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Prof. Goodrich

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OF THE
ORGANISM

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THE
SCIENCE & PHILOSOPHY
OF THE
ORGANISM

BY

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PREFACE TO THE SECOND EDITION

THE second edition of this work has been shortened by one-third of the original text, and can therefore be published in one volume. Everything that is not strictly relevant to the theme has been left out. The reader must refer to my other philosophical works for these topics, as, *e.g.*, the philosophy of history, the problem of metaphysics, etc.

But, on the other hand, everything that properly relates to the subject has been enlarged and improved, and thus, though it is shortened, this edition contains a more complete "Science and Philosophy of the *Organism*" than did the original text.

The book has, of course, been brought "up to date". Not, however, to the extent of my mentioning all biological details which have been discovered within the sphere of established problems. Only newly-established problems have been discussed, and such discoveries within the realm of old problems which mark a fundamental progress towards their solution. Neither the new problems nor the fundamental solutions are very numerous—at least in the sphere of biology proper, to the discussion of which this book is restricted quite intentionally, apart from a few remarks at the end.

As before, I am much obliged to my publishers, Messrs. A. & C. Black, Ltd., for their readiness to fulfil all my wishes.

HANS DRIESCH.

LEIPSIC, 1*st June* 1928.

EXTRACT FROM THE PREFACE TO THE FIRST EDITION

THIS work is not a text-book of theoretical biology; it is a systematic presentment of those biological topics which bear upon the true philosophy of nature. The book is written in a decidedly subjective manner, and it seems to me that this is just what "Gifford Lectures" ought to be. They ought never to lose, or even try to lose, their decidedly personal character.

My appointment as Gifford Lecturer, the news of which reached me in February 1906, came just at the right moment in the progress of my theoretical studies. I had always tried to improve my previous books by adding notes or altering the arrangement; I also had left a good deal of things unpublished, and thus I often hoped that I might have occasion to arrange for a new, improved, and enlarged edition of those books. This work then is the realisation of my hopes; it is, in its way, a definitive statement of all that I have to say about the Organic.

The lectures contained in this book were written in English by a German and delivered at a Scottish university. Almost all of the ideas discussed in it were first conceived during the author's long residence in Southern Italy. Thus this book may be witness to the truth which, I hope, will be universally recognised in the near future—that all culture, moral and intellectual and aesthetic, is not limited by the bounds of nationality.

HANS DRIESCH.

HEIDELBERG, *2nd January* 1908.

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INTRODUCTION

The Method

Every empirical problem may be studied in two different ways. We may begin with the naïve unbiassed analysis of the facts and then proceed to logical and theoretical discussion. Or we may begin with the discussion of logical and epistemological possibilities and illustrate them with facts later on. The second method may be more " philosophical " than the first ; the first method, nevertheless, is more natural psychologically, and, as it is the method applied by the author in his own scientific life, we shall accept it in this book, *i.e.* we will begin with the facts and will end with the philosophical discussion.

This implies that the first part of this book, the biological one in the proper sense, can be written from the point of view of what is generally called a naïve realism. We start from the thesis that there *is* or *exists* something in space, which we call *nature*, and of which one side is living or *organic*, whilst the other side is not. And we try to find out some *order* in the midst of the organic side of nature. This, at least, is to be our first task.

On Certain Characteristics of Biology as a Science

Practically, all of us know what a living being is, and therefore it is not necessary to formulate a definition of life, which, at the beginning of our studies, would be either provisional and incomplete, or else dogmatic. In some respects, indeed, a definition should rather be the end of a science than its opening.

Biology, the science of living nature, is the highest of all natural sciences, for it embraces as its final object the actions of man, at least in so far as actions also are phenomena observable on living bodies.

But biology is also the most difficult of all natural sciences, not only from the complexity of the phenomena which it studies, but in particular for another reason which is seldom properly emphasised, and therefore will well repay us for a few words devoted to it.

The experimenter in the inorganic fields of nature is not hampered by the specificity of composite objects: he " makes " all the combinations he wants. He is always able to have at his disposal red rays of a desired wave-length when and where he wants, or to have, at a given time and place, the precise amount of any organic compound which he wishes to examine. And he forces electricity and electro-magnetism to obey his will, at least with regard to space, time, and intensity of their appearance.

The biologist is not able to " make " specific forms of life, as the physicist has made red rays, or as the chemist has made a certain compound of carbon. The biologist is almost always in that strange plight in which the physicist would be if he always had to go to volcanoes in order to study the conductivity of heat, or if he had to wait for thunder-storms in order to study electricity. The biologist is dependent on the *specificity* of living objects as they occur in nature.

A few instances may show you what great inconveniences may hence arise to impede practical biological research. We later on shall have to deal with experiments on very young embryos: parts of the germ will have to be destroyed in order to study what will happen with the rest. Now, almost all germs are surrounded by a membrane; this membrane has to be detached before any operation is possible. But what are we to do if it is not possible to remove the membrane without killing the embryo? Or what if, as for instance in many marine animals, the membrane may be removed but the germs are killed by contact with sea-water? In both cases no experiments at all will be possible on a sort of germ which otherwise, for some special circumstances of its organisation, might have given results of importance. These results become impossible for only a practical and very secondary reason; but enough: they are impossible, and they might have thrown light on problems which now must remain problems. Quite the same thing may occur in experiments on physiology proper or functional physiology: one kind of animals survives the operation, the other kind does not, and therefore, for merely extrinsic reasons, the investigations have to be restricted to the first, though the second might have given more important results. And thus the biological experimenter always finds himself in a sort of dependence on his subjects, which can hardly be called pleasant. To a great extent the comparatively slow advance of biological sciences is due to this very fact: the unalterable specific nature of biological material.

But there is still another feature of biology dependent on the same fact. If a science is tied down to specific objects in every path it takes, it first, of course, has to know all about those objects, and that requires nothing else but plain description. We now understand why pure description, in the most simple sense of the word, takes up such an enormous part of every textbook of biological science. It is not only morphology, the science of form, that is most actively concerned with description; physiology also, in its present state, is pure description of what the functions of the different parts of the body of animals and plants actually *are*, at least for about nine-tenths of its range. It seems to me important to press this point very emphatically, since we often hear that physiology is from the very beginning a much higher sort of knowledge than morphology, inasmuch as it is rational. That is not at all true of the beginning of physiology: what the functions of the liver or of the root are has simply to be described just as the organisation of the brain or of the leaf, and it makes no difference logically that one species of description has to use the experimental method, while the other has not. The experiment, which only discovers what happens here or what happens there, possesses no kind of logical superiority over pure description at all.

THE DIFFERENT TYPES OF KNOWLEDGE ABOUT NATURE

Natural sciences cannot originate before the given phenomena of nature have been investigated, in at least a superficial and provisional manner, by and for the practical needs of man. But as soon as true science begins in any limited field, dealing, let us say, with animals or with minerals, it at once finds itself confronted by two very different kinds of problems.

In any branch of knowledge which practical necessities have separated from others, and which science now tries to study methodically, there occur general sequences in phenomena, general orders of events. This uniformity is revealed only gradually, but as soon as it has shown itself, even in the least degree, the investigator seizes upon it. He now devotes himself chiefly, or even exclusively, to the generalities in the sequences of all changes. He is convinced that there must be a sort of most general and at the same time of most universal connection about all occurrences. This most universal connection has to be found out ; at least it will be the ideal that always will accompany the inquiring mind during its researches. The " law of nature " is the ideal I am speaking about, an ideal which is nothing less than one of the postulates of the possibility of science at all.

Using for our purposes a word which has been already introduced into terminology by the philosopher Windelband,[1] we shall call that part of every branch of natural sciences which regards the establishment of a law of nature as its ideal, " nomothetic ", *i.e.* " law-giving ".

But while every natural science has its nomothetic side, it also has another half of a very different kind. This second half of every natural science does not care for the same general, the same universal, which is shown to us in every event in a different and specified kind : it is diversity, it is specification, that constitutes the subject of its interest. Its aim is to find a sufficient reason for the types of diversities, for the types of specifications. So in chemistry there has been found a

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[1] *Geschichte und Naturwissenschaft,* several editions.

systematic order in the long series of the compounds and of the elements; crystallography also has its different systems of crystals, and so on.

We have already employed the word by which we shall designate this second half of every natural science: it is the "systematic" side of science.

Nomothetic work on the one side and systematics on the other do, in fact, appear in every natural science, and besides them there are no other main parts. But "science" as a whole stands apart from another aspect of reality which is called "history". History deals with particulars, with particular events at a given time and a given place, whilst science always abstracts from the particular, even in its systematic half.

General Plan of this Book

Turning now to a sort of short outline of what is to be discussed in the whole of this book, it seems clear, without further analysis, that biology as a science has its nomothetic and its systematic part also; respiration and assimilation, for instance, have proved to be types of natural laws among living phenomena, and that there is a "system" of animals and plants is too commonly known to require further explanation here. Therefore we might study first biological laws, and after that biological systematics, and in the third place perhaps biological history. But that would hardly correspond to the philosophical aims of our lectures: our chief object is not biology as a regular science, as treated in text-books and in ordinary university lectures; our chief object is the Philosophy of the Organism, as aided and supported by scientific biology. Therefore a general acquaintance with biology must be assumed in these lectures, and the biological materials must be arranged according to their bearing on further, that is on philosophical, analysis.

That will be done, not, of course, to the extent of my regarding every one of my readers as a competent biologist; on the contrary, I shall explain most fully all points of biology proper, and even of the most simple and descriptive kind of biology, which serve as bases for philosophical analysis. But I shall do so only if they indeed do serve as such bases. All our biology will be not for its own sake, but for the sake of philosophy.

Whilst regarding the whole of the biological material with such aims, it seems to me best to arrange the properly scientific material which is to be the basis of my discussions, not along the lines which biology as an independent science would select, but to start from the three different kinds of fundamental phenomena which living bodies offer to investigation, and to attach all systematics exclusively to one of them. For there will not be very much for philosophy to learn from biological systematics at present.

Life is unknown to us except in association with individual bodies: we only know living individuals and call them organisms. It is the final object of all biology to tell us what it ultimately means to say that a body is "living", and in what sorts of relation body and life stand one to the other.

But at present it is enough to understand the terms "individual body" and "living" in the ordinary and popular sense.

Regarding living bodies in this unpretentious manner, and recollecting what the principal characters are of all bodies we know as living ones, we easily find that there are three features which are never wanting wherever life in bodies occurs. All living bodies are specific as to form—they "have" a specific form, as we are accustomed to say. All living bodies also exhibit metabolism; that is to say, they stand in a relation of interchange of materials with the surrounding medium, they take in and give out materials, but their form can remain unchanged during these processes. And, in the last place, we can say that all living bodies move; though this faculty is more commonly known among animals only, even elementary science teaches the student that it also belongs to plants.

Therefore we may ask for "laws of nature" in biology about form, about metabolism, and about movements. In fact, it is according to this scheme that we shall arrange the materials of the biological part of this book, though, as we cannot regard the three divisions as equally important in their bearing on our ultimate purposes, we shall not treat them quite on equal terms. It will appear that, at least in the present state of science, the problems of organic form and of organic movement have come into much closer relation to philosophical analysis than have most of the empirical data on metabolism.

It is *form* particularly which can be said to occupy the very centre of biological interest ; at least it furnishes the foundation of all biology. Therefore we shall begin our scientific studies with a full and thorough analysis of form. The science of living forms, later on, will afford us a key to study metabolism proper with the greatest advantage for our philosophical aims, and therefore the physiology of what is usually called the vegetative functions will be to us a sort of appendix to our chapters on form ; only the theory of a problematic " living substance " and of assimilation in the most general meaning of the word will be reserved for the philosophical part — for very good reasons, as I hope to show. But our chapters on the living forms will have yet another appendix besides the survey of the physiology of metabolism. Biological systematics almost wholly rests on form, on " morphology " ; and what hitherto has been done on the metabolical side of its problems consists of a few fragments, which are far from being an equivalent to the morphological system ; though, of course, it must be granted that, logically, systematics, in our general meaning of the word, as the sum of problems about the typically different and the specific, may be studied on the basis of each one of the principal characteristics of living bodies, not only on that of their forms. Therefore, systematics is to be the second appendix to the chief part of our studies in morphology ; and systematics, in its turn, will later on lead us to a short sketch of the historical side of biology, *i.e.*, to the theory of evolution in its different forms.

Goethe once said, that even in so-called facts there is more " theory " than is usually granted ; he apparently was thinking of what might be called the ultimate or the typical facts in science. It is with such typical or ultimate facts, which always relate to generalities, that we must become acquainted if our future philosophy is to be of profit to us.

GENERAL CHARACTER OF THE ORGANIC FORM

Our first discussion, it was said, is to be devoted wholly to organic forms. What then are the essentials of a living form, as commonly understood even without a special study of biology ?

Living bodies are not simple geometrical forms, not, like crystals, merely a typical arrangement of surfaces in space, to be reduced theoretically to an arrangement of elemental particles. Living bodies are *typically combined* forms ; that is to say, they consist of simpler parts of different characters, which have a special arrangement with regard to one another ; these parts have a typical form of their own and may again be combinations of more simple different parts. But besides that, living bodies have not always the same typically combined form during the whole of their life : they become more complicated as they grow older ; they all begin from one starting-point, which has little form at all, viz., the egg. So the living form may be called a " genetic form ", or a form considered as a process, and therefore *morphogenesis* is the proper and adequate term for the science which deals with the laws of organic forms in general ; or, if you prefer not to use the same word both for a science and for the subjects of that science, the *physiology of morphogenesis.*

Now, there are different branches of the physiology of morphogenesis or physiology of form. We may study, and indeed we at first shall study, what are the laws of the morphogenetic processes leading from the egg to the adult : that may be properly called physiology of development. But living forms are not only able to originate in one unchangeable way : they may restore themselves, if disturbed, and thus we get the physiology of restoration or restitution as a second branch of the science of morphogenesis. We shall draw very important data, some of the foundations indeed of our philosophical discussions, from the study of such restitutions. Besides that, it is to them that our survey of the problems of the physiology of metabolism is to be appended.

Living forms not only originate from the egg and are able to restore themselves, they also may give origin to other forms, guaranteeing in this way the continuity of life. The physiology of heredity therefore appears as the counterpart to those branches of the physiology of form which deal with individual form and its restitutions. And our discussion on heredity may be followed by our second appendix to this chief section on form, an appendix regarding the outlines of systematics and evolution.

Theoretical considerations on biology generally start, or, at least, used to start, from the evolution theory, discussing all other problems of the physiology of form by the way only, as things of secondary importance. You see from our programme, that we shall go just the opposite way: evolution will come last of all, and will be treated shortly; but the morphogenesis of the individual will be treated very fully and very carefully indeed.

Why then this deviation from what is the common practice? Because we do not know very much about evolution at all; because in this field we are just at the very beginning of what deserves the name of exact knowledge. But concerning individual morphogenesis we really know, even at present, if not very much, at least something, and that we know in a fairly exact form, aided by the results of experiments.

And it will not be without its reward, if we restrict our aims in such a manner, if we prefer to deal more fully with a series of problems which may seem at the first glance to be of less interest than others. After a few chapters we shall find already that we may decide one very important question about life merely by an analysis of individual form production, and without any regard to problematic and doubtful parts of biology: that we may decide the question, whether "life" is only a combination of chemical and physical events, or whether it has its elemental laws, laws of its own.

But to prepare the road that is to lead to such results, we first have to restrict our aims once more, and therefore the next chapter of this book, which eventually is to touch almost every concept of philosophy proper, will begin with the pure description of the individual development of the common sea-urchin.

SECTION A

THE CHIEF RESULTS OF ANALYTICAL BIOLOGY

PART I

THE INDIVIDUAL ORGANISM WITH REGARD TO FORM AND METABOLISM

A. ELEMENTARY MORPHOGENESIS

" EPIGENESIS "

THE organism is a specific individual body, built up by a typical combination of specific and different parts, all of them endowed with specific physiological functions. It is implied in the words of this definition that the organism is different, not only from crystals, as already mentioned, but also from all combinations of crystals, such as those called dendrites and others, which consist of a typical arrangement of identical units, the nature of their combination depending on the forces of every single one of their parts. For this reason dendrites, in spite of the typical features in their combination, must be called aggregates ; but the organism is not an aggregate even from the most superficial point of view.

We have said before, that the organism is not always the same in its individual life, that it has its development, leading from simpler to more complicated forms of combination of parts ; there is a " production of visible manifoldness " carried out during development, to describe the chief character of that process in the words of Wilhelm Roux. We leave it an open question in our present merely descriptive analysis, whether or not there was already a "manifoldness", in an invisible state, before development. In any case, there is a production of manifoldness *as far as we can see* even with our best instruments.

It certainly is of great importance to understand most clearly that there actually *is* a " production of *visible* manifoldness " with regard to form and to functions during ontogenesis in the descriptive sense ; the knowledge of the fact of this process must be the very foundation of all studies on the theory of development in any case, and therefore we will devote this chapter to studies in merely descriptive embryology.

But descriptive embryology, even if it is to serve merely as an instance of the universality of the fact of visible "epigenesis", can only be studied successfully with reference to a concrete case. We select the development of the common sea-urchin (*Echinus microtuberculatus*) as such a case, and we are the more entitled to select this organism rather than another, because most of the analytical experimental work, carried out in the interests of a real theory of development, has been done on the germs of this animal. Therefore, to know at least the outlines of the individual embryology of the Echinus may indeed be called the *conditio sine qua non* for a real understanding of what is to follow.

THE CELL [1]

You are aware that all organisms consist of organs and that each of their organs has a different function : the brain, the liver, the eyes, the hands are types of organs in animals, as are the leaves and the pistils in plants.

You are also aware that, except in the lowest organisms, the so-called Protista, all organs are built up of cells. That is a simple fact of observation, and I therefore cannot agree with the common habit of giving to this plain fact the title of cell-" theory ". There is nothing theoretical in it ; and, on the other hand, all attempts to conceive the organism as a mere aggregate of cells have proved to be wrong. It is *the whole* that uses the cells, as we shall see later on, or that may not use them : thus there is nothing like a cell-" theory ", even in a deeper meaning of the word.

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[1] E. B. Wilson, *The Cell in Development and Inheritance*, New York, Macmillan, many editions.

The cell may have the most different forms: take a cell of the skin, of a muscle, of a gland, of the wood in plants as typical examples. But in every case two parts may be distinguished in a cell: an outside part, the protoplasm, and an inside part, the nucleus, to leave out of special account several others, which, by the way, may only be protoplasmatic modifications.

Protoplasm is a mere name for what is not the nucleus; in any case it is not a homogeneous chemical compound; it consists of many such compounds and has a sort of architecture; all organic functions are based upon its metabolism. The nucleus has a very typical structure, which stands in a close relation to its behaviour during the most characteristic morphological period of the cell: during its division. Let us devote a few words to a consideration of this division and the part the nucleus plays in it; it will directly bear on future theoretical considerations about development.

There is a certain substance in every nucleus of a cell which stains most markedly, whenever cells are treated with pigments: the name "chromatin" has been given to it. The chromatin always gives the reaction of an acid, while protoplasm is basic; besides that, it seems to be a centre of oxidation. Now, when a division of a cell is to occur, the chromatin, which had been diffusely distributed before, in the form of small grains, arranges itself into a long and very much twisted thread. This thread breaks, as it were by sections, into almost equal parts, typical in number for each species, and each of these parts is split at full length. A certain number of pairs of small threads, the so-called "chromosomes", are the ultimate result of this process, which intentionally has been described a little schematically, the breaking and the splitting in fact going on simultaneously or occasionally even in reverse order. While what we have described is performing in the nucleus, there have happened some typical modifications in protoplasm, and then, by an interaction of protoplasmatic and nuclear factors, the first step in the actual division of the cell begins. Of each pair of the small threads of chromatin one constituent is moved to one side of the cell, one to the other; two daughter-nuclei are formed in this way; the protoplasm itself at the same time forms a circular furrow between them ; the furrow gets deeper and deeper ; at last it cuts the cell in two, and the division of the cell is accomplished.

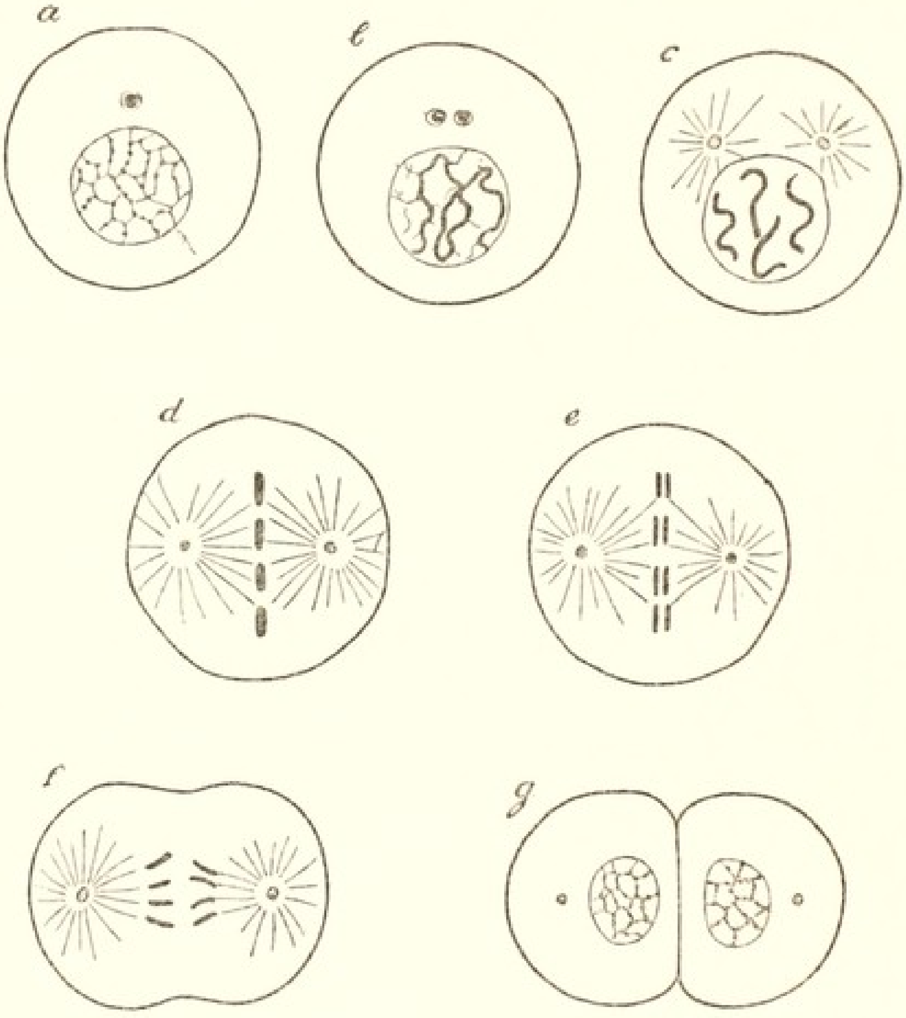

Fig. 1.—Diagram of Cell-Division (*after* Boveri).

a. Resting cell ; the chromatin distributed in the form of small granules inside the nucleus. Outside the nucleus is the " centrosome ", not mentioned in the text.
b. Beginning of division ; the chromatin arranged in the form of a long thread. Centrosome divided in two.
c. The thread of chromatin cut into four parts, the " chromosomes ".
d. The four parts of the chromatin arranged symmetrically between the centrosomes and the star-like " spheres ".
e. Each of the chromosomes split at full length.
f. Beginning of division of protoplasm ; the two parts of each chromosome separated.
g. End of cell-division.

Not only is the growth of the already typically formed organism carried out by a series of cell-divisions, but also development proper in our sense, as a " production of visible manifoldness ", is realised to a great extent by the aid of such divisions, which therefore may indeed be said to be of very fundamental importance (Fig. 1).

Each cell-division which promotes growth is followed by the enlargement of the two daughter-cells which result from it; these two daughter-elements attain the exact size of the mother-cell before division, and as soon as this size is reached a new division begins: so the growth of the whole is in the main the result of the growth of the elements. Cell-divisions during the first steps of embryology may behave differently, as will be described at a proper occasion.

THE EGG: ITS MATURATION AND FERTILISATION

We know that all the organs of an animal or plant consist of cells, and we know what acts a cell can perform. Now, there is one very important organ in all living beings, which is devoted to reproduction. This organ, the so-called ovary in animals, is also built up of cells, and its single cells are called the eggs; the eggs originated by cell-division, and cell-division is to lead from them to the new adult.

But, with a very few exceptions, the egg in the ovary is not able to accomplish its functions unless certain typical events have occurred, some of which are of a merely preparatory kind, whilst the others are the actual stimulus for development.

The preparatory ones are generally known under the name of "maturation". The egg must be "mature", in order that it may begin development, or even that it may be stimulated to it. Maturation consists of a rather complicated series of phenomena: later on we shall have occasion to mention, at least shortly, what happens in the protoplasm during its course; as to the nuclear changes during maturation it may be enough for our purposes to say, that there occur certain processes among the chromosomes which lead to an extension of half of them in the form of two very small cells, the "directive cells" or "directive or polar bodies", as they have been somewhat cautiously called.

The ripe or mature egg is capable of being fertilised.

Before turning to this important fact, which, by the way, will bring us to our specially chosen type, the Echinus, a few words may be devoted to the phenomenon of "parthenogenesis", that is to say, the possibility of development without fertilisation, since owing to the brilliant discoveries of the American physiologist, Jacques Loeb, this topic forms one of the centres of biological interest at present. It has long been known that the eggs of certain bees, lice, crayfishes, and other animals and also plants, are capable of development without fertilisation at all. Now, Richard Hertwig and T. H. Morgan already had shown that at least nuclear division may occur in the eggs of other forms—in the egg of the sea-urchin for instance—when these eggs are exposed to some chemical injuries. But Loeb[1] succeeded in obtaining a full development by treating the eggs of echinoderms with chloride of magnesium; thus artificial parthenogenesis had been discovered. Later researches have shown that artificial parthenogenesis may occur in all classes of the animal kingdom, and may be provoked by all sorts of chemical or physical means. We do not know at present in what the proper stimulus consists that must be supposed here to take the place of fertilisation; it seems, of course, highly probable that it is always the same in the last resort.

But enough about processes, which at present are of a highly scientific but hardly of any philosophic interest.

By fertilisation proper we understand the joining of the male element, the spermatozoon or the spermia, with the female element, the egg. Like the egg, the spermatozoon is but a cell, though the two differ very much from one another in the relation between their protoplasm and nucleus: in all eggs it is the protoplasm which is comparatively very large, if held together with somatic cells; in the spermatozoon it is the nucleus. A large amount of reserve material, destined for the growth of the future being, is the chief cause of the size of the egg protoplasm. The egg is quite or almost devoid of the faculty of movement; while, on the contrary, movement is the most typical feature of the spermia. Its whole organisation is adapted to movement in the most characteristic manner: indeed, most spermatozoa resemble a swimming infusorium, of the type of Flagellata—a so-called head and a moving tail are their two chief

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[1] *Amer. Journ. Physiol.* vols. iii. and iv., 1900.

constituents; the head is formed almost entirely of nuclear substance.

It seems that in most cases the spermatozoa swim around at random, and that their union with the eggs is assured only by their enormous number; only in a few cases in plants have there been discovered special stimuli of a chemical nature, which attract the spermia to the egg.

But we cannot enter here more fully into the physiology of fertilisation, and shall only remark that its real significance is by no means clear.[1]

The First Developmental Processes of Echinus

Turning now definitively to the special kind of organism, chosen of our type, the common sea-urchin, we properly begin with a few words about the absolute size of its eggs and spermatozoa. All of us are familiar with the eggs of birds and possibly of frogs; these are abnormally large eggs, on account of the very high amount of reserve material they contain. The almost spherical egg of our Echinus only measures about a tenth of a millimetre in diameter; and the head of the spermatozoon has a volume which is only the four-hundred-thousandth part of the volume of the egg! The egg is about on the extreme limit of what can be seen without optical instruments; it is visible as a small white point. But the number of eggs produced by a single female is enormous and may amount to hundreds of thousands. This is one of the properties which render the eggs of Echinus so very suitable for experimental research; and, moreover, they happen to be very clear and transparent, even in later stages, and to bear all kinds of operations well.

The spermia enters the egg, and it does so in the open water—another of the experimental advantages of our type. Only one spermia enters the egg in normal cases, and only

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[1] The older theories, attributing to fertilisation (or to "conjugation", *i.e.* its equivalent in Protozoa) some sort of "renovation" or "rejuvenescence" of the race, have been almost completely given up. (See Calkins, *Arch. für Entwickelungsmechanik*, xv., 1902). Teleologically, sexual reproduction has been considered as a means of variability (Weismann), but also as a means of preserving the type!

its head goes in. The moment that the head has penetrated the protoplasm of the egg a thin membrane is formed by the latter. This membrane is very soft at first, becoming much stronger later on; it is very important, for all experimental work, that by shaking the egg in the first minutes of its existence the membrane can easily be destroyed without any damage to the egg itself.

And now occurs the chief phenomenon of fertilisation: the nucleus of the spermatozoon unites with the nucleus of the egg. When speaking of maturation, we mentioned that half of the chromatin was thrown out of the egg by that process: now this half is brought in again, but comes from another individual.

It is from this phenomenon of nuclear union as the main character of fertilisation that almost all theories of heredity assume their right to regard the nuclei of the sexual cells as the true "seat" of inheritance. Later on, we shall have occasion to discuss this hypothesis from the point of view of logic and fact.

After the complete union of what are called the male and the female "pronuclei", the egg begins its development; and this development, in its first steps, is simply pure cell-division. We know already the chief points of this process, and need only add to what has been described that in the whole first series of the cell-divisions of the egg, or, to use the technical term, in the whole process of the "cleavage" or "segmentation", there is never any growth of the daughter-elements after each division, such as we know to occur after all cell-divisions of later embryological stages. So it happens, that during cleavage the embryonic cells become smaller and smaller, until a certain limit is reached; the sum of the volumes of all the cleavage cells together is equal to the volume of the egg.

But our future studies will require a more thorough knowledge of the cleavage of our Echinus. The first division plane, or, as we shall say, the first cleavage plane, divides the eggs into equal parts; the second lies at right-angles to the first and again divides equally: we now have a ring of four cells. The third cleavage plane stands at right-angles to the first two; it may be called an equatorial plane, if we compare the egg with a globe; it also divides equally, and so we now find two rings, each consisting of four cells, and one above the other. But now the cell-divisions cease to be equal, at least in one part of the egg: the next division, which leads from the eight- to the sixteen-cell stage of cleavage, forms four rings, of four cells each, out of the two rings of the eight-cell stage. Only in one half of the germ, which we shall call the upper one, or which we might call, in comparison with a globe, the northern hemisphere, are cells of equal size to be found; in the lower half of the egg four very small cells have been formed at one "pole" of the whole germ. We call these cells the "micromeres", that is, the "small parts", on the analogy of the term "blastomeres", that is, parts of the germ, which is applied to all the cleavage cells in general. The place occupied by the micromeres is of great importance to the germ as a whole: the first formation of real organs will start from this point later on. It is sufficient thus fully to have studied the cleavage of our Echinus up to this stage: the later cleavage stages may be mentioned more shortly. All the following divisions are into equal parts; there are no other micromeres formed, though, of course, the cells derived from the micromeres of the sixteen-cell stage always remain smaller than the rest. All the divisions are tangential; radial cleavages never occur, and therefore the process of cleavage ends at last in the formation of one layer of cells, which forms the surface of a sphere; it is especially by the rounding-up of each blastomere, after its individual appearance, that this real surface layer of cells is formed, but, of course, the condition, that no radial divisions occur, is the most important one in its formation. When 808 blastomeres have come into existence the process of cleavage is finished; a sphere with a wall of cells and an empty interior is the result. That only 808 cells are formed, and not, as might be expected, 1024, is due to the fact that the micromeres divide less often than the other elements; but, speaking roughly, of course, we may say that there are ten steps of cleavage-divisions in our form; 1024 being equal to 2^{10}.

We have learned that the first process of development, the cleavage, is carried out by simple cell-division. A few cases are known, in which cell-division during cleavage is accompanied by a specific migration of parts of the protoplasm in the interior of the blastomeres, especially in the first two or first four; but in almost all instances, cleavage is as simple a process of mere division as it is in our sea-urchin. Now, the second step in development, at least in our form, is a typical histological performance: it gives a new histological feature to all of the blastomeres: they acquire small cilia on their outer side, and with these cilia the young germ is able to swim about after it has left its membrane. The germ may be called a "blastula" at this stage, as it was first called by Haeckel, whose useful denominations of the first embryonic stages may conveniently be applied, even if one does not agree with most, or perhaps almost all, of his speculations (Fig. 2).

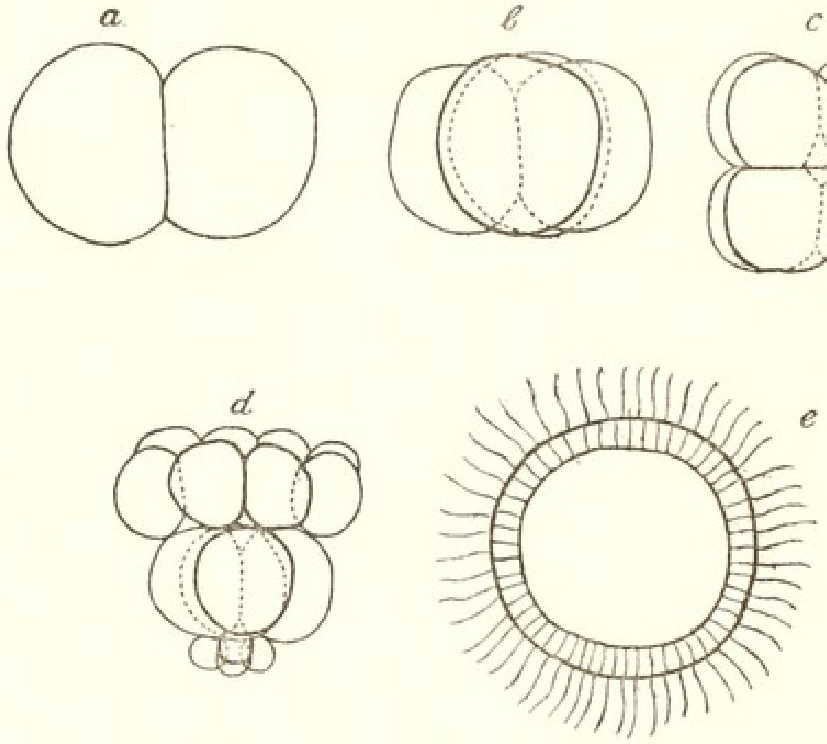

Fig. 2.—Early Development of Echinus, the Common Sea-urchin.

a. Two cells. *b.* Four cells. *c.* Eight cells, arranged in two rings of four, above one another.
d. Sixteen cells, four "micromeres" formed at the "vegetative" pole.
e. Optical section of the "blastula," a hollow sphere consisting of about one thousand cells, each of them with a small cilium.

It is important to notice that the formation of the

" blastula " from the last cleavage stage is certainly a process of organisation, and may also be called a differentiation with regard to that stage. But there is in the blastula no trace of one *part* of the germ becoming different with respect to others of its parts. If development were to go on in this direction alone, high organisatory complications might occur : but there would always be only one sort of cells, arranged in a sphere ; there would be only one kind of what is called " tissue ".

But in fact development very soon leads to true differences of the parts of the germ with respect to one another, and the next step of the process will enable us to apply different denominations to the different parts of the embryo.

At one pole of the swimming blastula, exactly at the point where the descendants of the micromeres are situated, about fifty cells lose contact with their neighbours and leave the surface of the globe, being driven into the interior space of it. Not very much is known about the exact manner in which these changes of cellular arrangement are carried out—whether the cells are passively pressed by their neighbours, or whether, perhaps, in a more active manner, they change their surface conditions ; therefore, as in most ontogenetic processes, the description had best be made cautiously in fairly neutral or figurative words.

The cells which in the above manner have entered the interior of the blastula are to be the foundation of important parts of the future organism ; they are to form its connective tissue, many of its muscles, and the skeleton. " Mesenchyme ", *i.e.* " what has been infused into the other parts ", is the technical name usually applied to these cells. We now have to learn their definite arrangement. At first they lie as a sort of heap inside the cell-wall of the blastula, inside the " blastoderm ", *i.e.* skin of the germ. But soon they move from one another, to form a ring round the pole at which they entered, and on this ring a process takes place which has a very important bearing upon the whole type of the organisation of the germ. You will have noticed that hitherto the germ with regard to its symmetry has been a monaxial or radial formation ; the cleavage stages and the blastula with its mesenchyme were forms with two different poles, lying at the ends of one single line, and round this line everything was arranged concentrically. But now what is called " bilateral symmetry " is established ; the mesenchyme ring assumes a structure which can be symmetrically divided only by one plane, but divided in such a way that one-half of it is the mirror image of the other. A figure shows best what has occurred, and you will notice (Fig. 3) two masses of cells in this figure, which have the forms of spherical triangles :

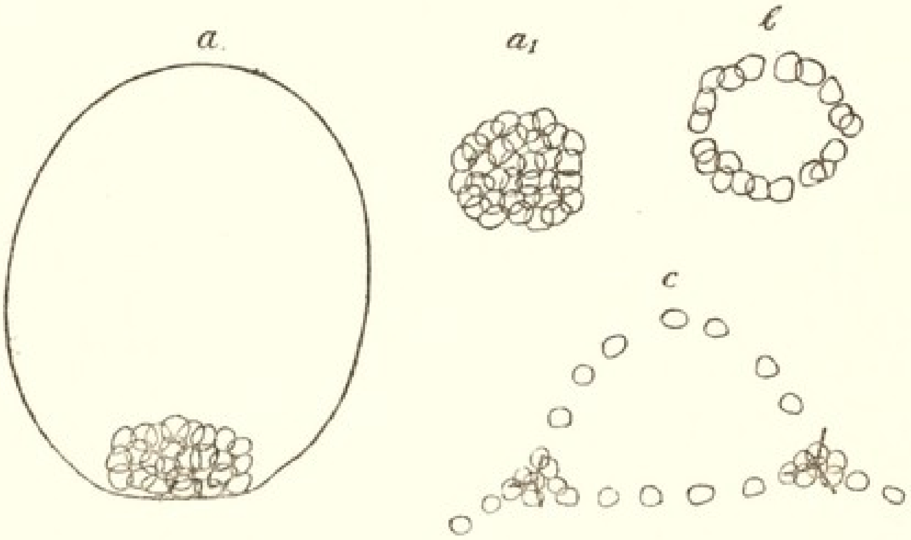

FIG. 3.—FORMATION OF MESENCHYME IN ECHINUS.

a. Outlines of blastula, side-view ; mesenchyme forms a heap of cells at the " vegetative " pole.
a_1. Heap of mesenchyme-cells from above.
b. Mesenchyme-cells arranged in a ring round the vegetative pole.
c. Mesenchyme-cells arranged in a bilateral-symmetrical figure ; primordia of skeleton in the midst of two spherical triangles.

it is in the midst of these triangles that the skeleton of the larva originates. The germ had an upper and a lower side before : it now has got an upper and lower, front and back, *right and left* half ; it now has acquired that symmetry of organisation which our own body has ; at least it has got it as far as its mesenchyme is concerned.

We leave the mesenchyme for a while and study another kind of organogenesis. At the very same pole of the germ where the mesenchyme cells originated there is a long and narrow tube of cells growing in, and this tube, getting longer and longer, after a few hours of growth touches the opposite pole of the larva. The growth of this cellular tube marks the beginning of the formation of the intestine, with all that is to be derived from it. The larva now is no longer a blastula, but receives the name of " gastrula " in Haeckel's terminology ; it is built up of the three " germ-layers " in this stage. The remaining part of the blastoderm is called "ectoderm", or outer layer ; the newly-formed tube, " endoderm ", or inner layer ; while the third layer is the " mesenchyme " already known to us.

The endoderm itself is a radial structure at first, as was the whole germ in a former stage, but soon its free end bends and moves against one of the sides of the ectoderm, against that side of it where the two triangles of the mesenchyme are to be found also. Thus the endoderm has acquired bilateral symmetry just as the mesenchyme before ; and as in this stage the ectoderm also assumes a bilateral symmetry in its form, corresponding with the symmetrical relations in the endoderm and the mesenchyme, we now may call the whole of our larva a bilateral-symmetrical organisation.

It cannot be our task to follow all the points of organogenesis of Echinus in detail. It must suffice to state briefly that ere long a second portion of the mesenchyme is formed in the larva, starting from the free end of its intestine tube ; that the formation of the so-called " coelum " occurs by a sort of splitting off from this same original organ ; and that the intestine itself is divided into three parts of different size and aspect by two circular sections.

But we must not, I think, dismiss the formation of the skeleton so quickly. I told you already that the skeleton has its first origin in the midst of the two triangular cell-masses of the mesenchyme ; but what are the steps before it attains its typical and complicated structure ? At the beginning a very small tetrahedron, consisting of carbonate of calcium, is formed in each of the triangles ; the four edges of the tetrahedron are produced into thin rods, and by means of a different organogenesis along each of these rods the typical formation of the skeleton proceeds. But the manner in which it is carried out is very strange and peculiar. About thirty of the mesenchyme cells are occupied in the formation of skeleton substance on each side of the larva. They wander through the interior space of the gastrula—which at this stage is not filled with sea-water but with a sort of gelatinous material—and wander in such a manner that they always come to the right places, where a part of the skeleton is to be formed ; they form it by a process of secretion, quite unknown in detail ; one of them forms one part, one the other, but what they form altogether is one whole.

When the formation of the skeleton is accomplished, the typical larva of our Echinus is built up ; it is called the "pluteus" (Fig. 4). Though it is far from being the perfect adult animal, it has an independent life of its own ; it feeds and moves about and does not go through any important changes of form for weeks. But after a certain period of this species of independent life as a "larva", the changes of form it undergoes again are most fundamental : it must be transformed into the adult sea-urchin, as all of you know. There are thousands and thousands of single operations of organogenesis to be accomplished before that end is reached ; and perhaps the strangest of all these operations is a certain sort of growth, by which the

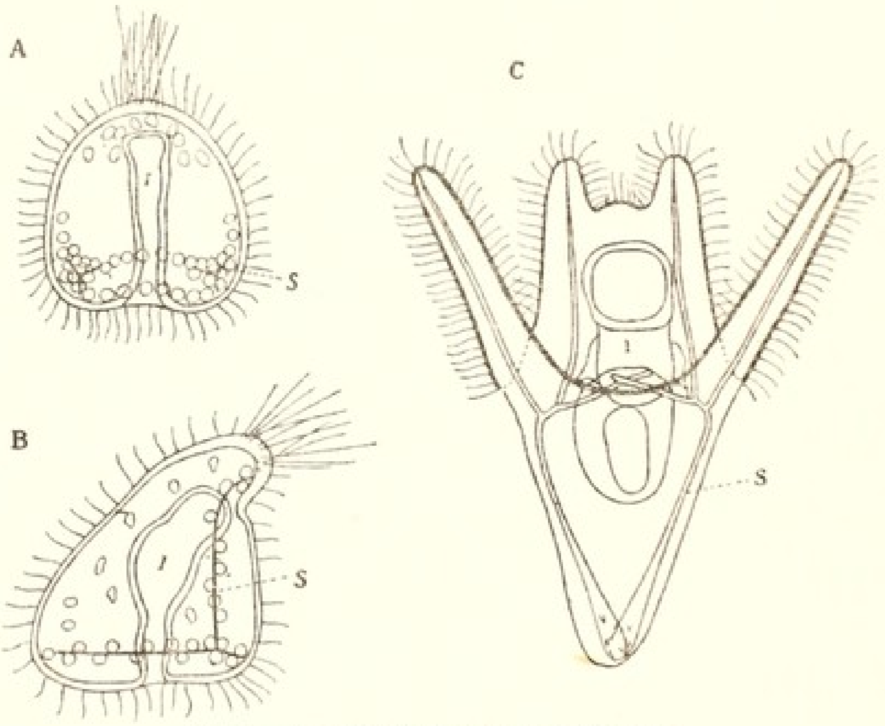

Fig. 4.—Larval Development of Echinus.

A. The gastrula.
B. Later stage, bilateral-symmetrical. Intestine begins to divide into three parts
C. Pluteus-larva. S=Skeleton. I=Intestine.

symmetry of the animal, at least in certain of its parts—not in all of them—is changed again from bilateral to radial, just the opposite of what happened in the very early stages!

But we cannot follow the embryology of our Echinus further here; and indeed we are the less obliged to do so, since in all our experimental work we shall have to deal with it only as far as to the pluteus larva. It is impossible under ordinary conditions to rear the germs up to the adult stages in captivity.

You now, I hope, will have a general idea at least of the processes of which the individual development of an animal consists. Of course the specific features leading from the egg to the adult are different in each specific case, and, in order to make this point as clear as possible, I shall now add to our description a few words about what may be called a comparative descriptive embryology.

Comparative Embryology

Even the cleavage may present rather different aspects. There may be a compact blastula, not one surrounded by only one layer of cells as in Echinus; or bilaterality may be established as early as the cleavage stage—as in many worms and in ascidians—and not so late as in Echinus. The formation of the germ layers may go on in a different order and under very different conditions: a rather close relative of our Echinus, for instance, the starfish, forms first the endoderm and afterwards the mesenchyme. In many cases there is no tube of cells forming the "endoderm", but a flat layer of cells is the first foundation of all the intestinal organs: so it is in all birds and in the cuttlefish. And, as all of you know, of course, there are very many animal forms which have no proper "larval" stage: there is one in the frog, the well-known "tadpole", but the birds and mammals have no larvae; that is to say, there is no special stage in the ontogeny of these forms which leads an independent life for a certain time, as if it were a species by itself, but all the ontogenetical stages are properly "embryonic"—the germ is always an "embryo" until it becomes the perfect young organism. And you also know that not all skeletons consist of carbonate of calcium, but that there are skeletons of silicates, as in Radiolaria, and of horny substance, as in many sponges. And, indeed, if we were to glance at the development of plants also, the differences would seem to us probably so great that all the similarities would disappear.

But there are similarities, nevertheless, in all development, and we shall now proceed to examine what they are. As a matter of fact, it was especially for their sake that we studied the ontogeny of a special form in such detail; one always sees generalities better if one knows the specific features of at least one case. What then are the features of most general and far-reaching importance which may be abstracted from the individual history of our sea-urchin, checked always by the teachings of other ontogenies, including those of plants?

THE FIRST STEPS OF ANALYTICAL MORPHOGENESIS

If we look back upon the long fight of the schools of embryologists in the eighteenth century about the question whether individual development was to be regarded as a real production of visible manifoldness or as a simple growth of visibly pre-existing manifoldness, whether, in the sphere of visibility, it was "epigenesis" or "evolutio", there can be no doubt, if we rely on all the investigations of the last hundred and fifty years, that, taken in the *descriptive sense,* the theory of epigenesis is right. Descriptively speaking, there *is* a production of manifoldness in the course of embryology: that is our first and main result. Any one possessed of an average microscope may any day convince himself personally that it is true.

In fact, true epigenesis, in the descriptive sense of the term, does exist. One thing is formed "after" the other; there is not a mere "unfolding" of what visibly existed already, though in a smaller form; there is no "evolutio" in the old meaning of the word.[1] Whether or not the theory

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[1] The word "evolution" in English usually serves to denote the theory of descent, that is, of a real relationship of all organisms. Of course, we are not thinking here of this modern and specifically English meaning of the Latin word *evolutio.* In its ancient sense, it means to a certain degree just

of *evolutio* may be maintained in a deeper sense of the word, will be discussed in a later chapter.

The totality of the line of morphogenetic facts can easily be resolved into a great number of distinct processes. We propose to call these " elementary morphogenetic processes " ; the turning in of the endoderm and its division into three typical parts are examples of them. If we give the name " elementary organs " to the distinct parts of every stage of ontogeny which are uniform in themselves and are each the result of one elementary process in our sense, we are entitled to say that each embryological stage consists of a certain number of elementary organs. The mesenchyme ring, the coelum, the middle-intestine, are instances of such organs. It is important to notice well that the word elementary is always understood here with regard to visible morphogenesis proper and does not apply to what may be called elementary in the physiological sense. An elementary process in our sense is every distinct act of form-building, and an elementary organ is the result of every one of such acts.

The elementary organs are typical with regard to their position and with regard to their histological properties. In many cases, they are of a very clearly different histological type, as, for instance, the cells of the three so-called germ-layers ; and in other cases, though apparently almost identical histologically, they can be proved to be different by their different power of resisting injuries or by other means. But there are not as many different types of histological structure as there are typically placed organs : on the contrary, there are many elementary organs of the same type in different typical parts of the organism, as all of you know to be the case with nerves and muscles. It will not be without importance for our future theory of development, carefully to notice this fact, that specialisation in the *position* of embryonic parts is more strict than in their histology.

the opposite ; it says that there is no formation of anything new, no transformation, but simply growth, and this is promoted not for the race but for the individual. Keeping well in mind these historical differences in the meaning of the word "evolutio", no mistakes, it seems to me, can occur from its use.

But elementary organs are not only typical in position and histology, they are typical also with regard to their form and their relative size. It agrees with what has been said about histology being independent of typical position, that there may be a number of organs in an embryonic stage, all in their most typical positions, which, though all possessing the same histology, may have different forms or different sizes or both : the single bones of the skeleton of vertebrates or of adult echinoderms are the very best instances of this most important feature of organogenesis. If we look back from elementary organs to elementary processes, the specialisation of the size of those organs may also be said to be the consequence of a typical duration of the elementary morphogenetic process leading to them.[1]

I hardly need to say that the histology, form, and size of elementary organs are equally an expression of their present or future physiological function. At least they prepare for this function by a specific sort of metabolism which sets in very early.

The whole sequence of individual morphogenesis has been divided by some embryologists into two different periods ; there is a first period, during which the foundations of the organisation of the "type" are laid down, and a second period, during which the histo-physiological specifications are modelled out (von Baer, Goette, Roux). Such a discrimination is certainly justified, if not taken too strictly ; but its practical application would encounter certain difficulties in many larval forms, and also, of course, in all plants.

Our mention of plants leads us to another analytical result. If an animal germ proceeds in its development from a stage d to the stage g, passing through e and f, we may say that the whole of d has become the whole of f, but we cannot say that there is a certain part of f which is d, we cannot say that f is $d+\alpha$. But in plants we can : the stage f is indeed equal to $a+b+c+d+e+\alpha$ in vegetable organisms ; all earlier stages

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[1] The phrase "*ceteris paribus*" has to be added of course, as the duration of each single elementary morphogenetic process is liable to vary with the temperature and many other conditions of the medium.

are actually visible as parts of the last one. The great embryologist, Carl Ernst von Baer, most clearly appreciated these analytical differences between animal and vegetable morphogenesis. They become a little less marked if we remember that plants, in a certain respect, are not simple individuals but colonies, and that among the corals, hydroids, bryozoa, and ascidia we find analogies to plants in the animal kingdom ; but nevertheless, the differences we have stated are not extinguished by such reasoning. It seems almost wholly due to the occurrence of so many foldings and bendings and migrations of cells and complexes of cells in animal morphogenesis that an earlier stage of their development seems *lost* in the later one ; those processes are almost entirely wanting in plants, even if we study their very first ontogenetic stages. If we say that almost all production of surfaces goes on outside in plants, inside in animals, we shall have adequately described the difference. And this feature again leads to the further diversity between animals and plants which is best expressed by calling the former "closed", the latter "open" forms : animals reach a point where they are finished, plants never are finished, at least in most cases.

We have already said that the embryological process appears under the form of a *production of visible manifoldness*, and it will be important for what is to follow to analyse the concept of *manifoldness* a little more in detail.

We call *manifold* everything that is not elemental, but is a combination of parts. And in the first place, we may speak of a *numerical* manifoldness, that is, one which only refers to the number of elements in question. In this respect, the atom of iron is more manifold than the atom of hydrogen ; for there are more electrons in the former.

But there may be a different *manifoldness of construction* in the realm of the same numerical manifoldness. A community of points which represents a flower has a higher degree of this sort of manifoldness than has the same community of points if arranged in squares, the *relations* between the points being more manifold in the first case than in the second.

Finally, there is what we shall call a *manifoldness by rank*, which may also have various degrees. A manifoldness of this sort is realised whenever a whole consists of parts which are wholes in themselves. A complicated engine is a good example of what we mean, and so also is the adult organism. The adult organism consists of organs, the organs of tissues, the tissues of cells, the cells of protoplasm, chromosomes, etc., these of molecules, the molecules of electrons and protons.

From our new points of view we may now say that, visibly, the embryological process produces a manifoldness of *high rank* out of a low rank manifoldness—an increase of *numerical* manifoldness, by assimilation, and of manifoldness of *construction* going hand-in-hand with this production.

This is also the ultimate foundation of the fact that embryology proceeds by steps or phases, *i.e.*, that the adult is not formed out of the egg by one single act ; or, in other terms, that embryology is a sequence of many single events in time.

All this will be very important in the course of our analytical work.

We have analysed our descriptions as far as we could, and yet we must confess that what we have found cannot be the last thing knowable about individual morphogenesis. There must be something deeper to be discovered : we only have been on the surface of the phenomena, we now want to get to the very bottom of them. Why then occurs all that folding, and bending, and histogenesis, and all the other processes we have described ? There must be something that drives them out, so to say. But how shall we discover it ?

Physicists always have used experiment and hypothetical construction. With these aids they have gone through the whole of the phenomena, and have erected the gigantic monument of modern physics.

It is the *method* of the physicists—not their *results*—that morphogenesis has to apply in order to make progress ; and this method we shall begin to apply in our next chapters.

But before saying any more about the exact rational and experimental method in morphology, we first shall have to analyse shortly some general attempts to understand morphogenesis by means of hypothetic construction exclusively. For such attempts have become very important as points of issue for really exact research.

B. EXPERIMENTAL AND THEORETICAL MORPHOGENESIS

1. The Foundations of the Physiology of Development. "Evolutio" and "Epigenesis"

THE THEORY OF WEISMANN

Of all the purely hypothetic theories on morphogenesis, that of August Weismann [1] can claim to have had the greatest influence, and to be at the same time the most logical and the most elaborated. The "germ-plasma" theory of the German author is generally considered as being a theory of heredity, and that is true inasmuch as problems of inheritance proper have been the starting-point of all his hypothetic speculations, and also form in some respects the most valuable part of them. But, rightly understood, Weismann's theory consists of two independent parts, which relate to morphogenesis and to heredity separately, and it is only the first which we shall have to take into consideration at present; what is generally known as the doctrine of the "continuity of the germ-plasm" will be discussed in a later chapter.

Weismann assumes that a very complicated organised structure, below the limits of visibility even with the highest optical powers, is the foundation of all morphogenetic processes, in such a way that, whilst part of this structure is handed over from generation to generation as the basis of heredity, another part of it is disintegrated during the individual development, and directs development by being disintegrated. The expression, "part" of the structure, first calls for some explanation. Weismann supposes several examples, several copies,

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[1] *Das Keimplasma*, Jena, 1892.

as it were, of his structure to be present in the germ cells, and it is to these copies that the word "part" has been applied by us: at least one copy has to be disintegrated during ontogeny.

The morphogenetic structure is assumed to be present in the nucleus of the germ cells, and Weismann supposes the disintegration of his hypothetic structure to be accomplished by nuclear division. By the cleavage of the egg, the most *fundamental* parts of it are separated one from the other. The word "fundamental" must be understood as applying not to organs or tissues, but to the chief relations of symmetry; the first cleavage, for instance, may separate the right and the left part of the primordial structure, the second one its upper and lower parts, and after the third or equatorial cleavage all the principal eighths of our minute organisation are divided off: for the minute organisation, it must now be added, had been supposed to be built up differently in the three directions of space, just as the adult organism is.

At the end of organogenesis the structure is assumed to have been broken up into its elements, and these elements, each of them localised in a particular cell, determine the fate of the single cells of the adult organism, the whole process having been accompanied by growth.

Here let us pause for a moment. There cannot be any doubt that Weismann's theory resembles to a very high degree some of the old "evolutio" doctrines of the eighteenth century; those doctrines, though not pretending to "see" the chick in the hen's egg, yet postulated its existence in a practically invisible form but *qua* chick with all its parts. Weismann's theory, however, is a little less crude. The chick *quâ* chick is not supposed to be present in the hen's egg before development, and ontogeny is not regarded as a mere growth of that chick in miniature; but what really is supposed to be present in the egg is nevertheless a something that in all its parts *corresponds* to all the parts of the chick, only under a somewhat different aspect, while all the relations of the parts of the one correspond to the relations of the parts of the other. Indeed, only on such an hypothesis of a fairly fixed and rigid relation between the parts of the morphogenetic structure could it be possible for the disintegration of the structure to go on, not by parts of organisation, but by parts of symmetry; which, indeed, is a very strange, but not an illogical, feature of Weismann's doctrine.

Weismann is absolutely convinced that there *must* be a theory of "evolutio" to account for the ontogenetic facts; that "epigenesis" has its place only in descriptive embryology, where, indeed, as we know, manifoldness in the *visible* sense is produced, but that epigenesis can never form the foundation of a real morphogenetic *theory*: theoretically one pre-existing material manifoldness is transformed into the other. An epigenetic *theory* would lead right beyond natural science, Weismann thinks, as in fact all such theories, if fully worked out, have carried their authors to vitalistic views. But vitalism is regarded by him as dethroned for ever.

Under these circumstances we have a good right, it seems to me, to speak of a *dogmatic* basis of Weismann's theory of development.

But to complete the outlines of the theory itself: Weismann was well aware that there were some grave difficulties attaching to his statements: all the facts of so-called adventitious morphogenesis in plants, of regeneration in animals, proved that the morphogenetic organisation could not be fully disintegrated during ontogeny. But these difficulties were not absolute: they could be overcome: indeed, Weismann assumes that in certain specific cases—and he regarded all cases of restoration of a destroyed organisation as due to specific properties of the subjects, originated by roundabout variations and natural selection—that in specific cases, specific arrangements of minute parts were formed during the process of disintegration, and were surrendered to specific cells during development, from which regeneration or adventitious budding could originate if required. "Plasma of reserve" was the name bestowed on these hypothetic arrangements.

Almost independently, another German author, Wilhelm Roux,[1] has advocated a theoretical view of morphogenesis which very closely resembles the hypothesis of Weismann.

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[1] *Die Bedeutung der Kernteilungsfiguren*, Leipzig, 1883.

But in spite of this similarity of the outset, we enter an altogether different field of biological investigation on mentioning Roux's name : we are leaving hypothetic construction, at least in its absoluteness, and are entering the realms of *scientific experiment in morphology.*

THE WORK OF WILHELM ROUX

We have already said that an hypothesis about the foundation of individual development was Roux's starting-point. Like Weismann, he supposed that there exists a very complicated structure in the germ, and that nuclear division leads to the disintegration of that structure. He next tried to bring forward what might be called a number of indicia supporting his view.

A close relation had been found to exist in many cases between the direction of the first cleavage furrows of the germ and the direction of the chief planes of symmetry in the adult : the first cleavage, for instance, very often corresponds to the median plane, or stands at right-angles to it. And in other instances, such as have been worked out into the doctrine of so-called "cell-lineages", typical cleavage cells were found to correspond to typical organs. Was not that a strong support for a theory which regarded cellular division as the principal means of differentiation ? It is true, the close relations between cleavage and symmetry did not exist in every case, but then there had always happened some specific experimental disturbances, *e.g.* influences of an abnormal direction of gravity on account of a turning over of the egg, and it was easy to reconcile such cases with the generally accepted theory on the assumption of what was called "anachronism" of cleavage.

But Roux was not satisfied with mere indicia ; he wanted a proof, and with this intention he carried out an experiment which has become very celebrated.[1] With a hot needle he killed one of the first two blastomeres of the frog's egg after the full accomplishment of its first cleavage, and then watched the development of the surviving cell. A typical half-embryo was

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[1] *Virchow's Archiv.* 114, 1888.

seen to emerge—an organism, indeed, which was as much a half as if a fully-formed embryo of a certain stage had been cut in two by a razor. It was especially in the anterior part of the embryo that its " halfness " could most clearly be demonstrated.

That seemed to be a proof of Weismann's and Roux's theory of development, a proof of the hypothesis that there is a very complicated structure which promotes ontogeny by its disintegration, carried out during the cell divisions of embryology by the aid of the process of nuclear division, the so-called " karyokinesis ". But things were far from being decided in a definitive manner.

THE EXPERIMENTS ON THE EGG OF THE SEA-URCHIN

Roux's results were published for the first time in 1888; three years later I tried to repeat his fundamental experiment on another subject and by a somewhat different method. It was known from the cytological researches of the brothers Hertwig and Boveri that the eggs of the common sea-urchin (*Echinus microtuberculatus*) are able to stand well all sorts of rough treatment, and that, in particular, when broken into pieces by shaking, their fragments will survive and continue to segment. I took advantage of these facts for my purposes. I shook the germs rather violently during their two-cell stage, and in several instances I succeeded in killing one of the blastomeres, while the other one was not damaged, or in separating the two blastomeres from one another.[1]

Let us now follow the development of the isolated surviving cell. It went through cleavage just as it would have done in contact with its sister-cell, and there occurred cleavage stages which were just half of the normal ones. The stage, for instance, which corresponded to the normal sixteen-cell stage, and which, of course, in my subjects was built up of eight elements only, showed two micromeres, two macromeres, and four cells of medium size, exactly as if a normal sixteen-cell stage had been cut in two; and the form of the whole was that of a hemisphere. So far there was no divergence from Roux's results.

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[1] *Zeitschr. wiss. Zool.* 53, 1891.

The development of our Echinus proceeds rather rapidly, the cleavage being accomplished in about fifteen hours. I quickly noticed, on the evening of the first day of the experiment, when the half-germ was composed of about two hundred elements, that the margin of the hemispherical germ bent together a little, as if it were about to form a whole sphere of smaller size, and, indeed, the next morning a *whole* diminutive blastula was swimming about. I was so much convinced that I should get Roux's morphogenetical result in all its features that, even in spite of this whole blastula, I now expected that the next morning would reveal to me the half-organisation of my subject once more; the intestine, I supposed, might come out quite on one side of it, as a half-tube, and the mesenchyme ring might be a half one also.

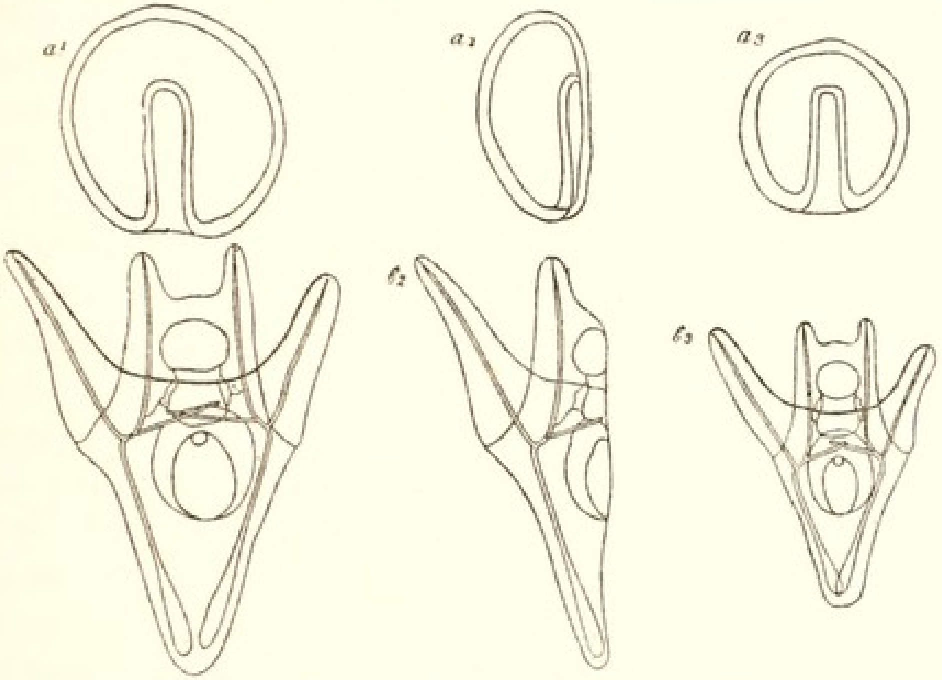

Fig. 5.—Illustration of Experiments on Echinus.

a_1 and b_1. Normal gastrula and normal pluteus.
a_2 and b_2. "Half"-gastrula and "half"-pluteus, that *ought* to result from one of the two first blastomeres, when isolated, according to the theory of "evolutio".
a_3 and b_3. The small *but whole* gastrula and pluteus, that actually *do* result.

But things turned out as they were bound to do and not as I had expected; there was a typically *whole* gastrula on my dish the next morning, differing only by its small size from a normal one; and this *small but whole* gastrula was followed by a whole and typical small pluteus-larva (Fig. 5).

That was just the opposite of Roux's result: one of the first two blastomeres had undergone a half-cleavage as in his case, but then it had become a whole organism by a simple process of rearrangement of its material, without anything that resembled regeneration, in the sense of a completion by budding from a wound.

If one blastomere of the two-cell stage was thus capable of performing the morphogenetical process in its totality, it became, of course, *impossible* to allow that nuclear division had separated any sort of "germ-plasm" into two different halves, and not even the protoplasm of the egg could be said to have been divided by the first cleavage furrow into unequal parts, as the postulate of the strict theory of so-called "evolutio" had been. This was a very important result, sufficient alone to overthrow at once the theory of ontogenetical "evolutio", the "Mosaiktheorie" as it had been called, in its exclusiveness.

After first widening the circle of my observations by showing that one of the first *four* blastomeres is also capable of performing a whole organogenesis, and that three of the first four blastomeres together result in an absolutely perfect organism, I went on to follow up separately one of the two fundamental problems which had been suggested by my first experiment: Was there anything more to find out about the importance or unimportance of the single *nuclear* divisions in morphogenesis? [1]

By raising the temperature of the medium or by diluting the sea-water to a certain degree it proved at first to be possible to alter in a rather fundamental way the type of the cleavage-stages without any damage to the resulting organism. There may be no micromeres at the sixteen-cell stage, or they may appear as early as in the stage of eight cells; no matter, the larva is bound to be typical. So it certainly is not necessary for all the cleavages to occur just in their normal order.

But of greater importance for our purposes was what followed. I succeeded in pressing the eggs of Echinus between two glass plates, rather tightly, but without killing them; the eggs became deformed to comparatively flat plates of a large diameter. Now, in these eggs all nuclear division occurred at

[1] *Zeitschr. wiss. Zool.* 55, 1892.

right-angles to the direction of pressure, that is to say, in the direction of the plates, as long as the pressure lasted ; but the divisions *began* to occur at right-angles to their former direction, as soon as the pressure ceased. By letting the pressure be at work for different times I therefore, of course, had it quite in my power to obtain cleavage types just as I wanted to get them. If, for instance, I kept the eggs under pressure until the eight-cell stage was complete, I got a plate of eight cells, one beside the other, instead of two rings, of four cells each, one above the other, as in the normal case ; but the next cell division occurred at right-angles to the former ones, and a sixteen-cell stage, of two plates of eight cells each, one above the other, was the result. If the pressure continued until the sixteen-cell stage was reached, sixteen cells lay together in one plate, and two plates of sixteen cells each, one above the other, were the result of the next cleavage.

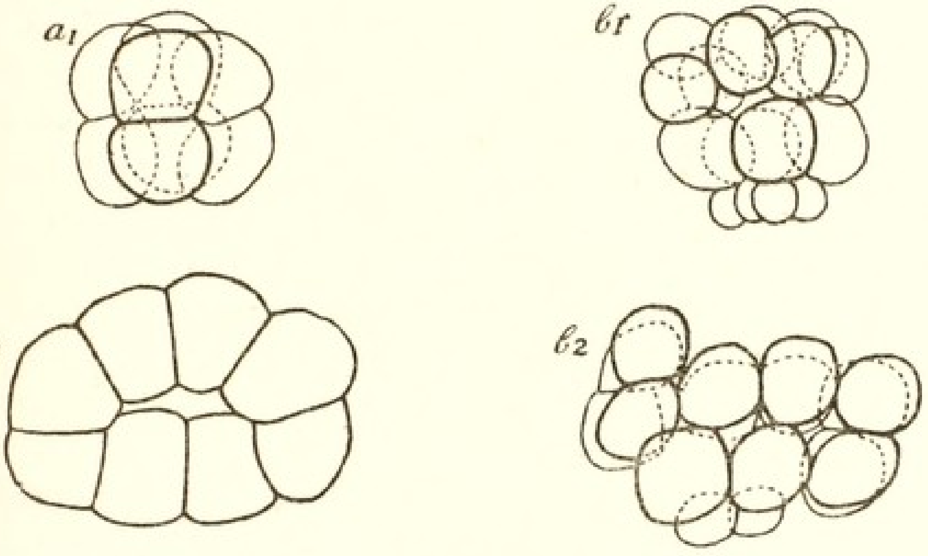

Fig. 6.—Pressure-experiments on Echinus.

a_1 and b_1. Two normal cleavage stages, consisting of eight and sixteen cells.
a_2 and b_2. Corresponding stages modified by exerting pressure until the eight-cell stage was finished. See text.

We are not, however, studying these things for cytological but for morphogenetical purposes, and for these the cleavage phenomenon itself is less important than the organogenetic result of it : all our subjects resulted in *absolutely normal* organisms. Now, it is clear that the spatial relations of the different nuclear divisions to each other are anything but normal in the eggs subjected to the pressure experiments; that, so to say, every nucleus has got quite different neighbours if compared with the "normal" case. If that makes no difference, then there *cannot* exist any close relation between the single nuclear divisions and organogenesis at all, and the conclusion we have drawn more provisionally from the whole development of isolated blastomeres has been extended and proved in the most perfect manner. There ought to result a morphogenetic chaos according to the theory of real "evolutio" carried out by nuclear division, if the positions of the single nuclei were fundamentally changed with regard to one another (Fig. 6). But now there resulted not chaos, but the normal organisation: therefore it was disproved, in the strictest way, that nuclear divisions have any bearing on the origin of organisation—at least, as far as the divisions during cleavage come into account.

On the egg of the frog (O. Hertwig), the annelids (E. B. Wilson), and ciona (T. H. Morgan) my pressure experiments have been carried out with the same result.[1]

An important experiment carried out by Spemann with the egg of the newt confirms the result of my pressure experiments in a different way: He corded the egg after fertilisation, by the aid of a hair, in such a way that one of the parts, which still were in communication by a bridge of protoplasm, was without the nucleus. Later on, at the stage of 8 or 16 cells, one of the nuclei migrated into that part. But *both* parts resulted in the formation of complete organisms, whilst, according to Weismann, that part which had received a nucleus of the 8- or 16-cell stage "should" have given but one-eighth or one-sixteenth of the organisation.

Finally, I have succeeded in raising *one giant* organism from *two* sea-urchin eggs, fused in the blastula stage; and the

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[1] In the pressure experiments I had altered the relative position of the nuclei *in origine*. In later years, I succeeded in disturbing the arrangement of the fully-formed cells of the eight-cell stage, and in getting normal larvae in spite of that in many cases. But as this series of experiments is not free from certain complications—which in part will be understood later on—it must suffice here to have mentioned them. (For further information, see my paper in *Archiv. f. Entwickelungsmechanik*, xiv., 1902, page 500.)

same result has been obtained with the egg of the newt by Mangold, in a slightly different way.

This, of course, is the real counterpart of my first experiments: in these, I got *many* (two or four) complete organisms from a material that normally should have given *one*; now, there is *one* instead of *many*. The second result is perhaps even more striking than the first. Both of them, in any case, contradict Weismann's hypothesis.

ON THE INTIMATE STRUCTURE OF THE PROTOPLASM OF THE GERM

Nuclear division, then, cannot be the basis of organogenesis, and all we know about the whole development of isolated blastomeres seems to show that there exists nothing responsible for differentiation in the protoplasm either.

But would that be possible? It cannot appear possible on a more profound consideration of the nature of morphogenesis, it seems to me: as the untypical agents of the medium cannot be responsible in any way for the origin of a form combination which is most typical and specific, there *must* be somewhere *in* the egg itself a certain factor which is responsible at least for the general orientation and symmetry of it. Considerations of this kind led me, as early as 1893,[1] to urge the hypothesis that there existed, that there *must* exist, a sort of intimate structure in the egg, including polarity and bilaterality as the chief features of its symmetry, a structure which belongs to every smallest element of the egg, and which might be imagined by analogy under the form of elementary magnets.[2] This hypothetic structure could have its seat in the protoplasm only. In the egg of echinoderms it would be capable of such a quick rearrangement after being disturbed, that it could not be observed but only inferred logically; there might, however, be cases in which its real discovery would be possible. Indeed Roux's frog-experiment seems to be a case where it is found to be at work: at least it seems very probable to

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[1] *Mitteil. Neapel.* 11, 1893.

[2] But the elementary magnets would have to be bilateral!

assume that Roux obtained half of a frog's embryo because the protoplasm of the isolated blastomere had preserved the "halfness" of its intimate structure, and had not been able to form a small whole out of it.

Of course, it was my principal object to verify this hypothesis, and such verification became possible in a set of experiments which my friend T. H. Morgan and myself carried out together,[1] in 1895, on the eggs of ctenophores, a sort of pelagic animals, somewhat resembling the jelly-fish, but of a rather different inner organisation. The zoologist Chun had found, even before Roux's analytical studies, that isolated blastomeres of the ctenophore egg behave like parts of the whole and result in a half-organisation like the frog's germ does; Chun had not laid much stress on his discovery, which now, of course, from the new points of view, became a very important one. We first repeated Chun's experiment and obtained his results, with the sole exception that there was a tendency of the endoderm of the half-larva of Beroë to become more than "half". But that was not what we chiefly wanted to study. We succeeded in cutting away a certain mass of the protoplasm of the ctenophore egg just *before* it began to cleave, without damaging its nuclear material in any way: in all cases, where the cut was performed at the side, there resulted a certain type of larvae from our experiments which showed exactly the same sort of defects as were present in larvae developed from one of the first two blastomeres alone.

The hypothesis of the morphogenetic importance of *protoplasm* had thus been proved. In our experiments there was all of the nuclear material, but there were defects on one side of the protoplasm of the egg; and the defects in the adult were found to correspond to these defects in the protoplasm.

And now O. Schultze and Morgan succeeded in performing some experiments which directly proved the hypothesis of the part played by protoplasm in the subject employed by Roux, *viz.*, the frog's egg. The first of these investigators managed to rear *two whole* frog embryos of small size, if he

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[1] *Arch. Entw. Mech.* 2, 1895.

slightly pressed the two-cell stage of that form between two plates of glass and turned it over; and Morgan,[1] after having killed one of the first two blastomeres, as was done in the original experiment of Roux, was able to bring the surviving one to a half or to a whole development according as it was undisturbed or turned. There cannot be any doubt that in both of these cases it is the possibility of a rearrangement of protoplasm, offered by the turning over, which allows the isolated blastomere to develop as a whole. The regulation of the frog's egg, with regard to its becoming whole, may be called *facultative,* whilst the same regulation of the egg of Echinus is *obligatory.* It is not without interest to note that the first two blastomeres of the common newt, *i.e.*, of a form which belongs to the other class of Amphibia, after a separation of *any* kind, *always* develop as wholes, their faculty of regulation being obligatory, like that of Echinus.

Whole or partial development may thus be dependent on the power of regulation contained in the intimate polar-bilateral structure of the protoplasm. Where this is so, the regulation and the differences in development are both connected with the chief relations of symmetry. The development becomes a half or a quarter of the normal because there is only one-half or one-quarter of a certain structure present, one-half or one-quarter with regard to the very wholeness of this structure; the development is whole, in spite of disturbances, if the intimate structure became whole first. We may describe the "wholeness", "halfness", or "quarterness" of our hypothetic structure in a mathematical way, by using three axes, at right-angles to one another, as the base of orientation. To each of these, x, y, and z, a certain specific state with regard to the symmetrical relations corresponds; thence it follows that, if there are wanting all those parts of the intimate structure which are determined, say, by a negative value of y, by minus y, then there is wanting half of the intimate structure; and this halfness of the intimate structure is followed by the halfness of organogenesis, the dependence of the latter on the intimate structure being established. But if regulation has

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[1] *Anat. Anz.* 10, 1895.

restored, on a smaller scale, the whole of the arrangement according to all values of x, y and z, development also can take place completely (Fig. 7).

I am quite aware that such a discussion is rather empty and purely formal, nevertheless it is by no means without

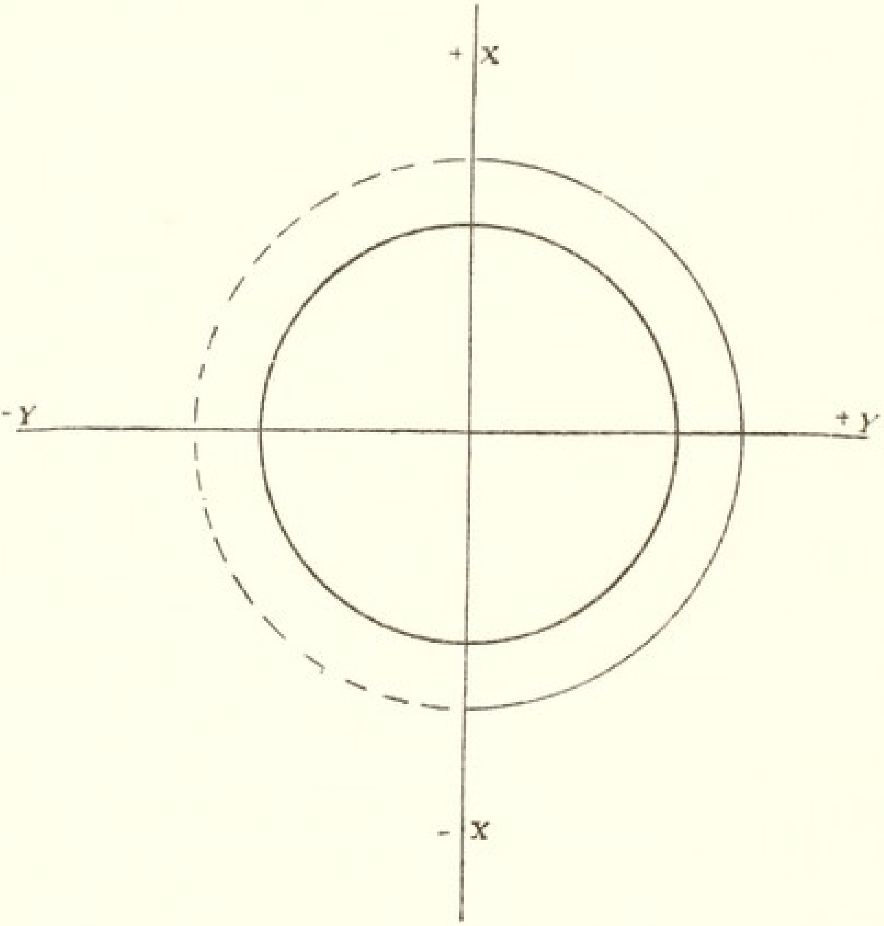

FIG. 7.—DIAGRAM ILLUSTRATING THE INTIMATE REGULATION OF PROTOPLASM FROM "HALF" TO "WHOLE".

The large circle represents the original structure of the egg. In all cases where cleavage-cells of the two-cell stage are isolated this original structure is only present as "half" in the beginning, say only on the right (+Y) side. Development then becomes "half", if the intimate structure remains half; but it becomes "whole" (on a smaller scale) if a new whole-structure (small circle!) is formed by regulatory processes.

value, for it shows most clearly the differences between what we have called the intimate structure of germs, responsible only for the general symmetry of themselves and of their isolated parts, and another sort of possible structure of the egg-protoplasm which we now shall have to consider, and which, at the first glance, seems to form a serious difficulty to our statements, as far at least as they claim to be of general importance. The study of this other sort of germinal structure at the same time will lead us a step further in our historical sketch of the first years of experimental embryology, and will bring this sketch to its end.

ON SOME SPECIFICITIES OF ORGANISATION IN CERTAIN GERMS

It was known already about 1890, from the careful study of what has been called "cell-lineage", that in the eggs of several families of the animal kingdom the origin of certain organs may be traced back to individual cells of cleavage, having a typical histological character of their own. In America especially such researches have been carried out with the utmost minuteness, E. B. Wilson's study of the cell-lineage of the Annelid *Nereis* being the first of them. If it were true that nuclear division is of no determining influence upon the ontogenetic fate of the blastomeres, only peculiarities of the different parts of the protoplasm could account for such relations of special cleavage cells to special organs. I advocated this view as early as in 1894, and it was proved two years later by Crampton, a pupil of Wilson's, in some very fine experiments performed on the germ of a certain mollusc.[1] The egg of this form contains a special sort of protoplasm near its vegetative pole, and this part of it is separated at each of the first two segmentations by a sort

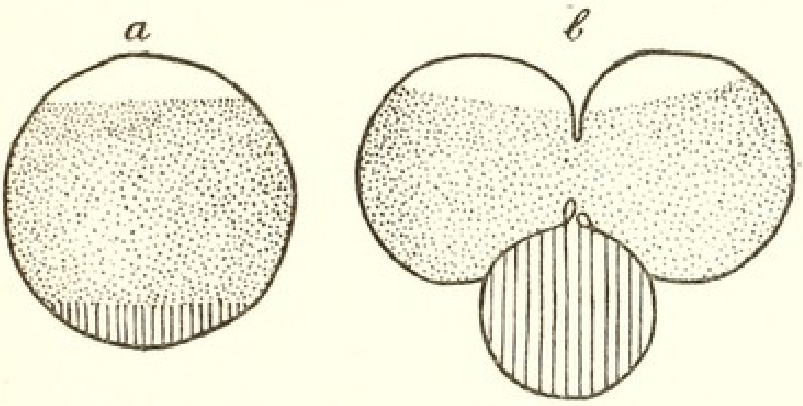

Fig. 8.—The Mollusc Dentalium (*after* E. B. Wilson).

a. The egg, consisting of three different kinds of protoplasmatic material.
b. First cleavage-stage. There are two cells and one "pseudo-cell", the yolk-sac, which contains no nucleus. This was removed in Crampton's experiment.

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[1] *Arch. Entw. Mech.* 3, 1896.

of pseudo-cleavage, leading to stages of three and five separated masses instead of two and four, the supernumerary mass being the so-called " yolk-sac " and possessing no nuclear elements (Fig. 8). Crampton removed this yolk-sac at the two-cell stage, and he found that the cleavage of the germs thus operated upon was normal except with regard to the size and histological appearance of one cell, and that the larvae originating from these germs were complete in every respect except in their mesenchyme, which was wanting. A special part of the protoplasm of the egg had thus been brought into relation with quite a special part of organisation, *and that special part of the protoplasm contained no nucleus.*

GENERAL RESULTS OF THE FIRST PERIOD OF EXPERIMENTAL EMBRYOLOGY

This experiment of Crampton's, afterwards confirmed by Wilson himself, may be said to have closed the first period of the new science of physiology of form, a period devoted almost exclusively to the problem whether the theory of nuclear division or, in a wider sense, whether the theory of a strict " evolutio " as the basis of organogenesis was true or not.

It was shown, as we have seen, that the theory of the " qualitatively unequal nuclear division " (" qualitativ-ungleiche Kernteilung " in German) certainly was not true, and that there also was no strict " evolutio " in protoplasm. Hence Weismann's theory was clearly disproved. There certainly is a good deal of real " epigenesis " in ontogeny, a good deal of " production of manifoldness ", not only with regard to visibility but in a more profound meaning. But some sort of pre-formation had also been proved to exist, and this pre-formation, or, if you like, this restricted evolutio, was found to be of two different kinds. First an intimate organisation of the protoplasm, spoken of as its polarity and bilaterality, was discovered, and this had to be postulated for every kind of germs, even when it was overshadowed by immediate obligatory regulation after disturbances. Besides that, there were cases in which a real specificity of special parts of the germ existed, a relation of these special parts to special organs; but this sort of specification also was shown to belong to the protoplasm.

It follows from all we have mentioned about the organisation of protoplasm and its bearings on morphogenesis, that the eggs of different animals may behave rather differently in this respect, and that the eggs indeed may be classified according to the degree of their organisation. Though we must leave a detailed discussion of these topics to zoology proper, we yet shall try shortly to summarise what has been ascertained about them in the different classes of the animal kingdom. A full regulation of the *intimate* structure of isolated blastomeres to a new whole has been proved to exist in the highest degree in the eggs of all echinoderms, medusae, nemertines, Amphioxus, fishes, and in one class of the Amphibia (the *Urodela*); it is facultative only among the other class of Amphibia, the *Anura*, and seems to be only partly developed or to be wanting altogether among ctenophora, ascidia, annelids, and mollusca. Peculiarities in the organisation of *specific parts* of protoplasm have been proved to occur in more cases than at first had been assumed; they exist even in the echinoderm egg, as experiments of later years have shown; even here a sort of specification exists at the vegetative pole of the egg, though it is liable to a certain kind of regulation; the same is true in medusae, nemertines, etc.; but among molluscs, ascidians, and annelids no regulation about the specific organisation of the germ in cleavage has been found in any case.

The differences in the degree of regulability of the intimate germinal structure may easily be reduced to simple differences in the physical consistency of their protoplasm.[1] But all differences in specific organisation must remain as they are for the present; it will be one of the aims of the future theory of development to trace these differences also to a common source.

That such an endeavour will probably be not without

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[1] It deserves notice, in this connection, that in some cases the protoplasm of parts of a germ has been found to be more regulable in the earliest stages, when it is very fluid, than later, when it is more stiff.

success, is clear, I should think, from the mere fact that differences with regard to germinal specific pre-formation do not agree in any way with the systematic position of the animals exhibiting them ; for, strange as it would be if there were two utterly different kinds of morphogenesis, it would be still more strange if there were differences in morphogenesis which were totally unconnected with systematic relationship : the ctenophores behaving differently from the medusae, and Amphioxus differently from ascidians.

SOME NEW RESULTS CONCERNING RESTITUTIONS

We now might close this chapter, which has chiefly dealt with the disproof of a certain sort of ontogenetic theories, and therefore has been almost negative in its character, did it not seem desirable to add at least a few words about the later discoveries relating to morphogenetic restorations of the adult. We have learnt that Weismann created his concept of " reserve plasma " to account for what little he knew about " restitutions "—that is, about the restoration of lost parts ; he only knew regeneration proper in animals and the formation of adventitious buds in plants. It is common to both of these phenomena that they take their origin from typically localised points of the body in every case ; each time they occur a certain well-defined part of the body is charged with the restoration of the lost parts. To explain such cases Weismann's hypothesis was quite adequate, at least in a logical sense. But at present, as we shall discuss more fully in another chapter, we know of some very widespread forms of restitution, in which what is to be done for a replacement of the lost is not entrusted to *one* typical part of the body in every case, but in which the whole of the morphogenetic action to be performed is transferred in its *single* parts to the *single* parts of the body which is accomplishing restoration : each of its parts has to take an individual share in the process of restoration, effecting what is properly called a certain kind of " re-differentiation " (" Umdifferenzierung "), and this share varies according to the relative position of the part in each case. Later on, these statements will appear in more correct form than at present, and then it will become clear that we are fully entitled to emphasise, at the end of our criticism of Weismann's theory, that his hypothesis relating to restorations can be no more true than his theory of development proper was found to be.

And now we shall pass on to our positive work.

We shall try to sketch the outlines of what might properly be called an *analytical theory of morphogenesis*; that is, to explain the sum of our knowledge about organic form-production, gained by experiment and by logical analysis, in the form of a real system, in which each part will be, or at least will try to be, in its proper place and in relation with every other part. Our analytical work will give us ample opportunity of mentioning many important topics of so-called general physiology also, irrespective of morphogenesis as such. But morphogenesis is always to be the centre and starting-point of our analysis. As I myself approach the subject as a zoologist, animal morphogenesis, as before, will be the principal subject of what is to follow.

2. Analytical Theory of Morphogenesis

We must now study morphogenesis in a systematic way, *i.e.* by dividing it into various characteristics and problems, as they offer themselves to the unbiassed observer. Six different problems will thus enter the scene—and a certain feature of one of them will force us to discuss the whole morphogenetic problem once more.

a. THE DISTRIBUTION OF MORPHOGENETIC POTENCIES

Prospective Value and Prospective Potency

Wilhelm Roux did not fail to see that the questions of the *locality* and the *time* of all morphogenetic differentiations had to be solved first, before any problem of causality proper could be attacked. From this point of view he carried out his fundamental experiments.

It is only in terminology that we differ from his views, if we prefer to call our introductory chapter an analysis of the *distribution of morphogenetic potencies*. The result will be, of course, rather different from what Roux expected it would be.

Let us begin by laying down two fundamental concepts. Suppose we have here a definite embryo in a definite state of development, say a blastula, or a gastrula, or some sort of larva: then we are entitled to study any special element of any special elementary organ of this germ with respect to what is actually to develop out of this very element in the future actual course of this embryology; it is the actual, *the real fate* of our element, that we take into account. I have proposed to call this real fate of each embryonic part in this very definite line of morphogenesis its *prospective value* ("prospective Bedeutung" in German). The fundamental question of the first chapter of our analytical theory of development may now be stated as follows: Is the prospective value of each part of any state of the morphogenetic line constant, *i.e.* is it unchangeable, can it be nothing but one; or is it variable, may it change according to different circumstances?

We first introduce a second concept: the term *prospective potency* ("prospective Potenz" in German) of each embryonic element. The term "prospective morphogenetic potency" is to signify the *possible fate* of each of those elements. With the aid of our two concepts, we are now able to formulate our introductory question thus: Is the prospective potency of each embryonic part fully given by its prospective value in a certain definite case; is it, so to say, identical with it, or does the prospective potency contain more than the prospective value of an element in a certain case reveals?

We know already from our historical sketch that the latter is true: that the actual fate of a part need not be identical with its possible fate, at least in many cases; that the potency of the first four blastomeres of the egg of the sea-urchin, for instance, has a far wider range than is shown by what each of them actually performs in even this ontogeny. There are more morphogenetic possibilities contained in each embryonic part than are actually realised in a special morphogenetic case.

As the most important special morphogenetic case is, of course, the so-called "normal" one, we can also express our formula in terms of special reference to it: there are more morphogenetic possibilities in each part than the observation of the normal development can reveal. Thus we have at once justified the application of analytical experiment to morphogenesis, and have stated its most important results.

As the introductory experiments have shown already that the prospective potency of embryonic parts, at least in certain cases, *can* exceed their prospective value, the concept of prospective potency at the very beginning of our studies puts itself in the centre of analytical interest, leaving to the concept of prospective value the second place only. For that each embryonic part actually has a certain prospective value, a specified actual fate in every single case of ontogeny, is clear from itself and does not affirm more than the reality of morphogenetic cases in general ; but that the prospective value of the elements may change, that there is a morphogenetic power in them which contains *more* than actuality—in other words, that the term " prospective potency " has not only a logical but a factual interest : all these points amount to a statement not only of the most fundamental introductory results but also of the actual *problems* of the physiology of form.

If at each point of the germ something else *can* be formed than actually is formed, why then does there happen in each case just what happens and nothing else ? In these words indeed we may state the chief problem of our science, at least after the fundamental relation of the superiority of prospective potency to prospective value has been generally shown.

We consequently may shortly formulate our first problem as the question of the *distribution* of the prospective morphogenetic potencies in the germ. Now, this general question involves a number of particular ones. Up to what stage, if at all, is there an absolutely equal distribution of the potencies over all the elements of the germ ? When such an equal distribution has ceased to exist at a certain stage, what are then the relations between the parts of different potency ? How, on the other hand, does a newly arisen, more specialised sort of potency behave with regard to the original general potency, and what about the distribution of the more restricted potency ?

The Potencies of the Blastomeres

At first we turn back to our experiments on the egg of the sea-urchin as a type of the germ in the very earliest stages. We know already that each of the first two, or each of the first four, or three of the first four blastomeres together may produce a whole organism. We may add that the swimming blastula, consisting of about one thousand cells, when cut in two quite at random, in a plane coincident with, or at least passing near, its polar axis, may form two fully developed organisms out of its halves.[1] We may formulate this result in the words: the prospective potency of the single cells of a blastula of Echinus is the same for all of them, at least around the axis; their prospective value is as far as possible from being invariable.

But we may say even a little more: what actually *will* happen in each of the blastula cells in any special case of development experimentally determined depends on the position of that cell in the whole, if the "whole" is put into relation with any fixed system of co-ordinates; or more shortly, "the prospective value of any blastula cell is a function of its position in the whole".

I know from former experience that this statement wants a few words of explanation. The word "function" is employed here in the most general, mathematical sense, simply to express that the prospective value, the actual fate of a cell, will change whenever its position in the whole is different.[2] The "whole" may be related to any three axes drawn through the normal undisturbed egg, on the hypothesis that there exists a primary polarity and bilaterality of the germ; the axes which determine this sort of symmetry may, of course, conveniently be taken as co-ordinates; but that is not necessary.

The Potencies of Elementary Organs in General

Before dealing with other very young germs, I think it advisable to describe first an experiment which is carried out at a later stage of our well-known form. This experiment will easily lead to a few new concepts, which we shall want later on, and will serve, on the other hand, as a basis of explanation for some results, obtained from the youngest germs of some other animal species, which otherwise would

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[1] If the plane of section passes near the equator of the germ, two whole larvae may be formed also, but in the majority of cases the "animal" half does not go beyond the blastula. The specific features of the organisation of the protoplasm come into account here.

[2] A change of the position of the cell is, of course, effected by each variation of the direction of the cut, which is purely a matter of chance.

seem to be rather irreconcilable with what our Echinus teaches us.

You know what a gastrula of our sea-urchin is. If you bisect this gastrula, when it is completely formed, or, still better, if you bisect the gastrula of the starfish, either along the axis or at right-angles to it, you get complete little organisms developed from the parts : the ectoderm is formed in the typical manner in the parts, and so is the endoderm; everything is proportionate and only smaller than in the normal case. So we have at once the important results, that, as in the blastula, so in the ectoderm and in the endoderm of our Echinus or of the starfish, the prospective potencies are the same for every single element : both in the ectoderm and in the endoderm the prospective value of each cell is a "function of its position" (Fig. 9).

But a further experiment has been made on our gastrula. If at the moment, where the material of the future intestine is most distinctly marked in the blastoderm, but not yet grown into a tube—if at this moment the upper half of the larva is separated from the lower by an equatorial section, you will get a complete larva only from that part which bears the "Anlage" of the endoderm, while the other half will proceed in morphogenesis very well but will form only ectodermal organs. By another sort of experiment, which we cannot fully explain here, it has been shown that the endoderm if isolated is also only able to form such organs as are normally derived from it.

And so we may summarise both our last results by saying : though ectoderm and endoderm have their potencies equally distributed amongst their respective cells, they possess different potencies compared one with the other. We may also say that they are *equipotential* in themselves, but of different potencies compared with each other.

So much for the conclusions that could be drawn from my own experiments. In recent years Spemann and his followers have shown in the embryo of the newt, v. Ubisch whilst working with the sea-urchin, that the *equipotentiality* of the early embryonic cells goes much further : the cells of the so-called germ

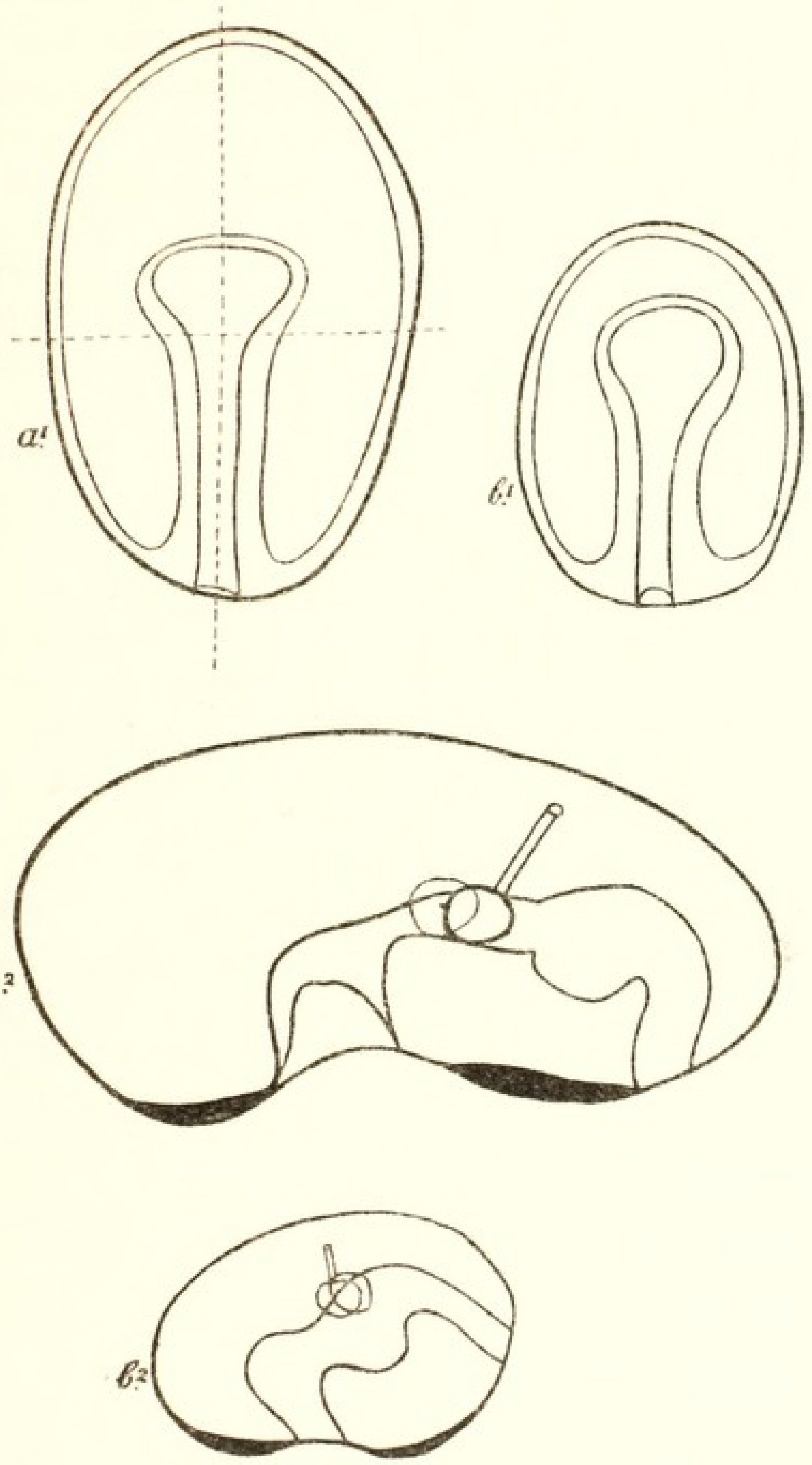

Fig. 9.—The Starfish, *Asterias*.

a^1. Normal gastrula ; may be bisected along the main axis or at right-angles to it (see dotted lines).
a^2. Normal larva, "*Bipinnaria*".
b^1. Small but whole gastrula that results by a process of regulation from the parts of a bisected gastrula.
b^2. Small *but whole* "*Bipinnaria*", developed out of b^1.

layers *may replace* one another under certain conditions, in any case so long as they have not yet acquired their definite histological structure, even though they are already in their typical position.

We shall come back to Spemann's experiments in another paragraph and therefore only note in this place that, in spite of them, certain potential restrictions of embryonic cells exist beyond any doubt, at least in later stages. But these potential restrictions may be due to mere secondary circumstances.

But those of you who are familiar with morphogenetic facts will object to me, that what we have stated about potential restrictions in ontogeny is not true in any case, and you will censure me for having overlooked regeneration, adventitious budding, and so on. To some extent the criticism would be right, but I am not going to recant ; I shall only introduce another new concept. We are dealing only with *primary* potencies in our present considerations, *i.e.* with potencies which lie at the root of true embryology, not with those serving to regulate disturbances of the organisation. It is true, we have in some way disturbed the development of our sea-urchin's egg in order to study it ; more than that, it would have been impossible to study it at all without some sort of disturbance, without some sort of operation. But, nevertheless, no potencies of what may properly be called the *secondary* or restitutive type have been aroused by our operations ; nothing happened except on the usual lines of organogenesis. It is true, some sort of regulation occurred, but that is included among the factors of ontogeny proper.

We shall afterwards study more fully and from a more general point of view this very important feature of "primary regulation" in its contrast to "secondary regulation" phenomena. At present it must be enough to say that in speaking of the restriction of the potencies in form-building we refer only to potencies of the primary type, which contain within themselves some properties of a (primary) regulative character.

The Morphogenetic Function of Maturation in the Light of Recent Discoveries

Turning again to more concrete matters, we shall first try, with the knowledge acquired of the potencies of the blastoderm and the so-called germ layers of Echinus, to understand certain rather complicated results which the experimental morphogenetic study of other animal forms has taught us. We know from our historical sketch that there are some very important aberrations from the type to which the Echinus germ belongs,[1] *i.e.* the type with an equal distribution of the potencies over all the blastomeres. We know not only that in cases where a regulation of the intimate structure of the protoplasm fails to occur a partial development of isolated cells will take place, but that there may even be a typical disposition of typical cells for the formation of typical organs only, without any regulability.

Let us first consider the last case, of which the egg of mollusca is a good type : here there is no equal distribution of potencies whatever, the cleavage-cells of this germ are a sort of real " mosaic " with regard to their morphogenetic potentialities. Is this difference between the germ of the echinoderms and the molluscs to remain where it is, and not to be elucidated any further ? Then there would be rather important differences among the germs of different animals, at least with regard to the degree of the specification of their cleavage cells; or if we ascribe differences among the blastomeres to the organisation of the fertilised egg ready for cleavage, there would be differences in the morphogenetic organisation of the egg-protoplasm : some eggs would be more typically specialised at the very beginning of morphogenesis than others.

In the first years of experimental embryology I pointed out that it must never be forgotten that the egg itself is the result of organogenesis. If, therefore, there are real mosaic-like specifi-

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[1] The reader will remember (see page 42, note 1), that even the germ of Echinus is not quite equipotential along its main axis, but it is equipotential in the strictest sense around this axis. The germs of certain medusae seem to be equipotential in every respect, even in their cleavage stages.

cations in some eggs at the beginning of cleavage, or during it, there may perhaps have been an *earlier* stage in the individual history of the egg which did not show such specifications of the morphogenetic structure. Two American authors share the merit of having proved this hypothesis. Conklin showed that certain intracellular migrations and rearrangements of material do happen in the first stages of ovogenesis in certain cases, but it is to E. B. Wilson [1] that science owes a proper and definitive elucidation of the whole subject. Wilson's researches, pursued not only by descriptive methods,[2] but also by means of analytical experiment, led him to the highly important discovery that the eggs of several forms (nemertines, molluscs), which *after* maturation show the mosaic type of specification in their protoplasm to a more or less high degree, fail to show any kind of specification in the distribution of their potencies *before* maturation has occurred. In the mollusc egg a certain degree of specification is shown already before maturation, but nothing to be compared with what happens afterwards ; in the egg of nemertines there is no specification at all in the unripe egg.

Maturation thus becomes a part of ontogeny itself ; it is not with fertilisation that morphogenesis begins—there is a sort of ontogeny anterior to fertilisation.

These words constitute a summary of Wilson's researches. Taken together with the general results obtained about the potencies of the blastula and the gastrula of Echinus, they reduce what appeared to be differences of degree or even of kind in the specification of the egg-protoplasm *to mere differences in the time of the beginning of real morphogenesis.* What occurs in some eggs, as in those of Echinus, at the time of the definite formation of the germ layers, leading to a specification and restriction of their prospective potencies, may happen very much earlier in other eggs. But there exists in *every* sort of egg an *earliest* stage, in which all parts of its protoplasm are equal

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[1] *Journ. Exp. Zool.* 1, 1904.

[2] Great caution must be taken in attributing any specific morphogenetic part to differently coloured or constructed materials which may be observed in the egg-protoplasm in certain cases. They may play such a part, but in other cases they certainly do not (see Lyon, *Arch. Entw. Mech.* 23, 1907). The final decision always depends on experiment.

as to their prospectivity, and in which there are no potential diversities or restrictions of any kind.

So much for differences in the *real material* organisation of the germ and their bearing on inequipotentialities of the cleavage cells.

The Intimate Structure of Protoplasm: Further Remarks

Where a typical half- or quarter-development from isolated blastomeres happens to occur, we know already that the impossibility of a regulation of the *intimate polar-bilateral* structure may account for it. As this impossibility of regulation probably rests on rather simple physical conditions,[1] it may properly be stated that equal distribution of potencies is not wanting but is only overshadowed here. In this respect there exists a logical difference of fundamental importance between those cases of so-called " partial " or (better) " fragmental " development of isolated blastomeres in which a certain embryonic organ is wanting, on account of its specific morphogenetic material being absent, and those cases in which the " fragmental " embryo lacks complete " halves " or " quarters " with regard to general symmetry, on account of the symmetry of its intimate structure being irregularly disturbed. This logical difference has not always received the attention which it undoubtedly deserves. Our hypothetical intimate structure in itself is, of course, also a result of factors concerned in ovogenesis. Only in one case do we actually know anything about its origin: Roux has shown that in the frog it is the accidental path of the fertilising spermatozoon in the egg which, together with the polar axis, normally determines the plane of bilateral symmetry; but this symmetry may be overcome and replaced by another, if gravity is forced to act in an abnormal manner upon the protoplasm — the latter showing parts of different specific gravity in the eggs of all Amphibia.

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[1] It seems that these physical conditions also—besides the real specifications in the organisation of the egg—may be different before and after maturation or (in other cases) fertilisation. (See Driesch, *Archiv. f. Entwickelungsmechanik*, 7, p. 98, and Brachet, *ibid.* 22, p. 325.)

The Neutrality of the Concept of " Potency "

Now we may close our rather long chapter on the distribution of potencies in the germ ; it has been made long, because it will prove to be very important for further analytical discussion ; and its importance, in great measure, is due to its freedom from prepossessions. Indeed, the concept of prospective potency *does not prejudice anything.* We have said, it is true, that limitations of potencies may be due to the presence of specific parts of organisation in some cases ; that, at least, they may be connected therewith. But we have not determined at all what a prospective potency really is, what the term really is to signify. It may seem that such a state of things gives an air of emptiness to our discussions, that it leaves uncertain what is the most important. But, I think, our way of argument, which tries to reach the problems of greatest importance by degrees, though it may be slow, could hardly be called wrong and misleading.

β. THE " MEANS " OF MORPHOGENESIS

We now proceed to an analysis of what may properly be called the *means* of morphogenesis, the word " means " being preferable to the more usual one " conditions " in this connection, as the latter would not cover the whole field. It is in quite an unpretentious and merely descriptive sense that the expression " means " *should* be understood at present ; what is usually called " conditions " is part of the morphogenetic means in our sense. We may say that morphogenetic *means* are circumstances which are necessary for a complete morphogenesis.

The Internal Elementary Means of Morphogenesis

We know that all morphogenesis, typical or atypical, primary or secondary, goes on by one morphogenetic elementary process following the other. Now, the very foundation of these elementary processes themselves lies in the elementary functions of the organism as far as they result in the formation of stable visible products. Therefore the elementary functions of the organism may properly be called the *internal* means of morphogenesis.

Secretion and migration are among such functions; and the same is true of cell division and growth and, last though not least, of the aggregative state of the organic substance in general, including so-called surface tension and osmotic pressure.

But let us observe that the elementary means of morphogenesis are far from being morphogenesis themselves. The word "means" itself implies as much. It would be possible to understand each of these single acts in morphogenesis as well as anything, and yet to be as far from understanding the whole as ever. All means of morphogenesis are only to be considered as the most general frame of events within which morphogenesis occurs.

We must be cautious in admitting that any organic feature has been explained, even in the most general way, by the action of physical forces. What at first seems to be the result of mechanical pressure may afterwards be found to be an active process of growth, and what at first seems to be a full effect of capillarity among homogeneous elements may afterwards be shown to depend on specialised metabolic conditions of the surfaces as its principal cause.[1] All these processes are only means of the organism, and can never do more than furnish the general type of events. They do not constitute life—they are *used* by life; let it remain an open question, for the present, how the phenomenon of "life" is to be regarded in general.

We do not by any means intend to discredit a thorough and detailed study of, say, osmosis or colloid chemistry in their relation to morphogenesis. On the contrary, we highly appreciate the results of such investigations, as they serve to *formulate very sharply the central biological problem.* But they never give us a solution of this problem.

Let us close this chapter with a few words on cell division.

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[1] According to Zur Strassen's results, the early embryology of *Ascaris* proceeds almost exclusively by cellular surface-changes: the most typical morphogenetic processes are carried out by the aid of this "means". As a whole, the embryology of *Ascaris* stands quite apart and presents a great number of unsolved problems.

The investigations of the last few years have made it quite clear that even in organisms with a high power of morphogenetic regulation it is always the form of the whole, but not the individual cell, which is subjected to the regulation processes. Starting from certain results obtained by T. H. Morgan, I was able to show that in all the small but whole larvae, reared from isolated blastomeres, the size of the cells remains normal, only their number being reduced; and Boveri has shown most clearly that it is always the size of the nucleus—more correctly, the mass of the chromatin—which determines how large a cell of a certain histological kind is to be. In this view, the cell appears even more as a sort of material used by the organism as supplied, just as workmen can build the most different buildings with stones of a given size.

The External Means of Morphogenesis

We now know what internal means of morphogenesis are, and so we may glance at some of the most important "outer means" or "conditions" of organisation.

Like the adult, the germ also requires a certain amount of heat, oxygen, and, when it grows up in the sea, salinity in the medium. For the germ, as for the adult, there exists not only a minimum but also a maximum limit of all the necessary factors of the medium; the same factor which at a certain intensity promotes development, disturbs it from a certain other intensity upwards.

Within the limits of this minimum and this maximum of every outside agent there generally is an increase in the rate of development corresponding to the increase of intensity of the agent. The acceleration of development by heat has been shown to follow the law of the acceleration of chemical processes by a rise of temperature; that seems to prove that certain chemical processes go on during the course of morphogenesis.

Almost all that has been investigated of the part played by the external conditions of development has little bearing on specific morphogenesis proper, and therefore may be left out of account here: we must, however, lay great stress on the general fact that there *is* a very close dependence of morphogenesis on the outside factors, lest we should be accused afterwards of having overlooked it.

Of course, all "external" means or conditions of morphogenesis can actually relate to morphogenetic processes only by becoming in some way "internal", but we unfortunately have no knowledge whatever how this happens. We at present are only able to ascertain what must necessarily be accomplished in the medium, in order that normal morphogenesis may go on, and we can only suppose that there exist certain specific internal general states, indispensable for organogenesis but inaccessible to present modes of investigation.

There are but few points in the doctrine of the external means or conditions of organogenesis which have a more special bearing on the specification of proper form, and which therefore require to be described here a little more fully. All these researches, which have been carried out almost exclusively by Herbst,[1] relate to the effect of the chemical components of sea-water upon the development of the sea-urchin. If we select the most important of Herbst's results, we must in the first place say a few words on the part taken by lime or calcium, not only in establishing specific features of form, in particular of the skeleton, but in rendering individual morphogenesis possible at all. Herbst has found that in sea-water which is deprived of calcium the cleavage cells and many tissue cells also completely lose contact with each other: cleavage goes on quite well, but after each single division the elements are separated; at the end of the process you find the 808 cells of the germ together at the bottom of the dish, all swimming about like infusoria. There seems to be some influence of the calcium salts upon the physical state of the surfaces of the blastomeres.

It is not without interest to note that this discovery has an important bearing on the technical side of all experiments dealing with the isolation of blastomeres. Since the separation

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[1] *Arch. Entw. Mech.* 17, 1904.

of the single cleavage elements ceases as soon as the germs are brought back from the mixture without lime into normal sea-water, it of course is possible to separate them up to any stage which it is desired to study, and to keep them together afterwards. Thus, if, for instance, you want to study the development of isolated cells of the eight-cell stage, you will leave the egg in the artificial mixture containing no calcium until the third cleavage, which leads from the four- to the eight-cell stage, is finished. The single eight cells brought back to normal sea-water at this point will give you the eight embryos you want. All researches upon the development of isolated blastomeres since the time of Herbst's discovery have been carried out by this method, and it would have been quite impossible by the old method of shaking to pursue the study into such minute detail as actually has been done.

Among all the other very numerous studies of Herbst, we need only mention that potassium is necessary for the typical growth of the intestine, just as this element has been found necessary for normal growth in plants, and that there must be the ion SO_4, or, in other terms, sulphur salts, present in the water, in order that the germs may acquire their pigments and their bilateral symmetry. This is indeed a very important result, though it cannot be said to be properly understood. It is a fact that in water without sulphates the larvae of Echinus retain the radial symmetry they have had in the very earliest stages, and may even preserve that symmetry on being brought back to normal sea-water if they have spent about twenty-four hours in the artificial mixture.

We may now leave the subject of Herbst's attempts to discover the morphogenetic function of the single constituents of normal sea-water, and may devote a few words to the other branch of his investigations, those dealing with the morphogenetic effects of substances which are not present in the water of the sea, but have been *added* to it artificially. Here, among many other achievements, Herbst has made the most important discovery that all salts of lithium effect radical changes in development.[1] I cannot describe fully here how

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[1] *Zeitschr. wiss. Zool.* 55, 1892; and *Mitt. Neapel.* 11, 1893.

the so-called " lithium larva " originates ; let me only mention that its endoderm is formed outside instead of inside, that it is far too large, that there is a spherical mass between the ectodermal and the endodermal part of the germ, that a radial symmetry is established in place of the normal bilateralism, that no skeleton exists, and that the mesenchyme cells are placed in a quite abnormal position. All these features, though abnormal, are typical of the development in lithium. The larvae present no really pathological appearance at all, and, therefore, it may indeed be said that lithium salts are able to change fundamentally the whole course of morphogenesis. It detracts nothing from the importance of these discoveries that, at present, they stand quite isolated : only with lithium salts has Herbst obtained such strange results ; and only upon the eggs of echinids, not even upon those of asterids, do lithium salts act in this specific way.

γ. THE FORMATIVE CAUSES OR STIMULI

The Definition of Cause

We cannot begin the study of the " causes " of the differentiation of form without a few words of explanation about the terminology which we shall apply. Causality is a very disputed concept ; many modern scientists, particularly in physics, try to avoid the concept of cause altogether, and to replace it by mere functional dependence, in the mathematical meaning of the term. They claim to express completely by an equation all that is discoverable about any sort of phenomena constantly connected.

I cannot convince myself that such a very restricted view is the right one : it is very cautious, no doubt, but it is incomplete, for the concept of the acting " cause " *is* a legitimate concept and we are *forced* to search for applications of it in Nature. On the other hand, it does not at all escape me that there are many difficulties, or rather ambiguities, in applying it.

We may call the " cause " of any event, the *sum total* of all the constellations of facts which must be completed in order that the event may occur; it is in this meaning, for instance, that the first principle of energetics applies the term in the words *causa aequat effectum.* But, by using the word only in this very general sense, we deprive ourselves of many conveniences in the further and more particular study of Nature. Would it be better to say that the "cause" of any event is the *very last* change which, after all the constellations necessary for its start are accomplished, must still take place in order that the event may actually occur? Let us see what would follow from such a use of the word causality. We here have an animal germ in a certain stage, say a larva of Echinus, which is just about to form the intestine; all the internal conditions are fulfilled, and there is also a certain temperature, a certain salinity, and so on, but there is no oxygen in the water: the intestine, of course, will not grow in such a state of things, but it soon will when oxygen is allowed to enter the dish. Is, therefore, oxygen the "cause" of the formation of the intestine of Echinus? Nobody, I think, would care to say so. By such reasoning, indeed, the temperature, or sodium, might be called the "cause" of any special process of morphogenesis. It, therefore, seems to be of little use to give the name of cause to that factor of any necessary constellation of events which accidentally happens to be the last that is realised. But what is to be done then?

Might we not say that the cause of any morphogenetic process is that typical property, or quality, or change on which its *specific* character depends—on which depends, for example, the fact that now it is the intestine which appears, while at another time it is the lens of the eye? We might very well, but we already have our term for this sort of cause, which is nothing else than our prospective potency applied to that elementary organ from which the new process takes its origin. The prospective potency indeed is the truly immanent cause of every specification affecting single organogenetic processes. But we want something more than this.

We may find what we want by considering that each single elementary process or development not only has its specification, but also has its specific and typical place in the whole—its *locality*. Therefore we shall call the " cause " of a single morphogenetic process, that occurrence on which depends its *localisation*, whether its specific character also partly depends on this " cause " or not.[1]

This definition of " cause " in morphology may be artificial; in any case it is clear. And at the same time the concepts of the prospective potency and of the " means " of organogenesis now acquire a clear and definite meaning: potency is the real basis of the specific character of every act in morphogenesis, and " means ", including conditions, are the sum of all external and internal general circumstances which must be present in order that morphogenetic processes may go on, without being responsible for their specificity or localisation.

It is implied in these definitions of cause and potency, that the former almost always will be of that general type which usually is called a stimulus. There is no quantitative correspondence between our " cause " and the morphogenetic effect.

Some Instances of Formative and Directive Stimuli

Again it is to Herbst that we owe not only a very thorough logical analysis of what he calls *formative* and *directive stimuli*[2] but also some important discoveries on this subject. We cannot do more here than barely mention some of the most characteristic facts.

Amongst plants it has long been known that the direction of light or of gravity may determine where roots or branches or other morphogenetic formations are to arise; in hydroids also we know that these factors of the medium may be at work[3] as morphogenetic causes, though most of the typical

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[1] In certain cases, part of the specific feature of the process in question may also depend on the " cause " which is localising it, *e.g.* in the galls of plants.

[2] Herbst, " Über die Bedeutung der Reizphysiologie für die kausale Auffassung von Vorgängen in der tierischen Ontogenese " (*Biol. Centralblatt*, vols. xiv., 1894, and xv., 1895); *Formative Reize in der tierischen Ontogenese*, Leipzig, 1901. These important papers must be studied by every one who wishes to become familiar with the subject.

[3] Compare the important papers by J. Loeb, *Untersuchungun zur physiologischen Morphologie der Tiere*, Würzburg, 1891–2.

architecture of hydroid colonies certainly is due to internal causes, as is also much of the organisation in plants.

Light and gravity are external formative causes; beside that they are merely "localisers". But there also are some external formative stimuli, on which depends not only the place of the effect, but also part of its specification. The galls of plants are the most typical organogenetic results of such stimuli. The potencies of the plant and the specific kind of the stimulus equally contribute to their specification; for several kinds of galls may originate on one sort of leaves.

No exterior formative stimuli are responsible for the intimate details of animal organisation; and one would hardly be wrong in saying that this morphogenetic independence in animals is due to their comparatively far-reaching functional independence of those external agents which have any sort of direction. But many organogenetic relations are known to exist *between* the single parts of animal germs, each of these parts being in some respect external to every other; and, indeed, it might have been expected already *a priori* that such formative relations between the parts of an animal embryo must exist, after all we have learned about the chief lines of early embryology. If differentiation does not go on after the scheme of Weismann, that is, if it is not carried out by true "evolutio" from within, how could it be effected except from without? Indeed, every embryonic part may, in some respect, be a possible cause for morphogenetic events which are to occur on every other part: it is here that the very roots of epigenesis are to be found.

Heliotropism and geotropism are among the well-known physiological functions of plants: the roots are seen to bend away from the light and towards the ground; the branches behave just in the opposite way. It now has been supposed by Herbst that such "directive stimuli" may also be at work among the growing or wandering parts of the embryo, that their growth or their migration may be determined by the typical character of other parts, and that real morphogenetic characters can be the result of some such relation; a sort of "chemotropism" or "chemotaxis" may be at work here. Herbst himself has discussed theoretically several cases of organogenesis in which the action of directive stimuli is very probable.

What has become actually known by experiment is not very much at present: the mesenchyme cells of Echinus are directed in their migration by specified places in the ectoderm (Driesch), the pigment cells of the yolk-sac of the fish Fundulus are attracted by its blood-vessels (J. Loeb), and the nerves of amphibian embryos, growing out from the ganglion cells of the central nervous system (His, Harrison), are attracted in some way on their path by the organs·which need innervation. Transplantation experiments (Detwiler, Weiss) have proved, however, that innervation may occur in very abnormal ways, an implanted leg, for example, being innervated by the trigeminous or facialis nerve, according to circumstances. The attractive relation among peripheral organs and nerves, therefore, is by no means specific.

The first case of an "internal formative stimulus" in the proper sense, that is, of one embryonic part causing another to appear, was discovered by Herbst himself. The arms of the so-called pluteus of the sea-urchin are in formative dependence on the skeleton—no skeleton, no arms; so many skeleton primordia,[1] in abnormal cases, so many arms; abnormal position of the skeleton, abnormal position of the arms: these three experimental observations form the proof of this morphogenetic relation.

It may be simple mechanical contact, or it may be some chemical influence that really constitutes the "stimulus" in this case; certainly, there exists a close and very specific relation of the localisation of one part of the embryo to another. Things are much the same in another case, which, after having been hypothetically stated by Herbst on the basis of pathological data, was proved experimentally by Spemann. The lens of the eye of certain Amphibia is formed of their skin in response to a formative stimulus proceeding from the

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[1] I use the word "primordia" for the German "Anlage"; it is better than the word "rudiment", as the latter may also serve to signify the very last stage of a certain formation that is disappearing (phylogenetically).

so-called primary optical vesicle. If this vesicle fails to touch the skin, no lens appears; and, on the other hand, the lens may appear in quite abnormal parts of the skin if they come into contact with the optic vesicle after transplantation.

But formative dependence of parts may also be of different types.

We owe to Herbst the important discovery that the eyes of crayfishes, after being cut off, will be regenerated in the proper way if the optic ganglion is present, but that an antenna will arise in their place if this ganglion has also been removed. There must in this case be some unknown influence of the formative kind on which depends, if not regeneration itself, at least its special character.

In other cases there seems to be an influence of the central nervous system on the regenerative power in general. Amphibia, for instance, are said to regenerate neither their legs (Wolff) nor their tail (Godlewski), if the nervous communications have been disturbed. But this influence is not of a specific nature (Weiss), and in other animals there is no such influence at all; in yet others, as for instance, in Planarians, it must seem doubtful at present whether the morphogenetic influence of the nervous system upon processes of restoration is more than indirect; the movements of the animal, which become very much reduced by the extirpation of the ganglia, being one of the main conditions of a good regeneration.

Of course, all we have said about the importance of special materials in the ripe germ, as bearing on specifically localised organisations, might be discussed again in our present chapter, and our intimate polar-bilateral structure of germs may also be regarded as embracing formative stimuli, at any rate as far as the actual poles of this structure are concerned. This again would bring us to the problem of so-called "polarity" in general, and to the "inversion" of polarity, that is, to a phenomenon well known in plants and in many hydroids and worms, viz., that morphogenetic processes, especially of the type of restitutions, occur differently, according as their point of origin represents, so to speak, the positive or the negative, the terminal or the basal end of an axis, but that under certain conditions the reverse may also be the case. But a fuller discussion of these important facts would lead us deeper and deeper into the science of morphogenesis proper, without being of much use for our future considerations.[1]

A few words may be devoted to the problem of the *determination of sex*, which, according to the latest researches, seems to depend on cytological events occurring in the very earliest embryonic stages, say even before ontogeny, and not on formative stimuli proper. It seems, indeed, as if the sexual products themselves would account for the sex of the individual produced by them, particularly if there were differences in their chromatin. But the problem is by no means solved. In the worm Bonellia external conditions *do* certainly play a rôle in sex determination (Baltzer, Herbst).

The influence of the *sexual* glands on the so-called *secondary* sexual characters of Vertebrates is beyond any doubt, as the transplantation experiments of Steinach have shown. But this statement must not be generalised and is certainly not true for Arthropods (Meisenheimer), where the secondary characters develop quite independently of the sex-glands. It is important to notice that, in Vertebrates, not the sex-cells themselves but certain intermediate cells are the source of the formative influence in question.

Very important additions to the theory of formative stimuli have recently been made by Spemann and his school (Mangold, Goerttler, etc.), by the aid of transplantation of embryonic parts, either in one and the same individual or from one individual to the other. These experiments, all of them carried out in embryos of the newt (Triton), have revealed quite an enormous variety of formative dependences. The authors speak of *homœogeneous induction*, if an implanted part makes other cells

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[1] A full analysis of the subject would not only have to deal with formative stimuli as inaugurating morphogenetic processes, but also with those stimuli which terminate or stop the single acts of morphogenesis. But little is actually known about this topic, and therefore the reader must refer to my other publications. I will only say here, that the end of each single morphogenetic act may either be determined at the very beginning or occur as an actual stopping of a process which otherwise would go on for ever and ever; in the first case some terminating factors are included in the very nature of the morphogenetic act itself.

equal to itself (morphological assimilation), whilst they call *heterogeneous* induction the action of formative stimuli proper. The roof of the primordial intestine, *e.g.*, induces heterogeneously the formation of the axial nervous system, whilst cells of this system, when abnormally transplanted, increase in number by morphogenetic assimilation.

The intimate nature of the morphogenetic influence is unknown. In any case, no nervous influence is in question. The concept of *hormon* (Starling), of so much use in physiology proper, may be applied here.

The ultimate source of all these formative influences is called *organiser* by Spemann,[1] and, in Triton, certain cells near the mouth of the gastrula constitute the organiser *kat' exochen*. The original organiser may induce secondary ones, etc. Later on we shall raise the question whether or not the sequence of organisers may in fact be dissolved into a play of single formative acts.

We have spoken of the morphogenetic potencies in a former paragraph, and may repeat in this place that the discoveries of the Spemann school have shown the embryo of Triton to be *equipotential* in quite an unexpected degree. Not only is every elementary organ equipotential in itself, as we already knew, but the so-called germ layers—in their " presumptive " state at least, *i.e.* as long as they have not yet reached their typical histological structure—are equipotential with regard to one another. " Presumptive " cells of the ectoderm may become mesoderm, etc.

It should well be kept in mind that this equipotentiality refers to what we have called primary potencies (page 58), and not to the secondary ones, which serve for regeneration.

δ. EMBRYOLOGY AND TIME

The duration of individual life is specific for each living species, and the same is true for the duration of the embryological process, the " speed " of embryology, as we may call it. Both statements require the addition of the words *ceteris*

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[1] Croonian Lecture, *Proc. Roy. Soc.* vol. cii., 1927.

paribus, for cold-blooded animals live longer in a low than in a high temperature (J. Loeb), and the duration of embryology depends on temperature, amount of oxygen, etc. But under equal conditions even two different species of sea-urchins differ in the *speed* of their embryology.

Steinach has shown that in vertebrates the duration of life may be increased by certain manipulations with the sexual glands; and Gudernatsch has discovered that the metamorphosis of tadpoles occurs much earlier than normally if they are fed with materials taken from the thyreoidea; whilst, according to Adler, no metamorphosis occurs, if the hypophysis or the thyreodea is extirpated, or if the tadpoles are fed with thymus material. All these results have been confirmed and elaborated in detail. But not very much is really understood in these cases; something of a chemical nature seems to play its rôle.

What seems to me to be most important with regard to the problem of *embryology and time* is the fact that every single embryological process occupies a particular and specific temporal position within a well-ordered sequence of events, *i.e.* a particular relative moment in this sequence at which it is *due*. It neither takes place earlier nor later—both words to be understood in a relative sense—and if, for some reason, it does not take place when *due*, it will *never* occur.

Herbst, *e.g.*, has oppressed the growth of the intestine in the gastrula of echinoderms by eliminating the element kalium from the sea-water. Everything else, then, goes on quite normally as far as the ectodermal organs are concerned. But there never will be any endoderm, even if the larvae are put back into normal sea-water.

Even the single steps in cleavage are *due* at specific relative moments. According to Boveri a whole normal egg may occasionally segment, as if it were one of the two or four first cleavage cells. In this case there have been nuclear divisions without any protoplasmic division in the egg. Let us assume that the two first divisions have affected the nucleus exclusively, whilst the third division has led to two equal cells. Then the next division will not lead to a stage of four equal cells, but will give us two mesomeres, one macromere and one micromere.

For at the fourth nuclear division micromeres are " due " (cp. p. 21).

This phenomenon of " being due " requires further investigation. And so does the question whether an embryonic process n happens to be realised because the process $n - 1$ *has occurred* or because the result of this process *does exist*, which, of course, is not the same. To this problem we shall come back later.

Certain observations in the course of Spemann's and Mangold's experiments (cp. p. 73 f.) tend in the same direction: implanted cells do not show their formative influence upon the cells of the host if the process in question is not " due ", *i.e.* if the host is " too old " already—though it may be a little " too young ". And this agrees with what Uhlenhuth and Kornfeld have called " synchronic metamorphosis " : if you implant embryonic eyes or gills of a salamander upon a host of greater age, they will change their structure according to the age of the host. The host gives the temporal rule.

To sum up : it seems as if there were a continuous stream of becoming at the basis of the embryological process, of which the visible embryonic phases are nothing but indexes. And this ultimate continuous foundation seems to give its *temporal position* to every single embryological performance.

All this relates to embryology proper exclusively. It does not relate to " secondary regulations " nor to the morphogenesis of " open forms " (p. 31) as, *e.g.*, the plants. The periodicity in the origin and the fall of the leaves of our trees, according to Klebs, has no internal but only external reasons, and the same is true for the alternation of the various generations of fungi and in many other botanical cases.

ε. THE MORPHOGENETIC HARMONIES

Let us now turn to considerations of a more abstract kind : we have become acquainted with some morphogenetic interactions among the parts of a developing embryo ; and, indeed, we can be sure that there exist far more of such interactions than we know at present.

But it is far from being true that the development of each embryonic part depends on the existence or development of every other one.

On the contrary, it is a very important and fundamental feature of organogenesis that it occurs in separate lines, that is to say, in lines of processes which may start from a common root, but which are absolutely independent of one another in their manner of differentiation. Roux has coined the term *self-differentiation* to denote this phenomenon, and we admit that this term may be conveniently used for the purpose, if only it can be kept in mind that its sense is always relative, and that it is also negative. Suppose a part, *A*, shows the phenomenon of self-differentiation: this means that the further development of *A* is not dependent on certain other parts, *B*, *C*, and *D*; it does *not* mean at all that *A* has not been formatively dependent on some other parts, *E* or *F*, at the time of its first appearance, nor does it imply that there might not be many formative actions among the constituents of *A* itself.

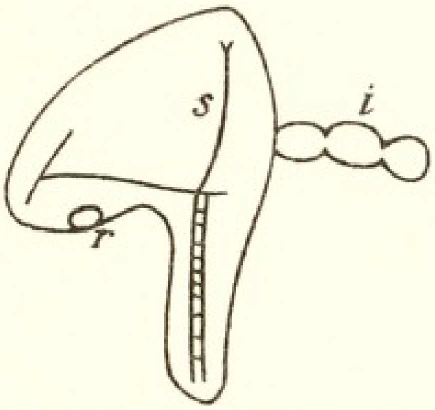

FIG. 10.—PLUTEUS-LARVA OF SPHAERECHINUS.

The Intestine (i) is developed outside instead of inside (by means of raising the temperature); but the mouth (r) is formed in its normal place. S = Skeleton.

We indeed are entitled to say that the ectoderm of Echinus shows "self-differentiation" with regard to the endoderm; it acquires its mouth, for instance, as has been shown by experiment, even in cases where no intestine is present at all (Fig. 10); but ectoderm and endoderm both are formatively dependent on the intimate and the material organisation of the blastoderm. In the same way, in the amphibian embryo, the formation of the "Anlage" of the legs and of the central nervous system are mutually independent.

The phenomenon of self-differentiation, properly understood, now may help to the discovery of one most general character of all development. If the phenomenon of self-differentiation really occurs in ontogeny in its most different aspects, and if, on the other hand, in spite of this relative morphogenetic independence of embryonic parts, the resulting organism is one whole in organisation and in function, some sort of *harmony of constellation*, as it may properly be styled, must be said to be one of the most fundamental characters of all production of individual form. In establishing this harmony, we do nothing more than describe exactly what happens: the harmony is shown by the fact that there *is* a whole organism at the end, in spite of the relative independence of the single events leading to it.

But still another sort of harmony is revealed in morphogenesis, by an analysis of the general conditions of the formative actions themselves. In order that these actions may go on properly, the possibility must be guaranteed that the formative causes may always find something upon which to act, and that those parts which contain the potencies for the next ontogenetic stage may properly receive the stimuli awaking these potencies: otherwise there would be no typical production of form at all. This, the second species of harmonious relations to be described in ontogeny, may be called *causal harmony*; the term simply expresses the unfailing relative condition of formative causes and cause-recipients.

Finally, in *functional harmony* we have an expression descriptive of the unity of organic function, and so we may state, as the latest result of our analytical theory of development up to this point, that individual morphogenesis is marked by a *threefold harmony* among its parts.

The three sides or parts of this threefold harmony are united in a very close way. They penetrate one another, as it were. For the embryological process lays the foundations of all the future functions of the adult; and, on the other hand, that process itself depends on a harmony of functions, every embryonic stage being also a functioning totality. We must never forget that the organism is in each of its stages a unity of form and of function, these two features being dependent on one another.

ζ. ON RESTITUTIONS [1]

At this stage we leave for a while our analytical studies of ontogeny proper. We must not forget that typical ontogenesis is not the only form in which morphogenesis can occur: the organic form is able to restore disturbances of its organisation, and it certainly is to be regarded as one of the chief problems of analytical morphogenesis to discover the specific and real stimulus which calls forth the restoring processes. For simply to say that the disturbance is the cause of the restoration would be to evade the problem instead of attacking it. But there are still some other problems peculiar to the doctrine of restitutions.

A few Remarks on Secondary Potencies and on Secondary Morphogenetic Regulations in General

We have only briefly mentioned in a previous chapter (page 58) that there exist many kinds of potencies of what we call the *secondary* or truly restitutive type, and that their distribution may be most various and quite independent of all the potencies for the primary processes of ontogeny proper. Let us first add a few words about the concept of "secondary restitution" and about the distribution of secondary potencies in general.

Primary ontogenetic processes founded upon primary potencies may *imply* regulation, or, more correctly, restitution in many cases: so it is when fragments of the blastula form the whole organism or when the mesenchyme cells of Echinus reach their normal final position by an attraction on the part

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[1] Driesch, *Die organischen Regulationen*, Leipzig, 1901; Morgan, *Regeneration*, New York, 1901.

of specific localities of the ectoderm in spite of a very abnormal original position enforced upon them by experiment. In these cases we speak of *primary* regulations or restitutions; disturbances are neutralised by *the very nature* of the process in question. We speak of *secondary* restitution whenever a disturbance of organisation is rectified by processes foreign to the realm of normality; and these abnormal lines of events are revealed to us in the first place by the activity of potencies which remain latent in ontogeny proper.

We know already that a certain kind of secondary restitution has been discovered, very contradictory to the theoretical views of Weismann; the process of restoration being carried out not by a definite part of the disturbed organisation, but by all the single elements of it. The problem of the distribution of secondary potencies in these cases of so-called "re-differentiation" is to form our special study in the next chapter.

In all other cases restoration processes start from specific localities; if they occur on the site of the wound which caused the disturbance, we speak of *regeneration*; if they occur at some distance from the wound, we call them *adventitious* processes.

Besides these three types of processes of restitution, there may be mentioned a fourth one, consisting in what is generally called *compensatory hypertrophy*; the most simple case of such a compensatory process is when one of a pair of organs, say a kidney, becomes larger after the other has been removed. But real compensatory differentiation occurs in the cases of so-called "hypertypy" as first discovered by Przibram and afterwards studied by Zeleny: here the two organs of a pair show a different degree of differentiation. Whenever the more specialised organ is removed the less developed one assumes its form. Similar cases, which might simply be called "compensatory heterotypy", are known in plants, though only relating to the actual fate of undifferentiated "Anlagen" in these organisms. A leaf may be formed out of the "Anlage" of a scale, if all the leaves are cut off, and so on.

Finally, at least in plants, a change of the directive irritability, of so-called "geotropism" for instance, in certain parts may serve to restore other more important parts.

In two of these general types of restitution, in regeneration proper and in the production of adventitious organs, the potencies which underlie these processes may be said to be "complex". It is a complicated series of events, a proper morphogenesis in itself, for which the potency has to account, if, for instance, a worm newly forms its head by regeneration, or if a plant restores a whole branch in the form of an adventitious bud.

Such generalisations as are possible about the distribution of complex potencies are also reserved for a special part of our future discussion.

Secondary restitution is always, like ontogeny, a process of morphogenesis, and therefore all the questions about single formative stimuli, and about internal and external conditions or means, occur again. But of course we cannot enter into these problems a second time, and may only say that, especially in regeneration proper, the specific type of the regenerative formation of any part may differ very much from the ontogenetic type of its origin: the end of both is the same, but the way can be even fundamentally different in every respect.

The Stimuli of Restitutions [1]

But now we turn to the important question: what is the precise stimulus [2] that calls forth processes of restitution; or, in other words, what must have happened in order that restitution may occur?

That the operation in itself, by its removing of mechanical

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[1] For a fuller analysis, compare my opening address delivered before the section of "Experimental Zoology" at the Seventh International Zoological Congress, Boston, 1907: "The Stimuli of Restitutions" (see Proceedings of that Congress).

[2] The problem of the stimulus of a secondary restitution as a whole must not be confused with the very different question, what the single "formative stimuli" concerned in the performance of a certain restitutive act may be. With regard to restitution as a *whole*, these single "formative stimuli" might properly be said to belong to its "internal means"—in the widest sense of the word.

obstacles, cannot be the true stimulus of any restitutions, is simply shown by all those restitutions that do not happen at the place of the wound. If we took a narrower point of view, and if we only considered regeneration proper from the wound itself, we might probably at first be inclined to advocate the doctrine that the removing of some obstacles might in fact be the stimulus to the process of restoration ; but, even then, why is it that just what is wanted grows out ? Why is there not only growth, but specific growth, growth followed by specification ? The removing of an obstacle could hardly account for that. But, of course, taking account of all the adventitious restitutions—that is, all restorations not beginning at the wound itself—the theory that the removing of obstacles is the stimulus to restoration becomes, as we have said, quite impossible.

But where then is the stimulus to be found ? There is another rather simple theory of the " Auslösung " of restitutions, which starts from the phenomena of compensatory hypertrophy and some occurrences among plants. The removal of some parts of the organism, it is said, will bring its other parts into better conditions of nutrition, and therefore these parts, particularly if they are of the same kind, will become larger. Granted for the moment that such a view may hold in cases when one of a pair of glands becomes larger after the other has been removed, or when pruning of almost all the leaves of a tree leads to the rest becoming larger, it certainly must fail to explain the fact that in other cases true *new* formations may arise in order to restore a damaged part, or that the latter may be regenerated in its proper way. For *merely quantitative* differences in the mixture of the blood or of the nourishing sap in plants can never be a sufficient reason for the highly typical and *qualitative* structure of newly formed restitutions. And even in the most simple cases of a mere increase in the size of some parts, that is in the simplest cases of so-called compensatory hypertrophy, it is at least doubtful, if not very improbable, that the compensation is accomplished in such a purely passive way, because we know that in other cases it is usually the growth of the young parts that actively attracts the nourishment: there is, first, differentiation and growth, and *afterwards* there is a change in the direction of the nourishing fluids.

The process of true regeneration, beginning at the locality of the wound itself, has been shown by Morgan, even as regards its rate, to occur quite irrespectively of the animal being fed or not. There could hardly be a better demonstration of the fundamental fact that food assists restitution, but does not "cause" it in any way.

But in spite of all we have said, there seems to be some truth in regarding the nutritive juices of animals and plants as somehow connected with the stimulus of restitutions: only in this very cautious form, however, may we make the hypothesis. It has been shown, for both animals and plants, that morphogenesis of the restitutive type may be called forth even if the parts now to be "regenerated" have not been actually removed; *e.g.* in the so-called super-regeneration of legs and tails in Amphibia, of the head in Planarians, of the root-tip in plants and in some other cases. Here it has always been a disturbance of the normal connection of some parts with the rest of the organism which proved to be the reason of the new formation. This shows that something to do with the communication among parts is at least connected with restitution, and this communication may go on either by the unknown action of specific tissues or by the aid of the blood or sap. But in what this change or break of specific communication consists, is absolutely unknown. One might suppose that each part of the organisation constantly adds some sort of ferment to the body fluids outside or inside the cells, that the removing of any part will change the composition of these fluids in this particular respect, and that this change acts as a sort of communication to summon the restituting parts of the whole to do their duty.[1]

But I see quite well that such a theory is not very satisfactory; for what has to be done in restitution in each

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[1] The so-called "inner secretion" in physiology proper would offer a certain analogy to the facts assumed by such an hypothesis. Compare the excellent summary given by E. Starling at the seventy-eighth meeting of the German "Naturforscherversammlung", Stuttgart, 1906.

case is not a simple homogeneous act, for which one special material might account, but is a very complicated work in itself. It was the defect of the theory of " organ-forming substances " as advocated by Sachs, that it overlooked this point.

So all we know about the proper stimuli of restitutions is far from resting on any valid grounds at all. No doubt, there will be something discovered some day, and the idea of the " whole " in organisation will probably play some part in it. For two facts must be well kept in mind : first, that in all restitutions the cells in action always perform that which is necessary in *this particular case* in order to restore normal organisation; and secondly, that the same cells *might* perform something else if required. Does it not seem, then, as if the cells had some " knowledge " about the specificity of the disturbance ? If so, there would be an analogy to—specific sensation.

But nothing more about this topic at present.

This is the first time that, hypothetically at least, the idea of *the whole* has entered into our discussion. The same idea may be said to have entered it already in a more implicit form in the statement of the threefold harmony in ontogeny.

Let us now see whether we can find the same problem of the " whole " elsewhere, and perhaps in more explicit and less hypothetical form. Let us see whether our analytical theory of development is in fact as complete as it seemed to be, whether there are no gaps left in it which will have to be filled up.

3. THE PROBLEM OF MORPHOGENETIC LOCALISATION

FIRST PROOF OF THE AUTONOMY OF LIFE

WE have come to the central point of the first part of this book; we shall try in this chapter to decide a question which is to give life its place in Nature, and biology its place in the system of sciences. One of the foundation-stones is to be laid, upon which our future philosophy of the organism will rest.

The General Problem

Our analytical theory of morphogenesis has been founded upon three elementary concepts — the prospective potency, the means, and the formative stimulus; and its principal object has been to show that all morphogenesis may be resolved into the three phenomena expressed by them. Have we indeed succeeded in attaining this object? Is it really possible to explain every morphogenetic event, at least in the most general way, by the aid of the terms potency, means, and stimulus?

All of these questions are apt to lead us to further considerations. Perhaps these considerations will give us a very clear and simple result by convincing us that it is indeed possible to analyse morphogenesis in our schematic way.

But if the answer were a negative one? What would that suggest?

The full analysis of morphogenesis into a series of single formative occurrences, brought about by the use of given means and on the basis of given potencies, might assure us, perhaps, that, though not yet, still at some future time, a further sort of analysis will be possible: the analysis into the elemental facts studied by the sciences of inorganic nature. The organism might prove to be a machine, not only in its functions but also in its very origin.

But what are we to say if even the preliminary analysis, which possibly might lead to such an ultimate result, fails ?

Let us, then, set to work. Let us try to consider most carefully the topic in which our concept of the formative cause or stimulus may be said to be centred, the *localisation* of all morphogenetic effects. Is it always possible, in fact, to account for the typical localisation of every morphogenetic effect by the discovery of a single specific formative stimulus ? You will answer me, that such an analysis certainly is not possible at present. But I ask you again, are there any criteria that it is possible, at least in principle ; or are there any criteria which will render such an aim of science impossible for all future time ?

The Morphogenetic " System "

We know from our experimental work that many, if not all, of the elementary organs in ontogeny show one and the same prospective potency distributed equally over their elements. If we now borrow a very convenient term from mechanics, and call any part of the organism which is considered as a unit from any morphogenetic point of view, a morphogenetic "*system*", we may sum up what we have learnt by saying that both the blastoderm of the echinoderms, at least around its polar axis, and also the germ-layers of these animals, are " systems " possessing an equal potentiality in all of their elements, or, in short, that they are *equipotential systems*.

But such a term would not altogether indicate the real character of these systems.

Later on, we shall analyse, more carefully than before, the distribution of potencies which are the foundation both of regeneration proper and of adventitious growth, and then we shall see that, in higher plants for instance, there is a certain " system " which may be called the organ proper of restitutions, and which also in each of its elements possesses the same restoring potency ; I refer to the well-known *cambium*. This cambium, therefore, also deserves the name of an " equipotential system ". But we know already that its potencies are of the *complex* type, that they consist in the faculty of producing the *whole* of such a complicated organisation as a branch or a root, that the term " equipotential system " is here only to signify that such a complicated unit may arise out of each of the cells of the cambium.

The potencies we have been studying in the blastula or gastrula of echinoderms are not of the complex type : our systems are equipotential to the extent that each of their elements may play every *single* part in the totality of what will occur in the whole system ; it is to this *single* part that the term " function of the position " relates. We therefore might call our systems equipotential systems with single potencies ; or, more shortly, *singular-equipotential* systems.

But even this terminology would fail to touch precisely the very centre of facts : it is not only the simplicity or singularity of their potencies which characterises the rôle of our systems in morphogenesis, but far more important with respect to the production of form are two other leading results of the experimental researches. The proper act to be performed by every element in each actual case is, in fact, a single one, but the potency of any element as such consists in the possibility of *many* single acts : that, then, might justify us in speaking of our systems as " indefinite equipotential ", were it not that another reason makes another title seem still more preferable. For the name of indefinite equipotential systems might also be applied to elementary organs, the single potencies of which are awaked to organogenesis by specific formative stimuli, as in the experiments carried out by Spemann and his school, where the reaction of one and the same cell varies according to the stimulus in question. But this is not the case in the system of which we are now speaking. There are, indeed, indefinite singular potencies at work in our systems during ontogeny ; but what happens to arise in every case out of the totality of the single acts performed by all of the single equipotential cells is not a sum induced from without, but a unit guaranteed from within. That is to say, there exists a sort of inner harmony in every case among the *real products* of our systems, these products being due to the inner forces of the systems exclusively. The term *harmonious-equipotential system*, therefore, seems to be the right one to denote them.

We now shall try, first, to analyse to its very extremes the meaning of the statement that a morphogenetic system is harmonious-equipotential.

The " Harmonious-Equipotential System "

We have an ectoderm of the gastrula of a starfish here before us ; we know that we may cut off any part of it in any direction, and that nevertheless the differentiation of the ectoderm may go on perfectly well and result in a typical little embryo, which is only smaller in its size than it would normally be. It is by studying the formation of the highly complicated ciliary band that these phenomena can be most clearly understood.

Now let us imagine our ectoderm to be a cylinder instead of being approximately a sphere, and let us imagine the surface of this cylinder unrolled. It will give us a plane of two definite dimensions, a and b. And now we have all the means necessary for the analytical study of the differentiation of an harmonious-equipotential system.

Our plane of the dimensions a and b is the basis of the normal, undisturbed development ; taking the sides of the plane as fixed localities for orientation, we can say that the actual fate, the " prospective value " of every element of the plane stands in a fixed and definite correlation to the length of two lines, drawn at right-angles to the bordering lines of the plane ; or, to speak analytically, there is a definite actual fate corresponding to each possible value of x and of y. Now, we have been able to state by our experimental work, that the prospective value of the elements of our embryonic organ is not identical with their " prospective potency ", or their possible fate, this potency being very much richer in content than is shown by a single case of ontogeny. What will be the analytical expression of such a relation?

Let us put the question in the following way: on what factors does the fate of any element of our system depend in all possible cases of development obtainable by means of operations? We may express our results in the form of an equation—

$$p.v.\ (X) = f\ (\ .\ .\ .\ ),$$

i.e. "the prospective value of the element X is a function of . . ."—of what?

We know that we may take off *any* part of the whole, as to *quantity*, and that a proportionate embryo will result, unless the part removed is of a very large size. This means that the prospective value of any element certainly depends on, certainly is a function of, the *absolute size* of the actually existing part of our system in the particular case. Let s be the absolute size of the system in any actual experimental case of morphogenesis: then we may write $p.v.\ (X) = f\ (s\ .\ .\ .\ )$. But we shall have to add still some other letter to this s.

The operation of section was without *any* restriction either as to the *amount* of the material removed from the germ or as to the direction of the cut. Of course, in almost every actual case there will be both a definite size of the actual system and a definite direction of the cut going hand-in-hand. But in order to study independently the importance of the variable *direction* alone, let us imagine that we have isolated at one time that part of our system which is bounded by the lines $a_1\ b_1$, and at another time an *equal* amount of it which has the lines $a_2\ b_2$ as its boundaries. Now, since in both cases a typical small organism may result on development, we see that, in spite of their equal size, the prospective value of every element of the two pieces cut out of the germ may vary even in relation to the direction of the cut itself. Our element, X, may belong to both of these pieces of the same size: its actual fate nevertheless will be different. Analytically, it may be said to change in correspondence to the actual position of the actual boundary lines of the piece itself with regard to the fundamental lines of orientation, a and b; let this actual position be expressed by the letter l, l marking the distance of one[1] of the actual boundary lines of our piece from a or b: then we are entitled to improve our formula by writing $p.v.\ (X) = f\,(s, l\ .\ .\ .\ )$ (Fig. 11).

But the formula is not yet complete: s and l are what the mathematicians call variables: they may have *any* actual value and there will always be a definite value of *p.v.*, *i.e.* of the actual fate which is being considered; to every value of s and l, which as we know are independent of each other, there corresponds a definite value of the actual prospectivity. Now, of course, there is also a certain factor at work in every actual case of experimental or normal development, which is *not* a variable, but which is the same in all cases. This factor is a something embraced in the prospective potency of our system, though not properly identical with it.

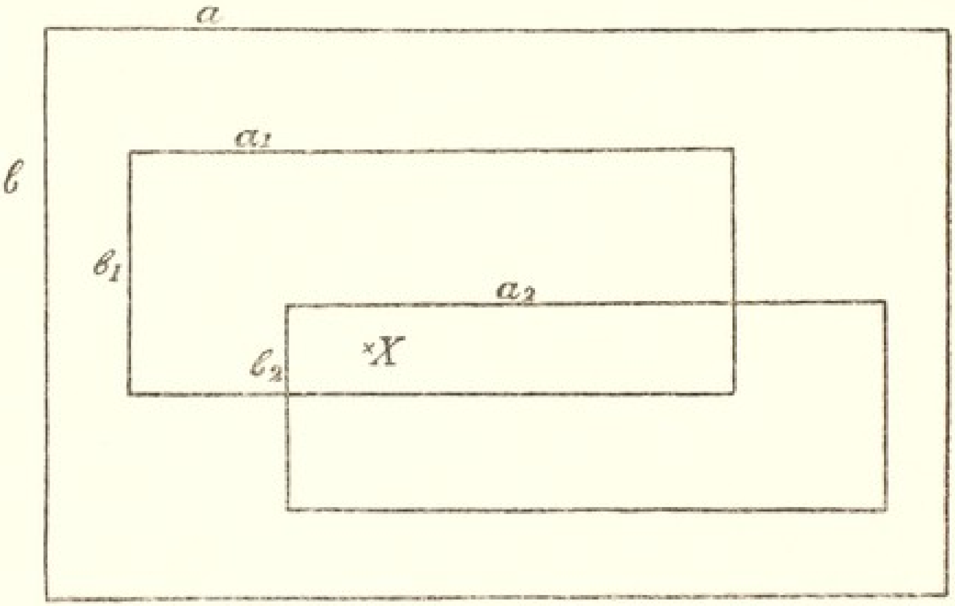

Fig. 11.—Diagram to show the Characteristics of an "Harmonious-Equipotential System."

The element X forms part of the systems $a\ b$ or $a_1\ b_1$ or $a_2\ b_2$; its prospective value is different in each case.

The prospective potency of our system, that is to say of each of its elements, is the sum total of what can be done

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[1] The distance of the other boundary line from a or b would be given by the value of s.

equally well by all ; but the fact that a typically proportionate development occurs in every possible case, proves that this sum comes into account, not merely as a sum, but as a sort of order : we may call this order the " relation of localities in the absolutely normal case ". If we keep in mind that the term " prospective potency " is always to contain this order, or, as we may also call it, this " relative proportionality ", which, indeed, was the reason for calling our systems " harmonious ", then we may apply it without further explanation in order to signify the *non-variable* factor on which the prospective value of any element of our systems depends ; and if we denote the prospective potency, embracing order, by the letter E, we are now able to complete our formula by saying $p.v.\ (X) = f\ (s, l, E)$.

So far the merely analytical study of the differentiation of harmonious-equipotential systems.[1]

Instances of " Harmonious-Equipotential Systems "

We must try at first to learn a few more positive facts about our systems, in order that we may know how important is the part which they play in the whole animal kingdom, and in order that our rather abstract analysis may become a little more familiar to us. We know already that many of the elementary morphogenetic organs have been really proved to be harmonious-equipotential systems, and that the same probably is true of many others ; we also know that the immature egg of almost all animals belongs to this type, even if a fixed determination of its parts may be established just after maturation. Moreover, we said, when speaking about some new discoveries on form-restitution, that there are many cases in which the processes of restitution do not proceed from single localities, the seat of complex potencies in the organism, but in which each *single* part of the truncated organism left by the operation has to perform one *single* act

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[1] A far more thorough analysis of this differentiation has been attempted in my paper, " Die Lokalisation morphogenetischer Vorgänge ; Ein Beweis vitalistischen Geschehens," Leipzig, 1899.

of restoration, the full restitution being the result of the totality of all.

Let me mention in the first place a few more purely embryological cases.

The mesenchyme cells of the sea-urchin form a harmonious-equipotential system ; for we may eliminate any number of these cells we like, or may change their relative position with respect to one another, and the skeleton is always normal. It is just as when 100 workmen have to construct a bridge and a certain number of them, *n*, fall ill and become unable to work. Then the rest, 100 - *n*,—(*n* being variable !)—must carry out the work, assuming that we cannot engage other workmen, and are *able* to do so !

Beautiful cases of equipotentiality have been discovered by Braus and Harrison : the *Anlage* of the limb of Amphibians, including the complicated skeleton, is equipotential to the very highest degree. You can do with this *Anlage* what you like : take off any part, unite two of them, turn it over, etc. The result is always normal.

The same is true with regard to regeneration : the small buds of cells, by which regeneration of the limbs of Amphibians begins, are equipotential. And it even seems, that the initial prolification of cells, which used to be the first step of regenerative processes, is harmonious-equipotential in *every* case.

But now let us give some details about some forms of restitution discovered during the last thirty years.

All of you have seen common sea-anemones or sea-roses, and many of you will also be familiar with the so-called hydroid polyps. *Tubularia* is one genus of them : it looks like a sea-anemone in miniature placed on the top of a stem like a flower. It was known already to Allman that *Tubularia* is able to restore its flower-like head when that is lost, but this process was taken to be an ordinary regeneration, until an American zoologist, Miss Bickford, succeeded in showing that there was no "regeneration" process at all, in the proper sense of the word, no budding of the missing part from the wound, but that the new tubularian head was restored by the combined work of many parts of the stem. Further analysis then taught us that *Tubularia* indeed is to be regarded as the perfect type of an harmonious-equipotential system: you may cut the stem at whatever level you like: a certain length of the stem will always restore the new head by the co-operation of its parts. As the point of section is of course absolutely *at our choice,* it is clear, without any further discussion, that the prospective value of each part of the restoring stem is a "function of its position", that it varies with its distance from the end of the stem; and so at once we discover one of the chief characteristics of our systems. But also the second point which enters into our formula can be demonstrated in *Tubularia*: the dependence of the fate of every element on the actual size of the system. You would not be able to demonstrate this on very long stems, but if you cut out of a *Tubularia* stem pieces which are less than ten millimetres in length, you will find the absolute size of the

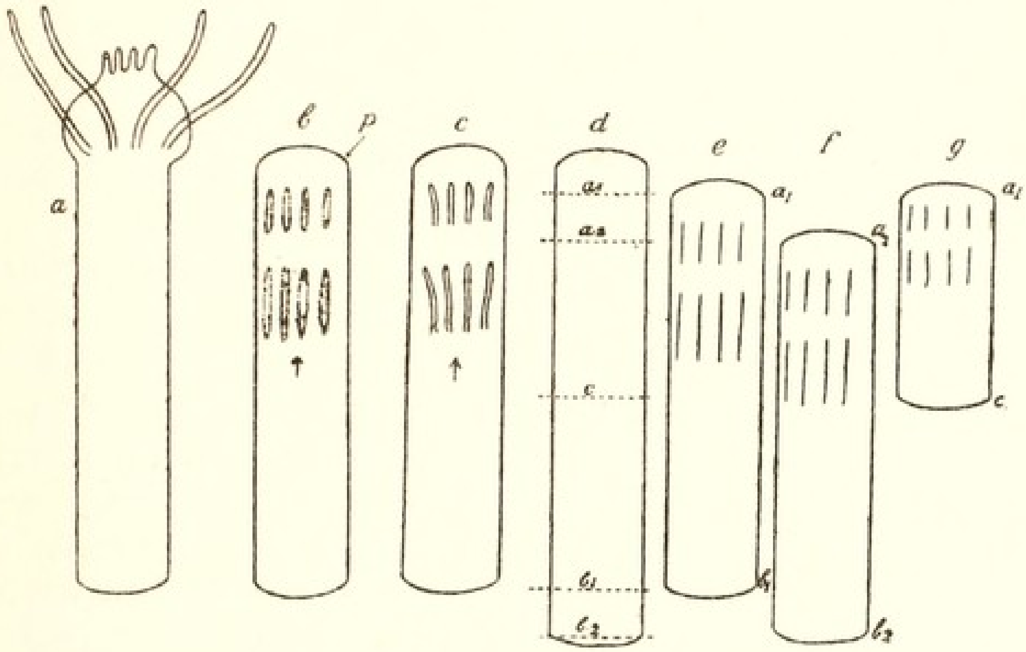

FIG. 12.—TUBULARIA.

a. Diagram of the "Hydranth", with its short and long tentacles.
b. Restitution of a new hydranth inside the perisarc (*p*).
c. The same—later stage; the tentacles are complete; the whole hydranth will be driven out of the perisarc by a process of growth that occurs at the locality marked ↑.
d. A stem of *Tubularia* cut either at a_1 b_1 or at a_2 b_2, or at a_1 c.
e. Position of tentacles in the piece cut at a_1 b_1.
f. ,, ,, ,, a_2 b_2, which is equal in length to a_1 b_1.
g. ,, ,, ,, a_1 c, which is half as long as a_1 b_1.

head restored to be in close relation to the length of the stem piece, and this dependence, of course, includes the second sort of dependence expressed in our formula.

The figures will serve to show you a little more concretely what has been described. The head of *Tubularia* consists of a sort of broad base with a thin proboscis upon it, both bearing a large number of tentacles ; these tentacles are the first things to be seen as primordia (" Anlagen ") in the process of restitution. You notice two rings of longitudinal lines inside the stem ; the lines will become walls and then will separate from the stem until they are only connected with it at their basal ends ; the new tentacles are ready as soon as that has happened, and a process of growth at the end will serve to drive the new head out of the so-called perisarc, or horny skeleton, which surrounds the stem. By comparing the two figures, 12 *e* and *g*, you easily find out that the absolute lengths of the two tentacle rings are very different, and that both are in proportion [1] to the actual size of the stem (Fig. 12).

So we find our formula $p.v.\ (X) = f\,(s,\ l,\ E)$ very well illustrated in *Tubularia*. The formula indeed may help us to predict, in any case, where a certain part of the polyp's organisation is to originate, at least if we know all that is included under our letter E, *i.e.* the normal proportion of our form.

Another very typical case of a morphogenetic system of the harmonious type is supplied by the phenomena of restoration in the ascidian *Clavellina*. I cannot fully describe the organisation of this form (Fig. 13 *a*), and it must suffice to say that it is very complicated, consisting of two very different chief parts, the branchial apparatus and the so-called intestinal sac ; if these two parts of the body of *Clavellina* are separated one from the other, each *may* regenerate the other in the typical way, by budding processes from the wound. But, as to the

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[1] This statement is *not strictly* correct for *Tubularia*. I found (*Archiv. f. Entwickelungsmechanik*, ix. 1899) that a reduction of the length of the stem is always followed by a reduction of the size of the hydranth-primordium, but there is no real proportionality between them. It is only for theoretical simplification that a strict proportionality is assumed here, both in the text and the diagram. But there is an almost strict proportionality in all cases of " closed forms ".

branchial apparatus, there *may* happen something very different: it may lose almost all of its organisation and become a small white sphere, consisting only of epithelia corresponding to the germ-layers, and of mesenchyme between them; and then, after a certain period of rest, a new organisation will appear. Now, this new organisation is not that of a branchial apparatus but represents a very small but complete ascidian (Fig. 13). Such a fact certainly seems to be very important, not to say very surprising. But still another phenomenon may be demonstrated on the animal, which seems to be even more important. You first isolate the branchial apparatus from the other part of the body, and then you cut it in two, in whatever direction you please. Provided they survive and do not die, as indeed many of them do, the pieces obtained by this operation will each lose their organisation, as did the whole branchial apparatus, and then will each acquire another one—and this new organisation is also that of a *complete* little *Clavellina*. So we see that not only is the branchial apparatus of our animal capable of being transformed into a whole animal by the

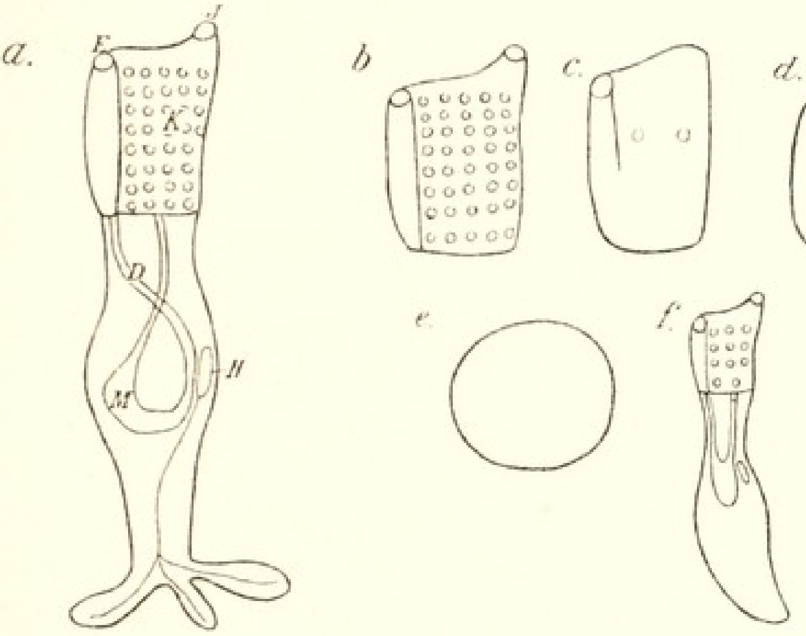

Fig. 13.—Clavellina.

a. Diagram of the normal animal: *E* and *J*=openings; *K*=branchial apparatus; *D*=intestine; *M*=stomach; *H*=heart.
b. The isolated branchial apparatus.
c-e. Different stages of reduction of the branchial apparatus.
f. The new *whole* little ascidian.

co-operative work of all its parts, but even each *part* of it may be transformed into a small *whole*, and it is quite at our disposal how large this part shall be, and what sort of a fragment of the original branchial apparatus it shall represent.

We could hardly imagine a better instance of an harmonious-equipotential system.

I cannot give you a description of all the other types of our systems subservient to restitution, and I can only mention here that the common hydra and the flatworm *Planaria* are very fine examples of them. But to one special case of harmonious equipotentiality you must allow me to direct your further attention.

It has been known for many years that the Protozoa are also capable of a restoration of their form and organisation after disturbances, if at least they contain a certain amount of their nuclear substance. This process of restoration used to be regarded as belonging to the common type of regeneration proper, until T. H. Morgan succeeded in showing that in the genus *Stentor* it follows just the very lines which we know already from our study of embryonic organs or from *Tubularia* : that an harmonious-equipotential system is at the basis of what goes on. Now, you know that all Protozoa are but one highly organised cell : we have therefore here an instance where the so-called " elements " of our harmonious-morphogenetic system are not cells, but something inside of cells ; and this feature must appear to be of very great moment, for it first shows, as we have already pointed out on another occasion, that morphogenesis is not necessarily dependent on cell-division, and it states at the same time that our concept of the harmonious-equipotential system may cover a very great area—that, in fact, it is a scheme of a very wide extent.

The Problem of the Factor E

We turn back again to considerations of a more abstract form. We left our analysis of the differentiation of the harmonious-equipotential systems, and particularly of the phenomena of localisation during this differentiation, at the point where we had succeeded in obtaining an equation as the expression of all those factors on which the prospective value, the actual fate, of any element of our systems depends. $p.v. (X) = f (s, l, E)$ was the short expression of all the relations involved; s and l, the absolute size of the system and the relative position of the element with respect to some fixed points, were independent variables; E was a constant, namely, the prospective potency, with special regard to the proportions embraced by it.

We shall now study the significance of the factor E.

What does this E mean? Is it a short expression merely for an actual sum of elemental agents having a common resultant? And, if so, of what kind are these agents? Or what may E mean, if it can be shown *not* to be a short sign for a mere sum?

No Explanation offered by "Means" or "Formative Stimuli"

For practical purposes it seems better if we modify the statement of our question. Let us put it thus: E is one of the factors responsible, among variables, for the localisation of organic differentiation; what then do we actually know about the causal factors which play a *localising* part in organogenesis? We, of course, have to look back to our well-studied "formative stimuli". These stimuli, be they "external" or "internal", come from without with respect to the elementary organ in which any sort of differentiation, and therefore of localisation, occurs: but in our harmonious systems no localising stimulus comes from without, as was the case, for instance, in the formation of the lens of the eye in response to the optical vesicle touching the skin. We know absolutely that it is so, not to speak of the self-evident fact that the general "means" of organogenesis have no localising value at all.[1]

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[1] One might object here that in a piece of a *Tubularia* stem, for instance, the tissues are in direct contact with the sea-water at the two points of the wounds only, and that at these very points a stimulus might be set up—say by a process of diffusion—which gradually decreases in intensity on its way inward. And a similar argument might apply to the small but whole blastula of Echinus, and to all other cases. But, in the first place, stimuli

Some authors have objected to my arguments that the germ, say in the shape of sixteen cells, might be regarded as a typically ordered physico-chemical system, in which all sorts of diffusions and other kinds of transport of materials might go on in a well-regulated pre-established way. Very well—for the case of *normal* embryology. But there are the results of experiment ! I take away one of the first four cleavage cells : the result is the normal one. And, if I may add another type of experiment not yet mentioned, the result is also the normal one if in the 16-cell stage I take, say, two micromeres, one macromere, and three mesomeres—that is, if I allow development to start from very " unharmoniously composed " conditions.

In face of such facts, the theory of the well-ordered pre-established system of surfaces, diffusions, etc., breaks down completely.

So we see there is nothing to be done, either with the means or with the formative stimuli ; both are entirely unable to account for those kinds of localisation during differentiation which appear in our harmonious systems.

But is there no possibility of explaining the phenomena of organogenetic localisation by any other sort of interaction of parts ? Two such possibilities may at the first glance seem to exist.

No Explanation offered by a Chemical Theory of Morphogenesis

Though never set forth in the form of a properly worked-out theory, the view has sometimes been advocated by

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which only differ in intensity could hardly call forth the typical and typically localised single features realised in differentiation. On the other hand—and this will overthrow such an hypothesis completely—the dependence of the single localised effects in every case on the *absolute size* of the fragment or piece chosen for restoration renders quite impossible the assumption that all the singularities in the differentiation of the harmonious systems might be called forth by single stimuli originating in two fixed places in an *independent* way. These would never result in any "harmonious", any proportionate structure, but a structure of the " normal " proportionality *and size* at its two ends and non-existent in the middle !

biologists, that a chemical compound of a very high degree of complication might be the very basis of both development and inheritance, and that such a chemical compound by its disintegration might direct morphogenesis.

Let us first examine if such a view may hold for the most general features of organic morphogenesis. It seems to me that from the very beginning there exists one very serious objection to every *purely* chemical theory of form-building,[1] in the mere fact of the possibility of the restoration of form starting from atypical localities. The mere fact, indeed, that there is such a thing as the regeneration of a leg of a newt—to say nothing about restitution of the harmonious type—simply contradicts,[2] it seems to me, the hypothesis that chemical disintegration of one compound may govern the course of morphogenetic events: for whence comes the re-existence of the hypothetical compound, newly to be disintegrated, after disintegration *has* been completed once already? And we even know that regeneration may go on several times running from the same locality, and that a regenerated part may later on be itself the starting-point of regeneration.

But, if we intentionally disregard this difficulty, in spite of its fundamental character, how could the hypothesis of chemical disintegration give the reason for the differentiation of our harmonious-equipotential systems, with special regard to the localisation of it; how could it account, in other words, for the appearance of typically localised specifications in an organ for which no external localising causes can be predicated?

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[1] Everything that is said in this paragraph against a "purely chemical" theory of morphogenesis is, of course, also valid against any theory which tries to explain morphogenesis exclusively by the dismingling of a given mixture.

[2] The question is rendered still more complicated by the fact that in the case of the regeneration, say, of a leg it is not the original "morphogenetic compound" which is again required for disintegration, after it has become disintegrated once already, but only a specific part of it: just that part of it which is necessary for producing the leg! On the other hand, it would be impossible to understand, on the basis of physical chemistry, how the isolated branchial apparatus of *Clavellina* could be transformed, by chemical processes exclusively, into a system of which only a certain *part* consists of that substance of which the starting-point had been composed in its *completeness*.

Let us remember that a few original intimate differences exist in our harmonious systems: the main directions of the intimate protoplasmic structure including polarity and bilaterality. There are therefore three times two specified poles in each of these systems, at least in bilateral organisms, but no other differences are present in them. A few very simple cases of harmonious differentiation might indeed be understood on the theory of a disintegrating chemical compound in connection with these few differences. Imagine that the original compound of the quantity a is disintegrated to the amount of a_1; from a_1 are formed the two more simple compounds, b and c, both of them in definite quantities; then we have the three chemical individuals, $a - a_1$, b and c, as the constituents of our harmonious system; and it now might be assumed, without any serious difficulty, though with the introduction of some new hypotheses, that the two poles of one of the fundamental axes of symmetry attract b and c respectively, $a - a_1$ remaining unattracted between them. We thus should have the three elementary constituents of the system separated into three parts, and as they all three are of a definite quantity, their separation would mean that the system had been divided into three parts, $a - a_1$, b and c, also with regard to its proper form. It is clear, that by taking away any part of the original system, by means of operations, there would be taken away a certain amount of the original compound; say that $\frac{a}{n}$ is left; then, of course, the three constituents after the partial disintegration would be $\frac{a - a_1}{n}$, $\frac{b}{n}$ and $\frac{c}{n}$, and so it follows that the proportionality of localisation would really be preserved in any case.

But these considerations, evident as they seem to be in the most simple case, fail to satisfy in a really general sense: for two different reasons. First, they could never account for the fact that the differentiated organism by no means consists of so many different compounds as it shows single parts of its differentiation, but that, on the contrary, it only consists, as we know, of a certain rather limited number of true different morphogenetic elements, these elements occurring again and again—as, for instance, nervous or muscular elements—but typical each time in locality, quantity, and form. And in the second place, the very *form* of elementary organs, their form as such, does not at all go hand-in-hand with chemical differences ; this feature alone would absolutely overthrow any sort of a chemical morphogenetic theory to account for the problem of localisation. Take the typically arranged ring of the mesenchyme cells in our Echinus-gastrula, with its two spherical triangles, so typically localised ; look at any sort of skeleton, in Radiolaria, or in starfishes, or in vertebrates : here you have form, real form, but form consisting of only one material. Not only is the arrangement of the elements of form typical here, *e.g.* the arrangement of the single parts of the skeleton of the hand or foot, but also the special form of each element is typical, *e.g.* the form of each single bone of the foot ; and on a *purely* chemical theory of morphogenesis the sufficient reason for the production of typical form in such a sense would be wanting. For atoms or molecules by themselves can only account for form which is arranged, so to speak, according to spatial geometry—as in fact they do in crystallography ; but they can never account for form such as the skeleton of the nose, or hand, or foot. You will answer me, perhaps, that there may be non-chemical agents in the germ,[1] responsible for typical form-localisation, but by such reasoning you would be departing from a *purely* chemical theory. Our next paragraph will be devoted to this side of the question.

That is the principal reason for rejecting all sorts of purely chemical morphogenetic theories put forward to explain the problem of localisation ; it is more explicit, and therefore, I suppose, still more convincing than the more general consideration that the very fact of restitutions in itself must contradict the hypothesis that a disintegration of compounds might be the directive agency in morphogenesis. To sum up : Specificity of organic form does not go hand-in-hand with specificity of chemical composition, and therefore cannot depend on it ; and besides that, specific organic form is such that it can never be

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[1] Besides the specified poles determined by the polar-bilateral structure of the protoplasm.

explained by atomic or molecular arrangement in the chemical sense ; for, to state it in a short but expressive manner, the " form " of an atom or molecule can never be that of a lion or a monkey. To assume that, would be to go beyond the limits of chemistry in chemistry itself.

No Machine Possible Inside the Harmonious Systems

And now we turn to the last possibility which is left to us in our endeavour to " understand " the localisation of the differentiation in our harmonious-equipotential systems by the means of physics and chemistry. Outside causes have failed to account for it ; chemical or any other kind of disintegration of a compound or mixture has failed too. But could there not exist some sort of complicated interactions amongst the parts of the harmonious systems themselves ? Could there not exist some kind of a real *machine* in the system, which, if once set going by fertilisation or its equivalent, would result in the differentiations that are to take place ? Then we might say that the " prospective potency " of the system is in fact that machine ; we should know what the letter E of our equation stood for : viz. a resultant action of many complicated elemental interactions, and nothing more.

We shall understand the word " machine " in a most general sense. A machine is a typical configuration of physical and of chemical constituents, by the acting of which a typical effect is attained. We, in fact, lay much stress upon embracing in our definition of a machine the existence of chemical constituents also ; we therefore understand by the word " machine " a configuration of a much higher degree of complication than for instance a steam-engine is. Of course, a machine whose acting is to be typical with regard to the three dimensions in space, has to be typically constructed with regard to these three dimensions itself ; a machine that was an arrangement of elements in a strict plane could never have typical effects at right-angles to that plane. This is a point which must well be kept in mind in all hypothetical considerations about machines that claim to explain morphogenesis.

It must be granted that a machine, as we understand the word, might very well be the motive force of organogenesis in general, if only normal, that is to say, if only undisturbed development existed, and if a taking away of parts of our systems led to fragmental development.

But we know that, at least in our harmonious-equipotential systems, quite another process occurs after parts have been taken away: the development that occurs is not fragmental but whole, only on a smaller scale.

And we know, further, that this truly whole development sets in irrespective of the amount and direction of the separation. Let us first consider the second of these points. There may be a whole development out of each portion of the system—above certain limits—which is, say, of the volume V. Good! Then there ought to exist a machine, like that which exists in the whole undisturbed system, in this portion V also, only of smaller dimensions; but it also ought to exist in the portion V_1 which is equal to V in amount, and also in V_2, in V_3, V_4, and so on. Indeed, there do exist almost indefinitely many V_n, all of which can perform the whole morphogenesis, and all of which therefore *ought* to possess the complete machine. But these different portions V_n are only partly different from each other in spatial relation. Many parts of V_2 are also parts of V_1 and of V_3 and of V_4, and so on; that is to say, the different volumes V_n overlap each other successively and in such a manner that each following one exceeds the preceding one in the line by a very small amount only. But what then about our machines? Every volume which may perform morphogenesis completely must possess the machine in its totality. As now every element of one volume may play any possible elemental rôle in every other, it follows that each part of the whole harmonious system possesses any possible elemental part of the machine equally well, all parts of the system at the same time being constituents of different machines.

A very strange sort of machine indeed, which is the same in all its parts (Fig. 14)!

But we have forgotten, I see, that in our operation the absolute amount of substance taken away from the system was also left to our choice. From this feature it follows that not only all the different V_n, all of the same size, must possess the hypothetic machine in its completeness, but that all amounts of the values $V_n - n$, n being variable, must possess the totality of the machine also: and all values $V_n - n$, with their variable n, may again overlap each other.

Here we are led to real absurdities!

But what is the conclusion of our rather wild considerations?

It seems to me that there is only one conclusion possible. *If* we are going to explain what happens in our harmonious-equipotential systems by the aid of causality based upon the constellation of single physical or chemical factors and events, there must be some such thing as a machine. Now, just the assumption of the existence of a "machine" proves to be absolutely absurd in the light of the experimental facts. *Therefore there can be neither any sort of a machine nor any sort of causality based upon constellation underlying the differentiation of harmonious-equipotential systems.*

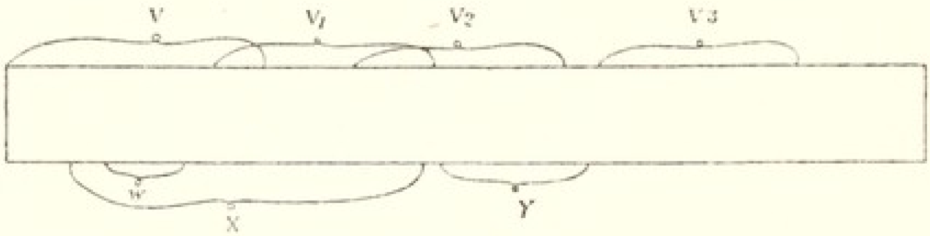

FIG. 14.—AN "HARMONIOUS-EQUIPOTENTIAL SYSTEM" OF WHATEVER KIND.

According to the "machine-theory" of life this system ought to possess a certain unknown very complicated machine *in its completeness*:
(*a*) in its total length,
and (*b*) in each of the equal volumes v, v_1, v_2, v_3, and so on,
and (*c*) in each of the unequal volumes w, x, y, and so on,
and (*d*) in every imaginable volume, no matter of what size.
Therefore the "machine-theory" of life is absurd.

For a machine, typical with regard to the three chief dimensions of space, cannot remain itself if you remove parts of it or if you rearrange[1] its parts at will.

Here we see that our long and careful study of morpho-

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[1] The pressure experiments and the dislocation experiments come into account here; for the sake of simplicity they have not been alluded to in the main line of our argument.

genesis has been worth while: it has afforded us a result of the very first importance.

The Autonomy of Morphogenesis proved

No kind of causality based upon the constellations of single physical and chemical acts can account for organic individual development; this development is not to be explained by any hypothesis about configuration of physical and chemical agents. Therefore there must be something else which is to be regarded as the sufficient reason of individual form-production. We now have got the answer to our question, what our constant E consists in. It is not the resulting action of a constellation. It is not only a short expression for a more complicated state of affairs, it expresses *a true element of nature.* Life, at least morphogenesis, is not a specialised arrangement of inorganic events; biology, therefore, is not applied physics and chemistry: life is something apart, and biology is an independent science.

All our results at present, indeed, are negative in their form; our evidence was throughout what is called *per exclusionem*, or indirect or apagogic. There were excluded from a certain number of possibilities all except one; a disjunctive proposition was stated in the form: E is either this, or that, or the other, and it was shown that it could not be any of all these except one, therefore it was proved to be that one. Indeed, I do not see how natural science could argue otherwise; no science dealing with inorganic phenomena does; something new and elemental must always be introduced whenever what is known of other elemental facts is proved to be unable to explain the facts in a new field of investigation.

We shall not hesitate to call by its proper name what we believe we have proved about morphogenetic phenomena. What we have proved to be true has always been called *vitalism*, and so it may be called in our days again. But if you think a new and less ambitious term to be better for it, let us style it the doctrine of the *autonomy of life*, as proved at least in the field of morphogenesis. I know very well that the word "autonomy" usually means the faculty of *giving* laws to oneself, and that in this sense it is applied with regard to a community of men, whilst in our phrase autonomy is to signify the *being subjected* to laws peculiar to the phenomena in question. But this meaning is etymologically defensible.

Vitalism then, or the autonomy of life, has been proved by us indirectly, and cannot be proved otherwise so long as we follow the lines of ordinary scientific reasoning.

"*Entelechy*"

But shall we not give a name to our vitalistic or autonomous factor E, concerned in morphogenesis? Indeed we will, and it was not without design that we chose the letter E to represent it provisionally. The great father of systematic philosophy, Aristotle, is also to be regarded as the founder of theoretical biology. Moreover, he is the first vitalist in history, for his theoretical biology is throughout vitalism; and a very conscious vitalism indeed, for it grew up in permanent opposition to the dogmatic mechanism maintained by the school of Democritus.

Let us then borrow our terminology from Aristotle, and let that factor in life phenomena which we have shown to be a factor of true autonomy be called *Entelechy*, though without identifying our doctrine with what Aristotle meant by the word *ἐντελέχεια*. We shall use this word only as a sign of our admiration for his great genius; his word is to be a mould which we have filled and shall fill with new contents. The etymology of the word *ἐντελέχεια* allows us such liberties, for indeed we have shown that there is at work a something in life phenomena "which bears the end in itself", *ὃ ἔχει ἐν ἑαυτῷ τὸ τέλος*.

Our concept of entelechy marks the end of our analysis of individual morphogenesis. Morphogenesis, we have learned, is "epigenesis" not only in the descriptive but also in the theoretical sense: manifoldness in space is produced where no manifoldness was, real "evolutio" is limited to rather insignificant topics. But was there nothing "manifold" previous to morphogenesis? Nothing certainly of an *extensive* character, but there was something else: there was entelechy, and thus we may provisionally call entelechy an "*intensive manifoldness*". That then is our result: not evolutio, but epigenesis—"epigenesis vitalistica".

The Logic of our First Proof of Vitalism

Let us devote the end of our present chapter to an account of the logical means by which it has been possible to develop what we hope will be regarded as a true *proof* of life autonomy.

Firstly, we have looked upon the phenomena of morphogenesis without any prepossessions; we may say that we have fully surrendered ourselves to them; we have not attacked them with any sort of dogmatism except the inherent dogmatism of all reasoning. But this dogmatism, if it may be called so, does not postulate that the results of the inorganic doctrines must hold for the organic world, but only that both the inorganic and the organic must be subject to certain most general principles.

By studying life as a given phenomenon, by fully devoting ourselves to our problem, we not only have analysed into its last elements what was given to us as our subject, but we also, more actively, have created new combinations out of those elements: and it was from the discussion of these positive constructions that our argument for vitalism was derived.

We have analysed morphogenesis into elementary processes, means, potency, formative stimulus, just as the physicist analyses mechanics into time, velocity, mass, and force; we have then rearranged our elements into "systems"—the equipotential systems, the harmonious-equipotential system in particular, just as the physicist composes his elements into the concepts of momentum or of kinetic energy or of work. And finally, we have discussed our compositions and have obtained our result, just as the physicist gets his ultimate results by discussing work and kinetic energy and momentum.

Of course the comparison is by no means intended to show that mechanics and biology are sciences of the same kind. In my opinion, they are not so at all; but nevertheless there do exist similarities of a logical kind between them.

And it is not the formal, logical character alone which allows us to compare biology with other natural sciences: there is still something more, there is one kind of assumption or postulate, or whatever you may choose to call it, without which all science whatever would be altogether *impossible*. I refer to the concept of *universality*. All concepts about nature which are gained by positive construction out of elements resulting from analysis, claim to be of *universal validity*; without that claim there could indeed be no science.

Of course this is no place for a discussion on methodology, and it therefore must suffice to make one remark with special regard to our purpose, which we should like to emphasise. Our concept of the harmonious-equipotential system—say rather, our concept of the prospective potency itself—presumes the understanding that indeed *all* blastomeres and *all* stems of *Tubularia*, including those upon which we have *not* carried out our experiments, will behave like those we have experimented with; and those concepts also presume that a certain germ of Echinus, *A*, the blastomeres of which were not separated, would have given two whole larvae, if separation had taken place, while another germ, *B*, which actually gave us two larvae after separation, would only have given one without it. Without this presumption the concept of "potency" is meaningless, and, indeed, every assumption of a "faculty" or a "possibility" would be meaningless in the whole area of science.

But this presumption can never be proved; it can only be postulated. It therefore is only with this postulate that our first proof of vitalism holds; but this restriction applies to *every* law of nature.

I cannot force you to agree with this postulate: but if you decline you are practically saying that there exists a sort of preestablished harmony between the scientific object and the scientist, the scientist always getting into his hands such objects only as have been "predestinated" from the very beginning to develop two larvae instead of one, and so on!

Of course, if that is so, no proof of natural laws is possible at all; but nature under such views would seem to be really daemonic.

And so, I hope, you will grant me the postulate of the universality of scientific concepts—the only " hypothesis " which we need for our argument.[1]

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[1] In the *Sitzungsberichte der Heidelberger Akademie der Wissenschaften* (1918, No. 3, and 1919, No. 18) I have published a very careful and thorough, quasi-mathematical, analysis of harmonious equipotentiality, which, so far, has not received much attention. Comp. also my little book *Der Begriff der organischen Form*, Berlin, 1919.

4. On Certain other Features of Morphogenesis advocating its Autonomy

Our next studies on the physiology of form will be devoted in the first place to some additional remarks about our harmonious-equipotential systems themselves, and about some other kinds of morphogenetic "systems" which show a certain sort of relationship with them. For it is of the greatest importance that we should become as familiar as possible with all those facts in the physiology of form upon the analysis of which are to be based almost all of the future theories that we shall have to develop in biology proper and philosophical.

ON CERTAIN COMBINED TYPES OF MORPHOGENETIC SYSTEMS

The type of the proper harmonious-equipotential system may go hand-in-hand with another type of "systems" which play a part in morphogenesis; a type which we have shortly mentioned already and which will be studied fully a few chapters later. We know that there are equipotential systems with complex potencies: that is to say, systems which may produce a whole organism equally well from any one of their elements; we know the cambium of Phanerogams to be such a system. Now it is easily understood that the germ of our Echinus, say in the stage of two or four or eight cleavage cells, is not only an harmonious-equipotential system, but a complex-equipotential system too. Not only may there arise a whole organism out of $\frac{2}{4}$ or $\frac{3}{4}$ or $\frac{3}{8}$, $\frac{4}{8}$, $\frac{5}{8}$, $\frac{6}{8}$, $\frac{7}{8}$ of its elements, in which cases the harmonious rôle of the single element with regard to its single performance in a totality is variable, but there may also arise four whole single larvae out of the four cells of the four-cell stage, or eight single whole larvae out of the eight-cell stage.[1] In these cases, of course, each of the four or eight elements has performed not a part of the totality, changing with its "position", but the totality itself. With respect to these possible performances the "systems" present in the four- or eight-cell stages of cleavage must be called complex-equipotential ones.

We propose to give the name of *mixed-equipotential systems* to all those equipotential systems which, at the same time, may be regarded as belonging to the harmonious or to the complex type. It is not only among cleavage-stages that they are to be found; you may also find them very clearly exhibited in our ascidian *Clavellina* for instance. We know already that the branchial apparatus of this form is typically harmonious-equipotential, but it is complex-equipotential too, for it also may regenerate what is wanting in the proper way, by a budding from the wound; and the same is true of many other cases, the flatworm *Planaria* for instance.

Another type of systems, which might be said to be of a higher degree, is exhibited in some very strange phenomena of regeneration. It was first shown by Godlewski that a whole tail may be regenerated from a wound inflicted on the body of a newt, even if this wound involves section of only a *portion* of the body-diameter. Section of the whole of the body-diameter of course would cause the formation of the whole tail also; but it was found that even an incomplete cross-section of the body is capable of performing the whole on a smaller scale. The series of possible cross-sections which are all capable of regeneration would have to be called a system of the complex type in this case; but, now we learn that every *single* cross-section is of the harmonious type, we must speak of *complex-harmonious systems*. What we have described is not the only instance of our new type of morphogenetic systems. Weiss has observed the regeneration of a complete foot from a partial section through the leg of the newt, and in the flatworm *Planaria* a partial cross-section is also capable of forming a whole structure, say a head, and all cases of

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[1] The eight larvae would be incomplete in some respect, but not with regard to symmetry. They would be "whole" ones, only showing certain defects in their organisation.

so-called " super-regeneration " after the infliction of a complicated wound probably belong here also.

You may say that our two additions to the theory of systems are merely formal, and indeed I am prepared to concede that we shall not learn anything altogether new from their discussion : their analysis would lead either to what was our " first proof " of the autonomy of life-phenomena or to what will be our " second " one. But the mere descriptions of the facts discovered here will interest you, I think, and will fill your minds with more vivid pictures of the various aspects of form-autonomy.

While dealing with our harmonious-equipotential systems as the starting-points of processes of restitution, *e.g.* in *Tubularia*, *Clavellina*, the flatworms, and other instances, we always have regarded cross-sections of the body as constituting the " elements " of equipotentiality. Now, cross-sections, of course, are by no means simple in themselves, but are made up of very different tissues, which are derivates of all three of the original germ layers—ectoderm, mesoderm, and endoderm. Owing to this composite character of the cross-sections, taken as elements of harmonious systems, a special phenomenon of morphogenesis is presented to us, which teaches somewhat more than the mere concept of harmonious-equipotentiality can express. If composite elements concerned in morphogenesis result in one whole organisation in spite of the development of the single tissues of these elements going on independently, then there must be a sort of correspondence or reciprocity of the harmonious development among these tissues themselves ; otherwise a proportionate form could not be the final result. We may conveniently speak of a *reciprocity of harmony* as existing between the single tissues or germ layers which constitute many harmonious-equipotential systems, and there can be little doubt that we have here an important feature with regard to general morphogenesis.

Some very interesting complicated forms of equipotentiality have, finally, been discovered in recent years, in particular by Harrison, Schaxel, Weiss, etc. All of them imply our ordinary harmonious-equipotentiality, but exceed its realm in various ways.

The "Anlage" of a left leg of Amphibian embryos or regenerating Amphibians, if transplanted to the right side of the body, may give a right leg, and *vice versa*. A bud of the foreleg, when implanted upon the locality of a hindleg, gives a hindleg, and, if it is implanted upon the wound of the tail, it even gives a tail. We may speak of *mirror equipotentiality* and *transgressing equipotentiality*.

Here we find an influence of the locality of implantation upon the fate of the transplanted cells, a real formative influence. And the possibility of such an influence shows that the community of the transplanted cells is not only equipotential in the ordinary sense, *i.e.* that not only every cell of that community can perform, harmoniously, every single act within a given totality of such acts, but that the *prospective area*, so to speak, is enlarged.

Do not these facts tend to suggest that, *in principle*, in animal embryos also, every cell can do everything—as we know, *e.g.*, from some lower forms of plants—and that restrictions of the prospective potency are nothing but a secondary phenomenon, due to a handicap, as it were ?

RESTITUTIONS OF THE SECOND ORDER

In the hydroid polyp *Tubularia*, already familiar to us as being a most typical representative of the harmonious-equipotential systems, a very interesting phenomenon has been discovered,[1] almost unparalleled at present but nevertheless of a general importance, a phenomenon that we may call a restitution of a restitution, or a restitution of the second order. You know that the first appearance of the new head of *Tubularia*, after an operation, consists in the formation of two rings of red lines, inside the stem, these rings being the primordia of the new tentacles. I removed the terminal ring by a second operation soon after it had arisen, disturbing in this way the process of restitution itself : and then the process

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[1] Driesch, *Arch. Entw. Mech.* 5, 1897.

of restitution itself became regulated. The organism indeed changed its course of morphogenesis, which was serving the purposes of a restitution, in order to attain its purpose in spite of the new disturbance which had occurred. For instance, it sometimes formed two rings out of the one that was left to it, or it behaved in a different way. As this difference of morphogenetic procedure is a problem by itself, to be discussed in the next paragraph, we shall postpone a fuller description of this case of a restitution of the second degree.

At present I do not see any way of proving independently the autonomy of life by a discussion of these phenomena; their analysis, I think, would again lead us to our problem of localisation and to nothing else; at least in such an exact form of reasoning as we demand.

ON THE "EQUIFINALITY" OF RESTITUTIONS[1]

I have told you already that *Tubularia* in the phenomena of the regulation of restitutions offers us a second problem of a great general importance, the problem of the *Equifinality of Restitutions*. There indeed may occur restitutions, starting from one and the same initial state and leading to one and the same end, but using very different means, following very different ways in the different individuals of one and the same species, taken from the same locality, or even colony.

Imagine that you have a piece of paper before you and wish to sketch a landscape. After drawing for some time you notice that you have miscalculated the scale with regard to the size of the paper, and that it will not be possible to bring upon the paper the whole of the landscape you want. What then can you do? You either may finish what you have begun to draw, and may afterwards carefully join a new piece of paper to the original one and use that for the rest of the drawing; or you may rub out all you have drawn and begin drawing to a new scale; or lastly, instead of continuing as you began, or erasing altogether, you may compromise as best you can by drawing here, and erasing there,

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[1] Driesch, *Arch. Entw. Mech.* 14, 1902.

and so you may complete the sketch by changing a little, according to your fancy, the proportions as they exist in nature.

This is precisely analogous to the behaviour of our *Tubularia. Tubularia* also may behave in three different ways, if, as I described to you, the terminal one of its two newly arisen rings of tentacle primordia is removed again. It may complete what is left, say the basal tentacle ring, then put forth from the horny skeleton (the "perisarc") the new head as far as it is ready, and finally complete this head by a regular process of budding regeneration. But it also may behave differently. It may "erase" by a process of retro-differentiation all that has been left of what had already been formed, and then may form *de novo* the totality of the primordia of a new head. Or, lastly, it may remove a part of the middle of the one ring of tentacle rudiments which was left, and may use this one ring for the formation of two, which, of course, will not be quite in the normal relations of place with regard to each other and to the whole, but will be regulated afterwards by processes of growth. Thus, indeed, there is a sort of equifinality of restitution: one starting-point, one end, but three different means and ways.

It would, of course, contradict the principle of univocality, as we shall see more fully later on, to assume that there actually are different ways of regulation whilst all the conditions and stimuli are the same. We are obliged to assume, on the contrary, that this is not the case, that there are certain differences in the constellation, say of the general conditions of age or of metabolism, which are responsible for any given individual choosing one process of restitution instead of another; but even then the phenomenon of equifinality remains very striking.

It has long been known that restitution in general does not always follow the same lines of morphogenesis as are taken by ontogeny, and it was this feature that once led Roux to point out that the adult forms of organisms seem to be more constant than their modes of origin. But, comparing ontogeny with restitution in general, we see that only the ends are the same, not the points of starting; the latter are normal or typical in ontogeny, non-typical in restitution. In the new discoveries of an equifinality of restitutions we have the *same* starting-point, which is decidedly non-typical, *i.e.* dependent on our arbitrary choice, leading by *different* ways always to the *same* end.

There may be many who will regard the fact of equifinality as a proof of vitalism. I should not like to argue in this easy way; I indeed prefer to include part of the phenomena of equifinality in our first proof of autonomy, and part in the second one, which is to follow.

Another important phenomenon of the equifinality of regulation was discovered by Morgan. A species of the flatworm *Planaria* was found to restore its totality out of small pieces either by regeneration proper, if the pieces were fed, or by a sort of rearrangement of material, on the basis of its harmonious-equipotentiality, if they were kept fasting. It is important to note that here we see one of the conditions determining the choice of the way to restoration, as we also do in the well-known equifinal restitutions of the root in plants, where the behaviour of the organism depends on the distance of the operation-wound from the tip.[1] In *Tubularia* the actual stage of restitution that has been already reached by the stem when the second operation takes place, may account for the specification of its future organogenesis, but this is not at all clearly ascertained at present.

Clavellina also shows equifinality in its restitution, as has already been shortly mentioned. The isolated branchial apparatus may restitute itself by retro-differentiation to an indifferent stage followed by renovation; or it may regenerate the intestine-sac in the proper way. Nothing is known here about the conditions, except perhaps that young individuals seem more apt to follow the first of these two ways, older ones the second; but there are exceptions to this rule.

The discussion of other instances of equifinality, though important in themselves, would not disclose anything funda-

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[1] The root may be restored by regeneration proper, or by the production of adventitious roots, or by one of the side-roots changing its geotropism from horizontal to positive, according to the smaller or greater distance of the wound from the tip.

mentally new, and so we may close the subject with the remark that nothing can show better than the fact of the equifinality of restitutions how absolutely inadequate all our scientific conceptions are when confronted with the actual phenomena of life itself. By analysis we have found differences of potencies, according as they are simple or complex ; by analysis we have found differences of "systems", differences of means, and indeed we were glad to be able to formulate these differences as strictly as possible : but now we see how, in defiance of our discriminations, one and the same species of animals behaves now like one sort of our " systems ", and now like the other ; how it uses now one sort of " potencies ", now another.

But even if it is granted that, in the presence of such phenomena of life, our endeavour seems to be like a child's play on the shores of the ocean, I do not see any other way for us to go, so long, at least, as our goal is human science—that is, a study of facts as demanded by our mental organisation.

Some Particular Features of Regeneration Proper

Regeneration may start from the same locality very many times (up to forty times have been observed). Can this be understood on mechanical lines ?

And the regenerated half of, say, Clavellina or the little annelid Amphiglaena may regenerate the original other half, if this is cut off after the first regeneration. And, then, the half that was regenerated from the regenerated half may again regenerate the other half, etc., etc., etc.

Is there still *the same* organism ? And *what* would be " the same " here ?

But we are still moving on the grounds of science proper.

C. ADAPTATION

1. INTRODUCTORY REMARKS ON REGULATIONS IN GENERAL

The Chief Forms of Regulation

WE have finished our long account of individual morphogenesis proper. If we look back upon the way we have traversed, and upon those topics in particular which have yielded us the most important general results, the material for the higher analysis which is to follow, it must strike us, I think, that all these results relate to regulations. In fact, it is " secondary " form-regulations, according to our terminology, that we have been studying under the names of equifinality, restitution of the second order, and so on, and our harmonious-equipotential systems have figured most largely in processes of secondary form-regulations also. But even where that has not been the case, as in the analysis of the potencies of the germ in development proper, form-regulations of the other type have been our subject, regulations of the primary or immanent kind, the connection of normal morphogenetic events being regulatory in itself. It was not, however, the phenomenon of organic regulation as such that afforded us the possibility of establishing our proof of the autonomy of morphogenesis : that possibility was afforded us by the analysis of the distribution of potencies ; but upon this distribution regulation is based, and thus we may be said to have studied some types of regulation more or less indirectly when analysing potencies.

It therefore seems to me that we shall have hopes of a successful issue to our inquiries, if we now, on passing to what is called the physiology of the vegetative functions, proceed to focus our attention on the concept of *regulation* as such.

But let us first try to give a proper definition of our concept. We shall understand by " regulation " any occurrence or group of occurrences on a living organism which takes place after any disturbance of its organisation or normal functional state, and which leads to a reappearance of this organisation or this state, or at least to a certain approach thereto. Organisation is disturbed by any actual removal of parts ; the functional state may be altered by any change among the parts of the organism on the one hand, by any change of the conditions of the medium on the other ; for physiological functioning is in permanent interaction with the medium. It is a consequence of what we have said that any removal of parts also changes the functional state of the organism, but nevertheless organisation is more than a mere sum of reactions in functional life. All regulations of disturbances of organisation may be called *restitutions*, while to regulations of functional disturbances we shall apply the name *adaptations*. It is with *adaptations* that we have to deal in the following.

SPECIFIC ADAPTEDNESS *NOT* " ADAPTATION "

It is important to keep well in mind our definition of adaptation, as by doing so we shall be able to exclude at once from our materials a large group of phenomena which occasionally have been called adaptations, but which, in fact, are not of the adaptation type and therefore cannot be said to afford those problems which possibly might have been expected. Typical structures or peculiarities in functional life cannot be called " regulations " simply because they serve to maintain the life of their bearer. The mere existence of protective colours, forms of mimicry, etc., therefore, shows mere *adaptedness*, not " adaptation ". And if the organism selects specific amounts of specific kinds of organic food or of salts out of the combinations of salts or organic food normally offered to it in the medium, there cannot be said to occur a " regulation " or " adaptation " with regard to the permeability of the cell, nor is it strictly a case of " regulation ", if so-called selective qualities are discovered in the processes of secretion, say of the epithelium of the kidney.

All these facts are typical and specific peculiarities in form or functioning which are duly to be expected, where a very typical and specific organisation of the most elaborated kind exists. Indeed, after studying such an organisation we must not be astonished that functions in organisms follow lines which certainly they would not have taken without it. Take the fact which is quoted very often, that the migration of compounds or of ions in the organisms can happen quite contrary to all the laws of osmosis, from the less concentrated to the more concentrated side of a so-called " membrane ". There *is* no simple " membrane " in the organism, but a complicated organisation of an almost unknown character takes its place, and nothing, indeed, is against the assumption that this organisation may include factors which actually drive ions or compounds to the side of higher concentration, which indeed drive them by " doing work ", if we like to speak in terms of energy ; and these factors included in organisation may very well be of a true physical or chemical nature.

In a more general form we now can sum up our discussion by saying : There never are adaptations where certain peculiarities of form are simply existing or where there are complications or even apparent deviations from the purely physico-chemical type of events which are, so to say, statical, *i.e.* fixed in quantity or quality, however peculiar or typically complicated they may be ; all such peculiarities, indeed, may properly be called " adapted ", that is to say, very well fitted to perform a specific part in the service of normal general functioning, and they are " adapted " to their part by virtue of a certain " adaptedness " of the organisation ; but they are not " adaptations " in the strict sense of the word.

PRIMARY AND SECONDARY ADAPTATIONS

We approach the subject of true adaptations, that is, of adapting processes, as soon as any kind of variation in form or functioning occurs which corresponds to a variation of any factor of the medium in the widest sense. But even here our work is by no means done by simply showing such a correspondence of outer and inner variations. We know very well already, from our former studies, that now we are faced by a further problem, that we are faced by the question whether we have to deal with simple primary kinds of adaptations or with the far more important secondary ones.

As the discrimination between primary and secondary regulations proves indeed to be of first-rate importance, you will allow me, I hope, to summarise our chief analytical statements regarding them in a most general form. We call primary regulatory any kind of morphogenetic or functional performance which, by its very intimate nature, always serves to keep the whole of organisation or of functions in its normal state. We call secondary regulations all features in the whole of morphogenesis or of functioning which serve to re-establish the normal state after disturbances along lines which are *outside the realm of so-called normality*. This analytical discrimination will help us very much to a proper understanding, though it will prove to be rather difficult in some cases clearly to separate primary adaptations from secondary ones on the one hand, and from mere adaptedness on the other.[1]

2. Morphological Adaptation

Morphological adaptation is a well-established fact, and I need only mention the striking differences between the land and water form of amphibious plants, or the differences between the same species of plants in the Alps and in the plains, or the very different aspect of the arms of an athlete and of an ascetic, to recall to your memory what is meant by this term.

Morphological adaptation is no part of individual morphogenesis proper, but occurs at the end of it ; at least, it almost never occurs previous to the full individual life of an organism, previous to its true functional life ; for it relates to the functions of the complete organism.

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[1] Comp. Ungerer, *Die Regulationen der Pflanzen*, 2nd ed., 1926, a very valuable book. Ungerer proposes to reserve the name of " adaptation " for the secondary ones exclusively, and to call all other cases " adaptedness " or " harmony ".

THE LIMITS OF THE CONCEPT OF MORPHOLOGICAL ADAPTATION

It is especially, though by no means exclusively, among plants that morphological adaptation assumes its most marked forms ; and this topic, indeed, may very easily be understood if we remember that plant-life is in the very closest permanent dependence on the medium, and that this medium is liable to many changes and variations of all kinds. In order to elucidate our problem, it therefore seems convenient to restrict our considerations for a while to the study of plants. There exist very many external formative stimuli in the morphogenesis of vegetation : would it then be possible to regard every effect of such an external formative stimulus as a real morphological adaptation ? No ; for that would not meet the point. The general *harmony* of form is indeed concerned if gravity forces roots to shoot forth below at a spot where they can enter the ground, or if light induces branches and leaves to originate at places where they can obtain it for assimilation ; but gravity and light themselves are mere formative stimuli—of the localising type—in these instances, for they relate only to the individual production of form, not to the functioning of already existing form. We therefore are warned not to confuse the effects of formative stimuli from without with real adaptive effects until we have fully analysed the particular case.

We have drawn a sharp line between causes and means of morphogenesis, applying the term " means " to those conditions of the morphogenetic process which relate neither to the specificity nor to the localisation of its constituents, though they are necessary for the accomplishment of the process in the most thorough manner. Would it be possible to connect our new concept of an adaptation with our well-established concept of a means of morphogenesis in such a way that we might speak of a morphological " adaptation " whenever any specific feature about morphogenesis proves to be immediately dependent for its success on some specific means, though it does not owe its localisation to that means as its " cause " ? It seems to me that such a view would also fall wide of the mark. It is well known, for instance, that the flowers of many plants never fully develop in the dark; light is necessary for their morphogenesis. Is, therefore, their growth in the presence of light to be called a morphological "adaptation" to light? Certainly not: they simply *cannot* originate without light, because they require it for some reason. It is precisely here that our conception of light as a "means" of morphogenesis is most fully justified. There are many such cases; and there are still others of an apparently different type, but proving the same. All pathological forms produced in plants by animal parasites or by parasitic fungi could hardly be called adaptations, but must be attributed to some abnormality of means or of stimuli. It may be that the organism reacts as well as possible in these cases, and that if it reacted otherwise it would die—we know absolutely nothing about this question. But even then there would only be some sort of regulation *in* the process of pathological morphogenesis, but *the process* itself could hardly be called adaptive.

So far we have only learned what is not to be regarded as morphological adaptation. No response to external formative stimuli is in itself an example of adaptation, nor are processes dependent for their existence on any kind of condition or means to be called, simply because they are dependent on them, adaptations to those agents. What then, after all, is a morphological adaptation?

Let us remember what the word adaptation is really to mean in our discussions: a state of functioning is adapted—a state of functioning must therefore have been disturbed; but as functioning itself, at least in plants, certainly stands in close relations to the medium, it follows that all adaptations are in the last resort connected with those factors of the medium which affect functioning. In being correctives to the disturbances of functioning they become correctives to the disturbing factors themselves.

But again, the question seems to arise whether these factors of the medium, when they provoke an adaptation by some change that is followed by functional disturbance, do so in the capacity of "causes" or of "means", and so if might seem that we have not gained very much so far by our analysis. The reproach, however, would not be quite justified, it seems to me: we indeed have gained a new sort of analytical concept, in the realm of causal concepts in general, by clearly stating the point that adaptations are related directly to functionality, and only indirectly, through functionality, to external changes. By the aid of this logical formulation we now are entitled to apply the term "cause", in our restricted sense of the word, to every change of the medium which is followed by any sort of adaptation in regard *to itself*. Our definition stated that a "cause" is any one of the sum of necessary factors from without that accounts either for the localisation *or* for *the specification* of the effect, and the definition holds very well in this case. Indeed, the specification of the effect is determined *by* the outside factor in every case of an adaptation *to* it, by the mere *fact* of its being a specific adaptation to this specific factor.

We must not forget that in this chapter we are not studying real individual morphogenesis as the realisation of what has been inherited, but that at present we regard morphogenesis proper as an accomplished fact. Morphogenesis proper has laid the general lines of organisation; and now adaptation during the functional life, so to speak, imposes a second kind of organisation upon the first. It is for that reason that the meaning of the word "cause" is now becoming a little different from what it was before.

In order to study a little more in detail what has been discovered about morphological adaptation in animals and plants, let us separate our materials into two groups, one of them embracing adaptations with regard to functional changes from without, the other adaptations to those functional changes which come from the very nature of functioning.

ADAPTATIONS TO FUNCTIONAL CHANGES FROM WITHOUT[1]

The differences between plants grown in very dry air, very moist air, and water, respectively, are most distinctly

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[1] Compare Herbst, *Biol. Centralbl.* 15, 1895; and Detto, *Die Theorie der direkten Anpassung*, Jena, 1904. A full account of the literature will be found in these papers.

seen in all the tissues that assist in what is called transpiration, that is, the exchange of water-vapour between the plant and the medium, but especially in the epidermis and the conductive fibres, both of which are much stronger in plants grown in the dry. Indeed, it seems from experiments that transpiration is the most essential factor to which " adaptation " occurs in amphibious plants, though the changes of the mechanical conditions according to the medium also seem to have some sort of structural effect. If plants stand very deeply in water, the conditions of illumination, so important for assimilation in plants, may have been altered, and therefore much of the structural change can be attributed also to them. It is unimportant in our general question what is due to one of these factors and what to the other. That there is a real sort of adaptation cannot be doubtful ; and the same is true, as experimental observations of the last few years have shown, with regard to the structural differences between so-called sun-leaves and shade-leaves of plants grown in the air : it has been actually shown here that the functional life of the former goes on better in the sun, of the latter better in the shade.

It is very important to emphasise this point, as the adaptive character of all sorts of structural differences in plants dependent on light and on moisture has lately been denied, on the supposition that there is only a stopping of organogenesis in the case of the more simple, a continuance in the case of the more complicated modification, but nothing else. Indeed, all morphological adaptation has been conceived as only consisting in differences dependent upon the absence or the presence of necessary means or causes of development, and as offering no problem of its own. We have gained the right position from which to oppose this argument, it seems to me, in our formula that all adaptations do relate *not* directly *to* the agents of the medium, but to changes of functional states induced *by* those agents ; that adaptations only *are* " adaptations " by being correctives to the functional state.

There simply *is* an " adaptation " of structure in *such* a sense in all the cases we have mentioned. We can say neither more nor less. Granted that one of the outside factors which comes into account is merely a necessary " means " : then why is the histological consequence of the presence of the means an actual adaptation to it as far as its relation to functioning is concerned; why is the consequence of its absence also an adaptation to this absence in its relation to functioning ? Why, to complete the series, is the degree of the consequence of its presence an adaptation to the degree of its presence ?

All these relationships, which are so many facts, have been absolutely overlooked by those who have been pleased to deny morphological adaptation to functional changes from without.

To do full justice to them, we may speak of " primary " regulative adaptations in all the cases mentioned above—applying the word "primary", just as was done with regard to restitutions, to the fact that there is some sort of regulation *in* the normal connection of processes. We reserve the title of " secondary adaptations " for cases such as those described, for instance, by Vöchting,[1] where not merely one and the same tissue originates adaptively with regard to the degree of its normal functioning, but where a profound disturbance of all functioning connections, due to the removal of portions of the organisation, is followed by histological changes at absolutely abnormal localities ; that is, where a real change of the *kind* of functioning is the consequence of the adaptation. It, of course, will be found very difficult to discriminate such phenomena from real restitutions, though logically there exists a very sharp line between them.

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[1] Vöchting (*Jahrb. wiss. Bot.* 34, 1899) forced the bulbs of plants to become parts of the stem, and parts of the stem to form bulbs ; in both cases the most characteristic changes in histology could be observed, being in part adaptations, but in part restitutions of the proper type. (See also my *Organische Regulationen*, 1901, p. 84.) A true and simple instance of a " secondary adaptation " seems to be furnished in a case described by Boirivant. In *Robinia* all the leaflets of a leaf-stalk were cut off : the leaf-stalk itself then changed its structure in order to assist assimilation, and also formed real stomata.

TRUE FUNCTIONAL ADAPTATION [1]

But all other cases of morphological adaptation among animals, and several in the vegetable kingdom too, belong to our second group of these phenomena, which in our analytical discussion we have called adaptations to functional changes that result from the very nature of functioning, and which we shall now call by their ordinary name, " functional adaptations ".

It was Roux who first saw the importance of this kind of organic regulation and thought it well to give it a distinguishing name. *By functioning the organisation of organic tissues becomes better adapted for functioning.* These words describe better than any others what happens. It is well known that the muscles get stronger and stronger the more they are used, and that the same holds for glands, for connective tissue, etc. But in these cases only quantitative changes come into account. We meet with functional adaptations of a much more complicated and important kind, when for instance, as shown by Babak, the intestine of tadpoles changes enormously in length and thickness according as they receive animal or vegetable food, being nearly twice as long in the second case. Besides this, the so-called mechanical adaptations are of the greatest interest.

It has long been known, especially from the discoveries of Schwendener, Julius Wolff, and Roux, that all tissues whose function it is to resist mechanical pressure or mechanical tension possess a minute histological structure specially suitable to their requirements. This is most markedly exhibited in the stem of plants, in the tail of the dolphin, in the arrangements of the lime lamellae in all bones of vertebrates. All these structures, indeed, are such as an engineer would have made them who knew the sort of mechanical conditions they would be called upon to encounter. Of course all these sorts of mechanically adapted structures are far from being " mechanically explained ", as the verbal expression might perhaps be taken to indicate, and as

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[1] Roux, *Gesammelte Abhandlungen*, vol. i., 1895; in particular, *Der Kampf der Teile im Organismus*, Leipzig, 1881.

indeed has sometimes been the opinion of uncritical authors. The structures exist *for* mechanics, not *by* it. And, on the other hand, all these structures, which we have called mechanically "adapted" ones, are far from being mechanical "adaptations", in our meaning of the word, simply because they are "adapted". Many of them indeed exist previous to any functioning; they are for the most part truly inherited, if for once we may make use of that ambiguous word.

But, the merely descriptive facts of mechanical adaptedness having been ascertained, there have now been discovered real processes of mechanical adaptations also. They occur among the statical tissues of plants, though not in that very high degree which sometimes has been assumed to exist; they also occur in a very high perfection in the connective tissue, in the muscles and in the bone tissue of vertebrates. Here indeed it has proved possible to change the specific structure of the tissue by changing the mechanical conditions which were to be withstood, and it is in cases of healing of broken bones that these phenomena have acquired a very great importance, both theoretically and practically: the new joints also, which may arise by force of circumstances, correspond mechanically to their newly created mechanical function.

We now, of course, have to ask ourselves if any more intimate analysis of these facts is possible, and indeed we easily discover that here also, as in the first of our groups of morphological adaptations, there are always single definite agents of the medium, which might be called "causes" or "means" of the adaptive effects, the word "medium" being taken as embracing everything that is external to the reacting cells. But of course also here the demonstration of single formative agents does not detract in the least from the adaptive character of the reaction itself. So we may say, perhaps, that localised pressure is the formative stimulus for the secretion of skeleton substance at a particular point of the bone tissue, or of the fibres of the connective tissue; the merely quantitative adaptations of muscles might even allow of a still more simple explanation. But adaptations remain adaptations in spite of that; even if they only deserve the name of "primary" regulations.

THEORETICAL CONCLUSIONS

We have stated in the analytical introduction to this chapter and elsewhere, that functional changes, which lead to morphological adaptations of both of our groups, may arise not only from changes of factors in the medium, but also from a removal of parts. As such removal is generally followed by restitution also, it is clear that restitutions and adaptations very often may go hand-in-hand, as is most strikingly shown in a fine series of experiments carried out by Vöchting, which we have already alluded to. Here again I should like to lay the greatest stress upon the fact that, in spite of such actual connections, restitutions and adaptations may always be separated from one another theoretically, and that the former are never to be resolved into sums of the latter. Such a view has been advocated by some recent authors, especially by Klebs, Holmes, and Child :[1] it is refuted, I think, by the simple fact that the first phase of every process of restitution, be it regeneration proper or be it a sort of harmonious differentiation, goes on without functioning at all, and only *for* future functioning.[2]

And there has been advocated still another view in order to amplify the sphere of adaptation : all individual morphogenesis, not only restitution, is adaptation, it has been said. In its strictest form such an opinion, of course, would simply be nonsense : even specific adaptive structures, such as those of bones, we have seen to originate in ontogeny previous to all specific functions, though for the help of them, to say nothing of the processes of the mere outlining of organisation during

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[1] What has been really *proved* to exist by the very careful studies carried out by Child, is only certain cases of functional adaptation to mechanical conditions of the strictest kind, and relating to the general mobility only, but nothing more ; such adaptations can be said to accompany restitution. See, for instance, *Journ. Exp. Zool.* 3, 1906, where Child has given a summary of his theory, and also his book *Physiol. Foundations of Behaviour*.

[2] Even in Vöchting's experiments (see page 126, note), in which adaptations are mixed with true restitutions in the closest possible manner, a few phenomena of the latter type could most clearly be separated. The stimulus which called them forth must have been one of the hypothetic sort alluded to in a former chapter (see page 81 f.). The best instances of true restitutions were offered in those cases, where, after the removal of all the bulbs, typical starch-storing cells were formed without the presence of any starch.

cleavage and gastrulation. But they are "inherited" adaptations, it has been answered to such objections. To this remark we shall reply in another chapter. It is enough to state at present that there *is* a certain kind of, so to speak, architectonic morphogenesis, both typical and restitutive, previous to specific functioning altogether.

If now we try to resume the most general results from the whole field of morphological adaptations, with the special purpose of obtaining new material for our further philosophical analysis, we have reluctantly to confess that, at present at least, it does not seem possible to gather any new real proof of life-autonomy, of "vitalism", from these facts, though of course also no proof against it.

We have stated that there is, in every case of both our types of adaptive events, a correspondence between the degree of the factor to which adaptation occurs and the degree of the adaptive effect. We here may speak of an *answering* between cause and effect with regard to adaptation, and so perhaps it may seem as if the concept of an "answering reaction" ("Antwortsreaktion"), which has been introduced into science by Goltz,[1] may come into account: but in our present cases "answering" only exists between a simple cause and a simple effect, and relates almost only to quantity and locality. There is therefore lacking the most important feature, which, as will be seen, would have made the new concept of value.

We only, I believe, can state the fact that there *are* relations between morphogenetic causes and effects which *are* adaptations, that functional disturbances or changes are followed by single histogenetic reactions from the organism, which are compensations of its disturbed or changed functional state. We are speaking of facts here, of very strange ones indeed. But I feel unable to formulate a real proof against all sorts of mechanism out of these facts: there *might* be a machine, to which all is due in a pre-established way. Of course we should hardly regard such a machine as very probable, after we have seen that it *cannot* exist in other fields of morphogenesis. But

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[1] *Beiträge zur Lehre von den Functionen der Nervencentren des Frosches*, Berlin, 1869.

we are searching for a new and independent proof ; and that is indeed not to be found here.

At present it must be taken as one of the fundamental *facts* of the organogenetic harmony, that the cells of functioning tissues do possess the faculty of reacting to factors which have changed the state of functioning in a way which normalises this state histologically. There is, however, one particular feature in all morphological adaptation, which, if further studied experimentally, might perhaps lead one day to a new and independent proof of vitalism.

It is a fact that all morphological adaptations start from cells which are not yet functioning but are in the so-called *embryonic* or indifferent condition.

This is a very important point in almost all morphological adaptation, whether corresponding to functional changes from without or resulting from the very nature of functioning. In fact, such cells as have already finished their histogenesis are, as a rule, only capable of changing their size adaptively, but are not able to divide into daughter-cells or to change their histological qualities fundamentally ; in technical terms, they can only assist " hypertrophy " but not " hyperplasia ". Any adaptive change of a tissue, therefore, that implies an increase in the number of cellular elements or a real process of histogenesis, has to start from " indifferent " cells, that is to say, cells that are *not yet* functioning in the form that is typical of the tissue in question ; and, strange to say, these " embryonic " cells—*i.e.* the " cambium " in higher plants and many kinds of cells in animals—*can* do what the functional state requires. We may speak of an *adaptive equipotentiality* of these cells. And this term is correct, even if the potencies of the indifferent cells relate only to histological types which are " normal " for the species in question.

3. Physiological Adaptation[1]

It is but a step from morphological adaptations to adaptations in physiology proper. The only difference between regulations of the first type and those which occur in mere functioning is, that the resulting products of the regulation are of definite shape and therefore distinctly visible in the first case, while they are not distinctly visible as formed materials but are merely marked by changes in chemical or physical composition in the latter.

Metabolism, it must never be forgotten, is the general scheme within which all the processes of life in a given living organism go on ; but metabolism means nothing else, at least if we use the word in its descriptive and unpretentious meaning, than change in the physical or chemical characteristics of the single constituents of that organism. In saying this, we affirm nothing about the physical or chemical nature of the actual processes leading to those physical or chemical characteristics, and by no means are these " processes " *a priori* regarded as being physical or chemical *themselves* : indeed, we have learned that in one large field, in the differentiation of our harmonious systems, they certainly are not. Now, if the metabolism does not end in any change of visible form, then true physiological processes, or more particularly physio-

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[1] General literature : Fröhlich, *Das natürliche Zweckmässigkeitsprincip in seiner Bedeutung für Krankheit und Heilung*, 1894. Driesch, *Die organischen Regulationen*, 1901. A. Tschermak, " Das Anpassungsproblem in der Physiologie der Gegenwart," in a collection of papers in honour of J. P. Pawlow, St. Petersburg, 1904. Bieganski, " Über die Zweckmässigkeit in den pathologischen Erscheinungen," *Annal. d. Naturphil.* 5, 1906. Among the general text-books of physiology those by Pfeffer (*Pflanzenphysiologie*, 1897–1904) and von Bunge (*Lehrbuch d. Phys. d. Menschen*, 1901) are the fullest on the subject of " regulations ". See also different papers on general pathology by Ribbert.

logical regulations, are going on before us. But we are dealing with morphogenetic events or regulations, if the result of metabolism is marked by any change in the constituents of form. This, however, may depend on rather secondary differences as to the nature of regulation itself, and any kind of metabolism may really be of the regulatory type, whether we actually see its result as a constituent of form, *e.g.* owing to the production of some insoluble compound, or whether we do not.

ON CERTAIN PRE-REQUISITES OF PHYSIOLOGICAL ADAPTATIONS IN GENERAL

We now must think of the general and important question, what types of adaptations may be expected in the field of physiology, and whether there may be certain classes of regulatory events which possibly might be expected to occur in the organism on *a priori* grounds, but which, nevertheless, are to be regarded as impossible after a more intimate analysis of its nature, even at the very beginning. Or, in other words, to what kinds of changes of the medium will an organism be found able or unable to adapt itself ?

We know that the *state of functioning* must be altered in order to call forth any sort of adaptation at all. Now, there can be no doubt that *a priori* it would seem to be very useful for the organism, if it never would let enter into its blood, lymph, etc., be it through the skin or through the intestine, any chemical compound that would prove to be a poison afterwards. In fact, a man, judging on the principle of the general usefulness of all the phenomena of the living, might suppose that there would exist a sort of adaptation against all poisons to the extent that they would never be allowed to enter the real interior of the body. We know that such reasoning would be incorrect. But we also can understand, I suppose, that an *a priori* analysis of a more careful kind would have reasoned differently. How could the functional state of the organism be changed, and how, therefore, could adaptation be called forth by any factor of the medium which had not yet entered the organism, but was only about to enter it ?

Not at all, therefore, is such a regulation to be expected as we have sketched; if there is to be any adaptation to poisons, it only can occur after the poison has really acted in some way, and in this case we shall indeed find regulations.

Very often, indeed, the question has been raised by the defenders of a mechanistic theory of life: Why then did the organisms not reject all poisons from the very beginning? We may now simply reply—How *could* they do so? How could they "know" what is a poison and what is not, unless they had experienced it?—if we are allowed for a moment to use very anthropomorphistic language.

We repeat, therefore, that the functional conditions of the organism must have been actually changed in order that an adaptation may occur. Nothing is more essential to a clear understanding of our problems than to keep fully in mind the exact sense of this definition.

Two Meanings of the Word "Function"

But the word "function" seems to require a still further explanation.

This word is generally used with two different meanings, which we shall call, respectively, the *proper function* and the *harmonious function*. The proper function of any organic cell is that which it immediately performs; the pancreas cells, *e.g.*, secrete trypsin. But the harmonious function is the effect of the performance of that cell upon the whole organism. The harmonious function of the pancreas cells, then, is to transform the food into substances which may be absorbed by the intestine and assimilated by the various tissues. The possibility of harmonious functioning rests upon the general "functional harmony" and the "harmony of constellation" of the organism (page 78).

Now we understand, so it seems to me, that that which starts adaptation is always a change in the totality of harmonious functioning, whilst the adaptation itself consists in a change of proper functioning. And this change occurs in such a way as to re-establish, more or less, the totality of harmonious functioning.

Some Particular Cases of Physiological Adaptation

If we now turn to particulars, we unfortunately see at once that, in wide areas of physiology, very many " adaptednesses " may be found, but very few real adaptations.

The so-called restoration of irritability in general and the regulation of temperature in warm-blooded animals may even be understood along physico-chemical lines.

As to the regulation of the permeability of cellular surfaces, serving the equilibrium of osmotic pressure, or the chemical composition of juices, or both, nothing has at present been established with absolute certainty. Almost every author has his own opinion about this subject, and I therefore omit all details.[1]

An " osmostat " seems to play a rôle here, just as in heat regulation a " thermostat ". This would signify mere adaptedness, the only true adaptation being realised, perhaps, in the fact that the osmostat adjusts itself by its own forces to a new equilibrium under abnormal conditions. But even this feature may be nothing but a *primary* regulation.

So-called adaptations of colour are mostly due to nervous influence, in the way of " seeing ", and, so far, do not belong to this chapter. If they are not, they probably rest upon a rather simple adaptedness.

The field of *metabolism* seems at the first glance to be really covered by adaptive regulations, but almost everything transpires to be pre-established, on the foundation of the given harmony of constellation and of functions in the adult organism.

In the state of fasting, however, there probably occurs a little more. In this state, oxydation, the necessary prerequisite of life, attacks the different tissues of the organism subjected to fasting in such an order that, after the combustion of the reserves, the most unimportant tissues with regard to life in general are destroyed first, the most important ones last. Thus in vertebrates, the nerve cells and the heart are preserved as long as possible ; in infusoria it is the nucleus ; in flatworms

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[1] For a fuller discussion compare the second German edition of this book (1921) and the paper of Fitting in *Jahrb. wiss. Bot.* 56.

it is the nerve cells and the sexual cells which longest resist destruction, whilst almost all the rest of the organisation of these animals may disappear. I should not say that we can do very much with these facts at present in our theoretical discussion, but they are certainly witness of certain adaptive powers.

Some other adaptations have been discovered in fungi. Fungi are known to be satisfied with one single organic compound instead of the group of three—fat, carbohydrate, and albumen—necessary for animals. Now, Pfeffer showed that the most different and indeed very abnormal compounds were able to bring his subjects to a perfect growth and morphogenesis; and, moreover, he found that, if several kinds of such food were offered together, they were consumed quite indifferently as to their chemical constitution, but only with regard to their nutritive value: that sort of food which had produced a better growth than another when both were offered separately was found to save the latter from consumption whenever both were offered together.

Here we are faced by one of the most typical cases of regulations in metabolic physiology: the organism is able to decompose compounds of the most different constitution, which have never been offered to it before; but, nevertheless, it must remain an open question whether real "secondary" regulation has occurred, as nothing is known in detail about the single steps of metabolism in these fungi. There *might* be some ferments equally able to destroy different classes of compounds, and that the most nutritive compound is used up first *may* be a question of physico-chemical equilibrium.

That is almost all that is actually known of adaptation with regard to the use of an abnormal food supply. Though important, it cannot be said to be very much.

IMMUNITY THE ONLY TYPE OF A SECONDARY PHYSIOLOGICAL ADAPTATION

There is only one class of physiological processes in which the type of the secondary regulation is realised beyond any doubt. The discoveries of the last decades have proved that the so-called *immunity* against diseases is but one case out of numerous biological phenomena in which there is an adaptive correspondence between abnormal chemical stimuli and active chemical reactions on the part of the organism and in its interior, exceeding by far everything that was formerly supposed to be possible in physiological regulation.

The adaptive faculty of the organism against inorganic poisonous substances is but small comparatively, and is almost always due not to a real process of active regulation but to the action of substances pre-existing in the organism —that is, to a sort of adaptiveness but not adaptation.

It is in the fight against animal and vegetable poisons, such as those produced by bacteria, by some plants and by poisonous snakes, that the true adaptation of the organism reaches its most astonishing degree. The production of so-called " anti-bodies " in the body fluids is not the only means applied against noxious chemical substances of this kind: the existence of so-called histogenetic immunity is beyond all doubt, and Metschnikoff[1] certainly was also right in stating that the cells of the organism themselves repel the attack of living bacteria. Cells of the connective tissue and the white blood cells, being attracted by them as well as by many other foreign bodies, take them in and kill them. This process, called "phagocytosis", is of special frequency among lower animals, but it also contributes to what is called inflammation in higher ones.[2] And there are still other kinds of defence against parasites, as for instance the horny or calcareous membranes employed to isolate trichinae and some kinds of bacteria. But all this is of almost secondary importance as compared with the adaptive faculties of the warm-blooded vertebrates, which produce anti-poisonous substances in their lymph and blood.

Discoveries of recent years have shown not only that against the " toxins " of bacteria, snakes, and some plants the organism

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[1] *Leçons sur la pathologie comparée de l'inflammation*, Paris, 1892.

[2] The other steps or phases in the process of inflammation have also been regarded as adaptive: the increased quantity of body fluid, for instance, is said to serve to dilute poisonous substances.

is able actively to produce so-called " anti-toxins "—that is, soluble substances which react with the toxins and destroy their poisonous character—whenever required, but that against *any* foreign body of the albumen group a *specific* reaction may occur, resulting in the coagulation of that body. But the destruction of the noxious substance or foreign albumen actually present is not all that is accomplished by the organism. " Acquired immunity " proper, that is, security against the noxious material for a more or less extensive period of the *future*, depends on something more. Not only is there produced as much of the so-called " anti-body " as is necessary to combine with the noxious, or at least foreign, substances which are present, but *more* is produced than is necessary in the actual case. On this over-production depends all active immunity, whether natural or, as in some kinds of vaccination, artificial; and so-called " passive " immunity, obtained by the transfusion of the serum of an actively immune organism into another, also depends upon this feature.

This phenomenon in particular—the production of *more* of the antitoxin or the " precipitin " than is actually necessary —seems to render almost impossible any merely chemical theory of these facts. The *reaction* between toxin and antitoxin, albumen and precipitin, is indeed chemical—it may, in fact, be carried out in a test-tube; but whether the *production* of the anti-body itself is also chemical or not could hardly be ascertained without a careful and unbiassed analysis.

And, indeed, here if anywhere we have the biological phenomenon of adaptation in its clearest form. There are very abnormal changes of the functional state of the organism, and the organism is able to compensate these changes in their minutest detail in almost any case. The problem of the *specification* of the reactions leading to immunity seems to me, as far as I can judge as an outsider, to stand at present in the very forefront of the science. There cannot be the slightest doubt that especially against all sorts of foreign albumens the reaction is as strictly specific as possible; but there are some typical cases of specificity in the production of antitoxins also. It is, of course, the *fact* of specific correspondence between stimulus and reaction that gives to immunity its central position among all adaptations, no matter whether the old hypothesis of the production of specific anti-bodies proves tenable, or whether, as has been urged more recently by some authors, the anti-body is always the same but reacts differently according to the medium. In the latter case it would be the medium that is regulated in some way by the organism in order to attain a specific adaptedness.

NO GENERAL POSITIVE RESULT FROM THIS CHAPTER

But now let us look back to the sum of all the physiological reactions studied, and let us see if we have gained a new proof of the autonomy of life from our long chapter.

We freely admit we have not gained any really new *proof*, but we may claim, I think, to have gained some new indicia for the statement that the organism is not of the type of a machine, in which every single regulation is to be regarded as properly prepared and outlined.

It is precisely in the field of immunity that such a machine-like preparation of the adaptive effects seems almost impossible to be imagined. How indeed could there be a machine, the chemical constituents of which were such as to correspond adaptively to almost every requirement—to say nothing of the fact that the production of *more* of the protecting substance than is actually necessary could hardly be said to be " chemical " ?

In fact, we are well entitled to say that we have reached here the very heart of life and of biology. If nevertheless we do not call the sum of our facts a real proof of vitalism, it is only because we feel unable to formulate the analysis of what happens in such a manner as to make a machine as the basis of all reactions absolutely unimaginable and unthinkable. There *might* be a true machine in the organism producing immunity with all its adaptations. We cannot disprove such a doctrine by demonstrating that it would lead to a real *absurdity*, as we did in our analysis of differentiation of form ; there is only a very high degree of improbability in our present case. But an indirect *proof* must reduce to *absurdity* all the possibilities except one, in order to be a proof.

Mechanistic explanations in all branches of functional physiology proper, so much in vogue in the past, can indeed be said to have failed all along the line : the only advantage they have brought to science is the clearer statement of problems to which we are now accustomed. But we are not fully entitled to say that there never will be any mechanistic explanation of physiological functions in the future. It may seem as improbable as anything can be ; but we wish to know not what is improbable but what is not possible.

Now, of course, you might answer me that after we have indeed shown that the *production of form*, as occurring on the basis of harmonious-equipotential systems, is a fact that proves vitalism, the acts taking place *on the basis* of that form after its production would have been proved to be vitalistic also, or at least to be in some connection with vitalistic phenomena. Certainly they would, and I myself, personally, should not hesitate to say so. But that is not the question. We have to ask : Is any new proof, *independent of every other*, to be obtained from the facts of physiological adaptation in themselves ? And there is really none. Mere regulatory correspondence between stimuli and reactions, even if it be of the adaptive type and occur in almost indefinite forms, never really disproves a machine as its basis so long as the stimuli and reactions are *simple* and uniform. Later on, however, we shall see that vitalism may be proved by such a correspondence if the two corresponding factors are *not* simple and not uniform.

We must clearly see at this point what it really was in our analysis of differentiation that allowed us to extract a real proof of vitalism from it. Not the mere fact of regulability, but certain specific relations of space, of locality, lay at the very foundation of our proof. These relations, indeed, and only these relations, made it possible to reduce *ad absurdum* any possible existence of a machine as the actual basis of what we had studied. In our next chapter again it will be space relations, though analysed in a different manner, that will enable us to add a second real proof of vitalism to our first one.

With this chapter we conclude the study of organic regulation in all its forms, as far as morphogenesis and metabolism are in question.

But our analysis of these regulations would be incomplete, and indeed would be open to objections, if we did not devote at least a few words to two merely negative topics, which will be taken more fully into consideration later on.

A FEW REMARKS ON THE LIMITS OF REGULABILITY

There has never been found any sort of " experience " in regulations about morphogenesis or in adaptations of the proper physiological type. Nothing goes on " better " the second time than it did the first time ;[1] everything is either complete, whenever it occurs, or it does not occur at all.

That is the first of our important negative statements about regulations ; the second relates to the phrase just used, " or it does not occur at all ". There are indeed limits of regulability ; adaptations are not possible to every sort of change of the physiological state : sickness and death could not exist if they were ; nor is restitution possible in all cases where it might be useful. It is a well-known fact that man is only able to heal wounds but is altogether destitute of the faculty of regeneration proper. But even lower animals may be without this faculty, as are the ctenophores and the nematodes for instance, and there is no sort of correspondence between the faculty of restitution and the place in the animal kingdom.

But no amount of negative instances can disprove an existing positive. Our analysis based upon the existence of regulations, therefore, is as little disparaged by cases where no regulability exists as optical studies are by the fact that they cannot be undertaken in absolute darkness.

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[1] The few cases of an " improvement " of morphogenetic acts in hydroids described by myself are too isolated at present to be more than mere problems (*Arch. Entw. Mech.* 5, 1897). The same is true, it seems to me, with regard to certain discoveries made by R. Pearl on *Ceratophyllum* (*Carnegie Inst. Wash. Publ.* No. 58, 1907) ; and by Zeleny on a medusa (*Jour. Exp. Zool.* 5, 1907).

D. INHERITANCE: SECOND PROOF OF THE AUTONOMY OF LIFE

ALL organisms are endowed with the faculty of re-creating their own initial form of existence.

In words similar to these Alexander Goette, it seems to me, has given the shortest and the best expression of the fact of inheritance. Indeed, if the initial form in all its essentials is re-created, it follows from the principle of univocality, that, *ceteris paribus*, it will behave again as it did when last it existed.

By the fact of inheritance life becomes a rhythmic phenomenon, that is to say, a phenomenon, or better, a chain of phenomena, whose single links reappear at constant intervals, if the outer conditions are not changed.

THE MATERIAL CONTINUITY IN INHERITANCE

It was first stated by Gustav Jaeger, and afterwards worked out into a regular theory by Weismann, that there is a *continuity* of material underlying inheritance. Taken in its literal meaning this statement is obviously self-evident, though none the less important on that account. For as all life is manifested on bodies, that is, on matter, and as the development of all offspring starts from parts of the parent bodies, that is, from the matter or material of the parents, it follows that in some sense there is a sort of continuity of material as long as there is life—at least in the forms we know of. The theory of the continuity of "germ-plasm" therefore would be true, even if germ-cells were produced by any and every part of the organism. That, as we know, is not actually the case: germ-cells, at least in the higher animals and in plants, are produced at certain specific localities of the organism only, and it is with regard to this fact that the so-called theory of the "continuity of germ-plasm" acquires its narrower and proper sense. There are distinct and specific lines of cell-lineage in ontogenesis, so the theory states, along which the continuity of germ-protoplasm is kept up, which, in other words, lead from one egg to the other, whilst almost all other lines of cell-lineage end in "somatic" cells, which are doomed to death. What has been stated here is a fact in many cases of descriptive embryology, though it can hardly be said to be more than that. But I regard it as very important that the fact of the continuity of some material as one of the foundations of inheritance has clearly been stated.

The important problem now presents itself: What is the material, the matter, which is handed down from generation to generation as the basis of inheritance? Weismann, as we know, regarded it as a very complicated structure, part of which by its disintegration became the foundation of individual embryology. We have disproved, on the authority of many facts, the latter part of this assumption; but of course the first part of it may turn out to be true in spite of this. We have no means at present to enable us to say *a priori* anything positive or negative about the important question of the nature of that matter, the continuity of which in inheritance is in some sense a self-evident fact, and we therefore shall postpone the answer until a later point of our analytical discussion.

One particular topic with regard to "material continuity" may, however, be stated before we proceed to any other discussion. The "continuity" must *not* be understood in the sense that, in a given species, exactly *the same* community of atoms, or electrons, or what you will, went through the whole line of generations. This is impossible for the fact of metabolism, *i.e.* dissimilation and assimilation. "The same" material, in the strict meaning of the word, only connects two generations in every case, and the material *sameness* that runs through all of them relates only to quality in general but not to a particular amount of matter as such.

So we see again (compare page 117) that the concept of *the same* implies a certain problem in biology, a problem that is to be discussed later.

THE COMPLEX-EQUIPOTENTIAL SYSTEM AND ITS RÔLE IN INHERITANCE [1]

We now begin the analytical study of inheritance, placing it upon as broad a basis as possible.

Our studies of morphogenetic restitution have shown us that besides the harmonious-equipotential systems another and widely different type of morphogenetic "systems" (*i.e.* unities consisting of elements equal in morphogenetic faculty) may also be the basis of restitution processes. Whilst in the harmonious system the morphogenetic acts performed by every single element in any actual case are single acts, the totality of all the single acts together forming the harmonious whole, in the other type of systems now to be examined, *complex* acts, that is, acts which consist of a manifoldness in space and in time, can be performed by *each single* element, and actually are performed by one or the other of them. We therefore have given the title of "complex-equipotential systems" to the systems in question, as all our denominations are based on the concept of the prospective morphogenetic potency, that is, of the possible fate of the elements.

The cambium of the Phanerogams may be regarded as the very type of a complex-equipotential system, promoting restitution of form. It runs through the whole stem of our trees, in the form of a hollow tube, placed between the inner and the outer cell-layers of the stem, and either branch or root may originate from any single one of its cells, just as circumstances require. We might call the cambium a system of the "complex" type, of course, even if every one of its constituents were able to form only a root or only a branch by way of restitution. But, in fact, one and the same element can form both of these complex-structures; it depends only on its relative position in the actual part of the stem isolated for

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[1] Driesch, *Organ. Regul.*, 1901.

the purposes of experiment, what will be accomplished in every case. Here we have a state of affairs which we shall encounter again when studying regeneration in animals: every element of the system may be said to contain potencies for the "ideal whole", though this ideal whole will never be realised in its proper wholeness.[1]

But there is no need to recur to the "ideal whole" in many other cases of adventitious restitution in plants. On isolated leaves of the well-known begonia, a whole plant, containing all the essential parts, may arise from any single cell[2] of the epidermis, at least along the veins; and in some liverworts it has been shown by Vöchting that almost every cell of the whole is able to reproduce the plant, as is also the case in many algae.

In the animal kingdom it is chiefly and almost solely the phenomena of regeneration proper which offer typical instances of our systems, since adventitious restitution, though occurring, for instance, in the restitution of the lens of vertebrates from the iris (G. Wolff), and though connected also with the events in regeneration proper,[3] is of but secondary importance in animal restitution, at least, if compared with restitution in plants. If we study the regeneration of a leg in the common newt, we find that it may take place from every section, the point of amputation being quite at our choice. We, therefore, can say without any doubt that the line of consecutive possible cross-sections forms a complex-morphogenetic system, as every one of them is able to give rise to a complex organ, viz. the foot and part of the leg. It is an open question whether

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[1] The "ideal whole" is also proved to exist, if any *given* "Anlage", say of a branch, is forced to give origin to a root, as has really been observed in certain plants. This case, like many other less extreme cases of what might be called "compensatory heterotypy", is best to be understood by the aid of the concept of "prospective potency". It is very misleading to speak of a metamorphosis here. See my *Organ. Regul.* pp. 77, 78.

[2] Winkler has discovered the important fact that the adventitious buds formed upon leaves may originate either from one single cell of the epidermis or from several cells together; a result that is very important with respect to the problem of the distribution of "potencies". (Compare p. 111.)

[3] The "regeneration" of the brain of annelids, for instance, is far better regarded as an adventitious formation than as regeneration proper: nothing indeed goes on here at the locality of the wound; a new brain is formed out of the ectoderm at a certain distance from it.

this complex system is to be called "equipotential" or not. It indeed seems to be inequipotential at the first glance, for each single section has to form a different organogenetic totality, namely, always that specific totality which had been cut off; but if we assume hypothetically that the real "Anlage" which is produced immediately by the cells of the wounded surface is the very same for all of them, and that it is the actual state of organisation which determines to what result this "Anlage" is to lead,[1] we may say that the series of consecutive cross-sections of a newt's leg does form a morphogenetic system of the complex-equipotential type, promoting secondary regulations of form.

Now all these difficulties vanish if we consider the regeneration of animals, such, for instance, as many worms of the annelid class or our familiar ascidian *Clavellina*, in which regeneration in both directions is possible. The wound at the posterior end of the one half which results from the operation forms a posterior body half; the wound at the anterior end of the other half forms an anterior one. Again, it is the ideal whole which we meet here: each section of the body indeed may be said to contain the potencies for the production of the totality, though actually this totality is always realised by the addition of two partial organisations. The title of complex-equipotential systems thus seems to be fully justified as applied to the systems which are the basis of regeneration: each section of the regenerating body may, in fact, produce the same complex whole, or may, if we prefer to say so, at least prepare the ground for that complex Anlage, out of which the complex totality is actually to arise, in the same manner.

It often occurs in science, that in rather strange and abnormal conditions something becomes apparent which

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[1] A full "analytical theory of regeneration" has been developed elsewhere (*Organ. Regul.* p. 44, etc.). I can only mention here that many different problems have to be studied by such a theory. The formation of the "Anlage" out of the body and the differentiation of it into the completely formed results of regeneration are two of them. The former embraces the question about the potencies not only of the regenerating body but of the elements of the "Anlage" also; the latter has to deal with the specific order of the single acts of regenerative processes. The cells of the "Anlage" have proved to be equipotential in the harmonious way (p. 92).

might have been found everywhere, which is lying before our eyes quite obviously. Are we not in just such a condition at present? In order to study the complex-equipotential systems, we turn to the phenomena of regeneration and of restitution in general; we occasionally even introduce hypotheses to render our materials more convenient for our purposes; and all the time there is one sort of complex-equipotential system in the body of every living being, which only needs to be mentioned in order to be understood as such, and which indeed requires no kind of preliminary discussion. The system of the *propagation cells*, in other words the *sexual organ*, is the clearest type of a complex-equipotential system which exists. Take the ovary of our sea-urchin, for instance, and there you have a morphogenetic system every element of which is equally capable of performing the same complex morphogenetic course—the production of the whole individual.

Further on we shall deal exclusively with this variety of our systems, and in doing so we shall be brought back to our problem of heredity.

The Second Proof of Life-Autonomy. Entelechy at the Bottom of Inheritance

After we had established the concept of the harmonious-equipotential system in a former chapter, we went on to study the phenomena of the *differentiation* of it, and in particular the problem of the localisation of all differentiations. Our new concept of the complex-equipotential system is to lead us to an analysis of a different kind: we shall pay special attention to the *origin*, to the *genesis* of our complex systems that show equipotentiality.

If we review the process of ontogenesis, we are able to trace back every complex system to a very small group of cells, and this small group of cells again to one single cell. So in plants the cambium may be shown to have originated in a sort of tissue-rudiment, established at a very early period, and the ovary may be demonstrated to be the outcome of a group of but a few cells, constituting the first visible " Anlage " of the reproductive organs. At the end then, or from another point of view at the beginning, a single cellular element represents the very primordial egg-cell. The primordial egg-cell has undergone a long line of consecutive divisions ; the single eggs are the last result of them.

We now proceed to some considerations which have a certain logical similarity to those which inaugurated our analysis of the differentiation of the harmonious-equipotential systems, though the facts in question are very different.

Viewed by itself without any kind of prepossessions, as it might be by anyone who faces a new problem with the single postulate of introducing new natural entities—to use the scholastic phrase—as little as possible, the development of the single egg might be regarded as proceeding on the foundation of a very complicated sort of machine, exhibiting a different kind of construction in the three chief dimensions of space, as does also the organism which is to be its result.

But could such a theory—irrespective of all the experimental facts which contradict it—could such a theory stand before the *one* fact, that there occurs a *genesis* of that complex-equipotential system, of which our one single egg forms a part ? Can you imagine a very complicated machine, differing in the three dimensions of space, to be divided hundreds and hundreds of times and in spite of that to remain always *the same whole* ? You may reply that during the period of cell-divisions there is still no machine, that the machine is established only after all the divisions are complete. Good ; but what then constructs this machine in the definitive cells of our systems, say in the eggs ? Another sort of machine perhaps ? That could hardly be said to be of much use. Or that entelechy of which we have spoken ? Then you would recur to our first proof of vitalism and would burden entelechy with a specific performance, that is, with the construction of the hypothetic machine which you are postulating in every single egg. But of course you would break the bounds of physics and chemistry even then.

It seems to me that it is more simple, and, so to say, more natural, not to recur to our first proof of life-autonomy in order to keep to the "machine theory" in this new branch of inquiry, but to consider facts as they offer themselves to analysis.

But then, indeed, we are entitled to draw an independent *second* proof of the autonomy of life from our analysis of the genesis of systems of the complex-equipotential type. We say it is a mere absurdity to assume that a complicated machine, typically different in the three dimensions of space, could be divided many, many times, and in spite of that always be the whole: therefore there cannot exist any sort of machine as the starting-point and basis of development.

Let us again apply the name entelechy to that which lies at the very beginning of all individual morphogenesis.

Entelechy thus proves to be also that which may be said to lie at the very root of inheritance,[1] or at least of the outcome of inheritance; the individual formation of the next generation is shown not to be performed by a machine but by a natural agent *per se*.

Our second vitalistic argument is not quite without importance for the first one.

People have said occasionally that my first proof of vitalism had not sufficiently considered the fact that an harmonious-equipotential system is full of nuclei, and that these nuclei might be machines.

We have now shown that this is impossible.

But let me add another remark: even if the nuclei were "machines", this would not suffice for a mechanistic explanation of the differentiation of an harmonious system. For the nuclei, as the experiments show, are all of the same type in such a system. Their totality as such is a *sum*, though (presumably) a sum of machines. But for a mechanistic explanation of harmonious differentiation we should be forced to consider the system in question as *one great super-machine*, embracing *ex hypothesi* many small machines, all of them alike. And just this super-machine, relating to the totality

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[1] And, of course, at the root of every new starting of certain parts of morphogenesis also, as in regeneration and in adventitious budding; these processes, as we know, being also founded upon "complex-equipotential systems", which have had their "genesis".

of the system, cannot exist. Thus even the view that the single nuclei are machines would not help us, quite apart from the fact that this view is wrong.

THE SIGNIFICANCE OF THE MATERIAL CONTINUITY IN INHERITANCE

But what about the material continuity appearing in inheritance, which we have said to be almost self-evident, as life is only known to exist on material bodies? Is there not, in fact, a serious contradiction in admitting at the same time entelechy on the one side and a sort of material condition on the other as the basis of all that leads to and from inheritance? Not at all, so it seems to me.

Let us try to comprehend what is meant by the statement that entelechy *and* something material are at work in inheritance at the same time. Entelechy has ruled the individual morphogenesis of the generation which is regarded as being the starting-point for inheritance, and will rule also the morphogenesis of the generation which is to follow; entelechy determines the egg to be what it is, and the morphogenesis starting from this egg to be what it is also. Entelechy, at present, is not much more for us than a mere word, to signify the autonomous, the irreducible of all that happens in morphogenesis with respect to *order*, in the one generation and in the next. But may not the material continuity which exists in inheritance account perhaps for the material elements *which are to be ordered*? In such a way, indeed, I hope we shall be able to reconcile entelechy and the material basis of heredity. May it not be that there exist some "means" for morphogenesis, which are handed down from generation to generation, always controlled by entelechy, and which constitute the real significance of the continuity of matter during inheritance?

MENDELISM

Discoveries of the last decades show that such means of a material character, though not the foundation of that order of processes which is inherited, are nevertheless among the most necessary conditions for the accomplishment of inheritance in general. It is scarcely necessary to remind you that for very many years all concrete research on heredity proper—that is, the actual comparison of the various specific characters in the generations of the grandfather, the father, and the child—was due to Galton. You may also be aware that, in spite of Galton's inestimable services, it was not till 1900 that one of the important principles concerned in inheritance was found independently by de Vries, Correns, and Tschermak, and that this principle happened to be one that *had* been discovered already, stated with the utmost clearness and precision by the Augustinian monk, Gregor Mendel, as early as 1865, though it had been completely forgotten ever since.

The so-called " rule of Mendel " is based upon experiments with hybrids, that is, with the offspring of parents belonging to different varieties; but it relates not to the characters of the generation resulting immediately from hybridisation, the "first" generation of hybrids, as we shall call it, but to the characters of that generation which is the result of crossing the hybrids with each other, provided that this leads to any offspring at all. There are many cases indeed, both amongst animals and plants, where the offspring of the hybrids, or in other terms the " second " generation, is found to consist of individuals of three different types—the mixed[1] type of the hybrids themselves, and the two pure types of the grandparents. Whenever the individuals of the " second " generation are separated into these three different types, hybrids are said to " split ". It is the fact of this splitting on the one hand, and on the other hand a certain statement about the numbers of individuals in the three different types of the " second " generation, that give its real importance to Mendel's rule.

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[1] For the sake of simplicity, I shall not deal here with those cases of hybridisation in which one quality is " recessive ", the other " dominant ", but only allude to the cases, less numerous though they be, where a real mixture of maternal and paternal qualities occurs. And I also omit all exceptions based upon a " binding " of properties, etc. For a full discussion, compare the works of Bateson, T. H. Morgan, etc.

From the fact of the splitting of hybrids in the second generation most important consequences may be drawn for the theory of inheritance ; the split individuals, if crossed with each other, always give an offspring which remains pure ; there is no further splitting and no other change whatever. The germ-cells produced by the split individuals of the second generation may therefore be said to be "pure", as pure as were those of the grandparents. But that is as much as to say that the pureness of the germ-cells has been preserved in spite of their passing through the " impure " generation of the hybrids, and from this fact it follows again that the union of characters in the hybrids must have been such as to permit pure separation : in fact, the germ-cells produced by Mendelian hybrids may hypothetically be regarded as being pure themselves.

We have not yet considered one feature of all experiments in hybridisation, which indeed seems to be the most important of all for the theory of inheritance, if taken together with the fact of the pureness of the germs. The rule of Mendel always relates to *one single* character of the species or varieties concerned in hybridisation, and if it deals with more than one character, it regards every one of them *separately* ; indeed, the rule holds for every one of them irrespective of the others. We cannot study here how this most important fact of the independence of the single characters of a species with regard to inheritance leads to the production of new races, by an abnormal mixture of those characters. We only take advantage of the fact theoretically, and in doing so, I believe, we can hardly escape the conclusion that the independence of the single characters in inheritance, taken together with the pureness of the germ-cells in the most simple form of hybrids, proves that there occurs in inheritance a sort of handing over of single and separate morphogenetic agents which relate to the single morphogenetic characters of the adult.

Mendelism and Cytology

Modern cytology now strongly supports this view.

The discoveries of Rauber, Boveri, and Herbst had shown that it is the *nucleus* of the germ-cells that plays the most important part in inheritance, the protoplasm being only responsible for certain properties of the offspring that are of minor importance.[1] Herbst, *e.g.*, was able to show that hybrids of echinoderms become the more of the " maternal " type the more there is chromatin in the fertilised egg derived from the mother.[2]

But it is the modern theory of *maturation* and *fertilisation* in particular that has supported the Mendelian law most strongly : in maturation half of the chromosomes are eliminated from the egg and the spermia ; fertilisation restores the total number again. Then separation follows again in the next maturation, etc., etc.

But the individuality of the chromosomes is *preserved* throughout the line of these processes and, on the other hand, the separation of the chromosomes in maturation is quite *ad libitum* and does not relate to the very same chromosome groups that had been united by the preceding fertilisation.

Let me give an example.

Let us assume that we have ripe eggs and ripe spermiae, of different varieties. Each of them contains n chromosomes, which we will call $A, B, C \ldots$ in the egg, and $a, b, c \ldots$ in the spermia. Fertilisation occurs and the number of chromosomes is now $A, B, C \ldots + a, b, c \ldots = 2n$ in each egg.

And now we take account only of the chromosomes called A and a.

The next maturation then will lead to a separation again of the chromosomes, and thus we get what we will briefly call A-eggs, a-eggs, A-spermiae and a-spermiae.

The next fertilisation then gives us fertilised eggs of the types: AA, Aa, aA, aa, that is, $\frac{1}{4}$ pure A's, $\frac{1}{4}$ pure a's, and $\frac{1}{2}$ Aa's, *i.e. mixed* eggs.

But these numbers, $\frac{1}{4}$, $\frac{1}{4}$, $\frac{1}{2}$, are just the same numbers that occur in Mendelian " splitting ". Thus there is a correspondence among two kinds of splitting, the cytological and the Mendelian, and we are therefore fully entitled to regard the first of these splittings as the foundation of the second.

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[1] Compare my studies on Echinoderm hybrids, *Arch. Entw. Mech.* vii., 1898.

[2] *Arch. Entw. Mech.* xxvii. and xxxiv., and *Sitzungsber. Acad. Heidelberg*, 1913, No. 8.

So much for the more general outlines of the relations between Mendelism and cytology.

If, now, we introduce the modern name of *genes* for the ultimate material units transported in propagation from one generation to the next, we are entitled to say that inheritance has as its material basis the uniting and splitting of genes.[1]

But the genes as *material* entities, of whatever kind, *cannot*, by themselves, account for inheritance.

In the first place, their community is most decidedly an *aggregate*. This is a fact. But even if we knew nothing about this fact, we should have to postulate it. For, according to our second vitalistic argument, there *cannot* be a structure of the type of a well-ordered machine of three dimensions, which divides indefinite times and remains what it has been.

Thus entelechy and genes are working together. Entelechy uses the genes as its *means*, and all *order* in morphogenesis is exclusively due to entelechy.

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[1] We have omitted all details intentionally and only add that there are many genes in one chromosome, and that, in the state of " synapsis ", single genes may be interchanged among two corresponding chromosomes. See Morgan, etc.

CONCLUSIONS FROM THE FIRST MAIN PART OF THIS BOOK

IN finishing our chapter on inheritance, we at the same time have finished the first main part of this book—that part of it which has been devoted exclusively to the study of the morphogenesis of the *individual*, including the functioning of the adult individual form.

The chief result of the first main part of this book has been to prove that an autonomy of life phenomena exists at least in some departments of individual morphogenesis, and probably in all of them ; the real starting-point of all morphogenesis cannot be regarded as a machine, nor can the real process of differentiation, in all cases where it is based upon systems of the harmonious-equipotential type. There cannot be any sort of machine in the cell from which the individual originates, because this cell, including both its protoplasm and its nucleus, has undergone a long series of divisions, all resulting in equal products, and because a machine cannot be divided and in spite of that remain what it was. There cannot be, on the other hand, any sort of machine as the real foundation of the whole of an harmonious system, including many cells and many nuclei, because the development of this system goes on normally, even if its parts are rearranged or partly removed, and because a machine would never remain what it had been in such cases.

Once more we repeat, at this resting-point in our discussions, that both of our proofs of life-autonomy have been based upon a careful analysis of certain facts about the distribution of morphogenetic potencies in two classes of morphogenetic systems, and upon nothing else. To recall only one point, we have not said that regeneration, merely because it is a kind of restitution of the disturbed whole, compels us to admit that biological events happen in a specific and elemental manner, but, indeed, regeneration *does* prove vitalism, because it is founded upon the existence of certain complex-equipotential systems, the analysis of the genesis of which leads to the understanding of life-autonomy. This distinction, in fact, is of the greatest logical importance.

PART II

SYSTEMATICS AND HISTORY

I. THE PRINCIPLES OF SYSTEMATICS

Rational Systematics

All systematics which deserves the predicate " rational " is founded upon a concept or upon a proposition, by the aid of which a totality of specific diversities may be understood. That is to say : every system claiming to be rational gives us a clue by which we are able to apprehend either that there cannot exist more than a certain number of diversities of a certain nature, or that there can be an indefinite number of them which follow a certain law with regard to the character of their differences.

Solid geometry, which states that only five regular bodies are possible, and points out the geometrical nature of each of these bodies, is a model of what a rational system should be. The theory of conic sections is another. Take the general equation of the second degree with two unknowns, and study all the possible forms it can assume by a variation of its constants, and you will understand that only four different types of conic sections are possible—the circle, the ellipse, the hyperbola, and the parabola.

The system of chemical elements and compounds approaches the ideal type of a rational system in a high degree. In crystallography a similar end has been reached and systematics has here accounted for the limited number and fixed character of the possible forms of crystalline symmetry. Certain hypotheses about the possible forms of geometrical equilibrium among the ultimate elements of matter are the foundation of rational systematics in these cases.

It is not difficult to understand the general logical type of all rational systems, and logic indeed can discover it without appealing to concrete sciences or to geometry. Rational systematics is always possible whenever there exists any fundamental concept or proposition which carries with it a principle of division. The so-called " genus ", as will easily be perceived, then embraces all its " species " in such a manner that all peculiarities of the species are represented already in properties of the genus, only in a more general form, in a form which is still unspecified. The genus is both richer in content and richer in extent than are the species, though it must be added that its richness in content is, as it were, only latent : but it may come into actuality by itself and without any help from without.

In fact, all rational systems with regard to the relations of symmetry in natural bodies deal ultimately with space ; or better, all systems in such fields are able to become rational only if they happen to turn into questions of special symmetry.

All other genera and species, whether of natural bodies or of facts, can be related only on the basis of empirical abstraction, *i.e.* can never attain rationality : here, indeed, the genus is richer in extent, but poorer in content, than are the species. The genus is transformed into the species, not by any inherent development of latent properties, but by a mere process of addition of characteristic points. It is impossible to deduce the number or law or specifications of the species from the genus. Mere " classification ", if we may reserve the honourable name of systematics for the rational type, is possible here, a mere statement in the form of a catalogue, useful for orientation but for nothing more. We may classify all varieties of hats or of tables in the same way.

Biological Systematics

At this point we return from our logical excursion to our proper subject of biology ; for I am sorry to say biological systematics is at present of our second type of systematics throughout: it is classification pure and simple. We have a catalogue in our hands, but nothing more.

Such a statement of fact conveys not a particle of censure, casts not the least reflection on the gifted men who created the classification of animals or plants. It is absolutely necessary to have such a catalogue, and indeed the catalogue of the organisms can be said to have been improved enormously during the advance of empirical and descriptive biological science. Any classification improves as it becomes more "natural", as the different possible schemes of arrangement, the different reasons of division, agree better and better in their results; and, in fact, there has been a great advance of organic classification in this direction. The "natural" system has reached such perfection, that what is related from one point of view seems nearly related also from almost all points of view which are applicable, at least from those which touch the most important characteristics. There has been a real weighing of all the possible reasons of division, and that has led to a result which seems to be to some extent final.

But, nevertheless, we do not understand the *raison d'être* of the system of organisms; we are not at all able to say that there *must* be these classes or orders or families and no others, and that they must be such as they are.

Shall we ever be able to understand that? Or will organic systematics always remain empirical classification? We cannot answer this question. If we could, indeed, we should have what we desire! As simple relations of space are certainly not the central point of any problematic rational organic systematics even of the future, the question arises whether there could be found any principle of another type which could allow an inherent sort of evolution of latent diversities, as do all judgments about spatial symmetry. At the end of the second part of this book, we shall be able to say a few more words about this important point.

The concept of what is called a "type", due almost wholly to Cuvier and Goethe, is the most important of all that classification has given to us. Hardly second in importance is the discovery of the "correlation of parts", as a sort of connection which has the character of necessity without being immediately based upon causality. Rádl seems to be the only modern author who has laid some stress on this topic. The harmony which we have discovered in development is also part of this correlation. When, later on, we come to discuss analytically our well-established entelechy as the ultimate basis of individual organisation, we shall be able to gain more satisfactory ideas with respect to the meaning of the non-causal but necessary connection, embraced in the concepts of type and of correlation of parts.

The type is a sort of irreducible arrangement of different parts; the correlation deals with the degree and the quality of what may be called the actual make of the parts, in relation to one another: all ruminants, for instance, are cloven-footed; the so-called dental formulae are characteristic of whole groups of mammals. Of course all such statements are empirical and have their limits: but it is important that they are possible.[1]

It has been the chief result of comparative embryology to show that the type as such is more clearly expressed in developmental stages than it is in the adults, and that, therefore, the embryological stages of different groups may be very much more similar to each other than are the adults: that is the truth contained in the so-called "biogenetisches Grundgesetz". But the specific differences of the species are not wanting in any case of ontogeny, in spite of such similarities in different groups during development, and a careful observer may even attribute a cell of a blastula to a particular species.

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[1] Recent years have created the beginnings of a systematics based on chemical differences of metabolism and its products: such differences in fact have been found to go hand-in-hand with diversities of the type in some cases (v. Bunge, Przibram, etc.).

2. THE THEORY OF DESCENT

GENERALITIES

IT is most generally conceded at the present time that the actually existing state of all organisms whatsoever is the result of their history. What does that mean? What are the foundations upon which the assumption rests? What is the relation of systematics to history? In raising such questions and considerations we are treading the ground sacred to the theory of descent.[1]

The theory of descent is the hypothetic statement that the organisms are really allied by blood among each other, in spite of their diversities. The question about their so-called monophyletic or polyphyletic origin is of secondary importance compared with the statement of relationship in general.

There are two different groups of facts which have suggested the idea of transformism: none of these facts can be said to be conclusive, but there certainly is a great amount of probability in the whole if taken together.

The first group of evidences which lead to the hypothesis of the real relationship of organisms consists of facts relating to the *geographical* distribution of animals and plants and to *palaeontology*. As to geography, it seems to me that the results of the floral and faunal study of groups of islands are to be mentioned in the first place. If, indeed, on each of the different islands, *A B C* and *D*, forming a group, the species of a certain genus of animals or plants are different in a certain respect, and show differences also compared with the species living on the neighbouring continent, of which

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[1] I do not say "evolution", as I shall use this word in quite a particular sense later on, and as we do not know *a priori* whether phylogeny is a true "evolution" or not.

there is geological evidence that the islands once formed a part, whilst there is no change in the species on the continent itself for very wide areas, then, no doubt, the hypothesis that all these differing species once had a common origin, the hypothesis that there is a certain community among them all, will serve to elucidate in some way what would seem to be very abstruse without it. And the same is true of the facts of palaeontology. In the geological strata, forming a continuous series, you find a set of animals, always typical and specific for every single stratigraphical horizon, but forming a series just as do those horizons. Would not the whole aspect of these facts lose very much of its peculiarity if you were to introduce the hypothesis that the animals changed with the strata? The continuity of life, at least, would be guaranteed by such an assumption.

The geographical and geological evidences in favour of the theory of descent are facts taken from sciences which are not biology proper; they are not facts of the living, but only facts about the living. That is not quite without logical importance, for it shows that not biology alone has led to the transformism hypothesis. Were it otherwise, transformism might be said to be a mere hypothesis *ad hoc*; but now this proves to be not the case, though we are far from pretending that transformism might be regarded as resting upon a real *causa vera*.

But let us study the second group of facts which support the theory of descent. It is a group of evidences supplied by biology itself that we meet here, there being indeed some features in biology which can be said to gain some light, some sort of elucidation, if the theory of descent is accepted. Of course, these facts can only be such as relate to specific diversities, and indeed are facts of systematics; in other words, there exists something in the very nature of the system of organisms that renders transformism probable. The system of animals and plants is based upon a principle which might be called the principle of *similarities and diversities by gradation*; its categories are not uniform but different in degree and importance, and there are different kinds of such differences.

No doubt, some light would be shed upon this character of the system, as revealed by comparative anatomy and embryology, if we were allowed to assume that the relation between similarities and diversities, which is gradual, corresponded to a blood-relationship which is gradual also.

The theory of descent as such, however, without a real knowledge of the dynamic *factors* which are concerned in transformism, or of the law of transformism, does not yet tell us very much.

Imagine so-called historical geology, without any knowledge of the physical and chemical factors which are concerned in it: what would you have except a series of facts absolutely unintelligible to you? Or suppose that some one stated the cosmogenetic theory of Kant and Laplace without there being any science of mechanics: what would the theory mean to you? Or suppose that the whole history of mankind was revealed to you, but that you had absolutely no knowledge of psychology: what would you have but facts and facts and facts again, with not a morsel of real explanation?

But such is the condition in which pure phylogeny stands. If it is based only on the pure theory of transformism, there is nothing explained at all. It was for this reason that the philosopher Liebmann complained of phylogeny that it furnishes nothing but a "gallery of ancestors". And this gallery of ancestors set up in phylogeny is not even certain; on the contrary, it is absolutely uncertain, and very far from being a fact. For there is no sound and rational principle underlying phylogeny; there is mere fantastic speculation. How could it be otherwise where all is based upon suppositions which themselves have no leading principle at present? I should not like to be misunderstood in my polemics against phylogeny. I fully grant you that it may be possible in a few cases to find out the phylogenetic history of smaller groups with some probability, if there is some palaeontological evidence in support of pure comparative anatomy; and I also do not hesitate to allow that such a statement would be of a certain value with regard to a future discovery of the "laws" of descent. But it is quite another thing with phylogeny on the larger scale. Far more eloquent than any amount of polemics is the fact that vertebrates, for instance, have already been "proved" to be descended from, firstly, the amphioxus; secondly, the annelids; thirdly, the *Sagitta* type of worms; fourthly, from spiders; fifthly, from *Limulus*, a group of crayfishes; and sixthly, from echinoderm larvae. That is the extent of *my* acquaintance with the literature, with which I do not pretend to be specially familiar. Emil du Bois-Reymond said once that phylogeny of this sort is of about as much scientific value as are the pedigrees of the heroes of Homer, and I think we may fully endorse his opinion on this point. We must, therefore, search for the dynamic factors which promote phylogeny.

HISTORY AND SYSTEMATICS

But first a few words should be devoted to the relations between history and systematics in biology. Is there no contradiction between historical development and a true and rational system which, we conceded, might exist some day in biological sciences, even though it does not at present? By no means. A totality of diversities is regarded from quite different points of view if taken as the material of a system, and if considered as realised in time. We have said that chemistry has come very near to proper rational systematics; but the compounds it deals with at the same time may be said to have originated historically also, though not, of course, by a process of propagation. It is evident at once that the geological conditions of very early times prohibited the existence of certain chemical compounds, both organic and inorganic, which are known at present. None the less these compounds occupy their proper place in the system. And there may be many substances theoretically known to chemical systematics which have never yet been produced, on account of the impossibility of arranging for their proper conditions of appearance, and nevertheless they must be said to "exist". "Existence", as understood in systematics, is independent of special space and of special time, as is the existence of the laws of nature:

we may speak of a Platonic kind of existence here. Of course it does not contradict this sort of ideal existence if reality proper is added to it.

Thus the problem of systematics remains, no matter whether the theory of descent be right or wrong. There always remains the question about the totality of diversities in life : whether it may be understood by a general principle, and of what kind that principle would be. As, in fact, it is most probably by history, by descent, that organic systematics is brought about, it of course most probably will happen some day that the analysis of the causal factors concerned in the history will serve to discover the principle of systematics also.

The Prerequisites of the Theory of Descent and our Knowledge about them

The theory of descent, of whatever form it may be, has two absolutely indispensable prerequisites : there must exist some sort of *deviation from inheritance* in some cases, and the result of this deviation must be *inheritable itself*. Otherwise no phylogeny would be possible.

Now deviations from inheritance are known in four different forms. Let us enumerate them, and let us try to find out whether their results are themselves inheritable or not.

There is, first, *continuous variation* in the proper sense. All the individuals of the offspring of a pair of animals (or of a parthenogenetic female) are different from each other. And they are different—what is important to notice—even if mother and father belong to the same *pure line* (Johannsen), *i.e.* if they are not " mutants " with regard to one another in even the slightest way. Continuous variations follow the " law of errors " as mathematically formulated by Gauss and Galton. Their results are *not* inheritable, and therefore have no bearing upon the theory of descent. Even if you select two extremes for propagation, you get an offspring with the same error curve. These variations are probably due to the contingent variation of the medium, which also obeys the law of errors.

Secondly, there is *adaptive variation*, studied in a former part of this book. This is not exactly a " deviation " from inheritance. For the totality of adaptive potencies of a given species is inherited, and it simply depends on the conditions, met by an individual, which potency will become effective. (This point of view, by the way, may also be applied to variation proper.) *Nothing* is known with certainty about the inheritance of adaptations, *i.e.* about the so-called " inheritance of acquired characters ", with the exception, perhaps, that the effect of a change of conditions in some (botanical) cases may require several generations before it becomes quite definite. Guyer's experiments on rabbits, it is true, may mark the beginning of a positive knowledge in this field, but they are rather fragmentary at present and not quite undisputed. About Kammerer's experiments nothing can be said, until they have been confirmed by a competent author. Inheritance of adaptations, by the way, would not be a very useful event for the organism, unless it would serve to strengthen adaptive results under permanently equal conditions. It might even be said to be in opposition to the real value of adaptation itself.

In the third place there is *Mendelian variation*. As the single properties of an organism split and combine separately, we may raise new " races " by Mendelian experiments. We may start from a plant with white flowers covered with hairs and from another with red naked ones, and, at the end, we may have before us red flowers covered with hairs and white naked ones. These results, originated as they are at the very basis of all inheritance, are, of course, inheritable themselves. But they do not help us much for phylogeny. For only a regrouping of pre-existing properties, nothing " new ", stands in question.

Ultimately there is *mutation* (de Vries), which marks a real break of inheritance. Its results are inheritable. This is so-called " discontinuous variation ". Its steps may be comparatively great or very small (Jennings). They are never of such importance as to lead to the formation of a really new " species ". The origin of mutations is unknown. They seem to be due to " inner forces " ; but the medium, though in a very unspecified way, may give a sort of stimulus to those forces. Very rich feeding, *e.g.*, has often had a considerable number of mutations as its consequence. No plan or law in the sequence of mutations has so far been discovered.

This is all we know, in a positive way, about the "prerequisites" of phylogeny. In fact, it is not very much. And, thus, it is not very surprising that scientists have tried to attack the problem of descent in a merely constructive, hypothetical way. Let us then study the principal forms of this sort of theory.

3. THE PRINCIPLES OF DARWINISM

THERE is no need in our times to explain in a full manner the theory known under the name of Darwinism. All of you know this theory, at least in its outlines, and so we may enter at once upon its analytic discussion. A few words only I beg you to allow me as to the name of " Darwinism " itself. Strange to say, Darwinism, and the opinion of Charles Darwin about the descent of organisms, are two different things. Darwin, the very type of a man devoted to science alone and not to personal interests,—Darwin was anything but dogmatic, and yet Darwinism is dogmatism in one of its purest forms. Darwin, for instance, gave the greatest latitude to the nature of the variations which form the battleground of the struggle for existence and natural selection ; and he made great allowances for other causal combinations also, which may come into account besides the indirect factors of transformism. He was Lamarckian to a very far-reaching extent. And he had no definite opinion about the origin and the most intimate nature of life in general. These may seem to be defects but really are advantages of his theory. He left open the question which he could not answer, and, in fact, he may be said to be a good illustration of what Lessing says, that it is not the possession of truth but the searching after it that gives happiness to man.

How different is this from what many of Darwin's followers have made out of his doctrines ; how far is " Darwinism " removed from Darwin's own teaching and character !

It is to Darwinism of the *dogmatic* kind, however, that our next discussions are to relate, for, thanks to its dogmatism, it has the advantage of allowing the very sharp formulation of a few causal factors, which *a priori* might be thought tc be concerned in organic transformism, though we are bound to say that a really searching analysis of these factors ought to have led to their rejection from the very beginning.

The logical structure of dogmatic Darwinism reveals two different parts, which have nothing at all to do with one another.

NATURAL SELECTION

We shall first study that part of it which is known under the title of natural selection, irrespective of the nature of the causes of primary differences, or, in other words, the nature of variability. This part may be said to belong to Darwin's personal teachings and not only to "Darwinism". The offspring of a certain number of adults show differences compared with each other; there are more individuals in the offspring than can grow up under the given conditions, therefore there will be a struggle for existence amongst them which only the fittest will survive; these survivors may be said to have been "selected" by natural means.

It must be certain from the very beginning of analysis that natural selection, as defined here, can only eliminate what cannot survive, what cannot stand the environment in the broadest sense, but that natural selection never is able to create diversities. It always acts negatively only, never positively. And therefore it can "explain"—if you will allow me to make use of this ambiguous word—it can "explain" only why certain types of organic specifications, imaginable *a priori*, do *not* actually exist, but it never explains at all the existence of the specifications of animal and vegetable forms that are actually found. In speaking of an "explanation" of the origin of the living specific forms by natural selection, one therefore confuses the sufficient reason for the non-existence of what there is not, with the sufficient reason for the existence of what there is. To say that a man has explained some organic character by natural selection is, in the words of Nägeli, the same as if some one who is asked the question, "Why is this tree covered with these leaves?" were to answer, "Because the gardener did not cut them away." Of course that would explain why there are no more leaves than those actually there, but it never would account for the existence and nature of the existing leaves as such. Or do we understand in the least why there are white bears in the Polar Regions if we are told that bears of other colours could not survive ?

In denying any real explanatory value to the concept of natural selection, I am far from denying the action of natural selection. On the contrary, natural selection, to some degree, is *self-evident* ; at least as far as it simply states that what is incompatible with permanent existence cannot exist permanently. Chemical compounds, indeed, which decompose very rapidly under the conditions existing at the time when they originated may also be said to have been eliminated by " natural selection ". It is another question, of course, whether in fact all eliminations among organic diversities are exclusively due to the action of natural selection in the proper Darwinian sense. It has been pointed out already by several critics of Darwinism, and most clearly by Gustav Wolff, that there are many cases in which an advantage with regard to situation will greatly outweigh any advantage in organisation or physiology. In a railway accident, for instance, the passengers that survive are not those who have the strongest bones, but those who occupied the best seats ; and the eliminating effect of epidemics is determined at least as much by localities, *e.g.* special houses or special streets, as by the degree of immunity. But, certainly, natural selection is a *causa vera* in many other cases.

Natural selection has a certain important logical bearing on systematics, as a science of the future, which has scarcely ever been alluded to. Systematics of course has to deal with the totality of the *possible*, not only of the *actual* diversities ; it therefore must remember that more forms may be possible than are actual, the word " possible " having reference in this connection to originating, not to surviving. Moreover, systematics is concerned not only with what has been eliminated by selection, but also with all that might have originated from the eliminated types. By such reasoning natural selection gains a very important aspect—but a logical aspect only.

CONTINGENT VARIATION

The second doctrine of dogmatic Darwinism states that all the given diversities among the organisms that natural selection has to work upon are offered to natural selection by continuous variation; that is, by variation as studied by means of statistics.

Now we know already that the effects of this sort of variation are not inherited. We might, however, put real mutations of very small extent in their place; we should then be employing a *causa vera*. But these mutations, according to orthodox Darwinism, must be looked upon as *contingent, i.e.* as not being subject to any plan or direction.

The question, then, is, what may be explained by *contingent mutation* and *natural selection*.

I cannot enter here into the whole subject of Darwinian criticism. Our aims are of a positive character. So I shall only mention that dogmatic Darwinism has been found to be unable to explain every kind of mutual adaptations, *e.g.* those existing between plants and insects; that it can never account for the origin of those properties that are indifferent to the life of their bearer, being mere features of organisation as an arrangement of parts; that it fails in the face of all portions of organisation which are composed of many different parts—like the eye—and nevertheless are functional units in any passive or active way; and that, last not least, it has been found to be quite inadequate to explain the first origin of all newly formed constituents of organisation even if they are not indifferent: for how could any rudiment of an organ, which is not functioning at all, not only be useful to its bearer, but be useful in such a degree as to decide about life or death?

It is only for one special feature that I should like to show, by a more full analysis, that dogmatic Darwinism does not satisfy the requirements of the case. The special strength of Darwinism is said to lie in its explaining everything that is useful in and for organisms; the competitive factor it introduces does indeed seem to secure at least a relative sort of adaptedness between the organism and its needs. But, in spite of that, we shall now see that Darwinism fails absolutely to explain those most intimate organic phenomena which may be said to be the *most* useful of all.

Darwinism in its dogmatic form is not able to explain the origin of any sort of organic *restitution* ; it is altogether impossible to account for the restitutive power of organisms by the simple means of contingent mutation and natural selection in the struggle for existence. Here we have the logical *experimentum crucis* of Darwinism.

Let us try to study in the Darwinian style the origin of the regenerative faculty, as shown in the restitution of the leg of a newt. All individuals of a given species of the newt, say *Triton taeniatus*, are endowed with this faculty ; all of them, therefore, must have originated from ancestors which acquired it at some time or other. But this necessary supposition implies that all of these ancestors must have lost their legs in some way, and not only one, but all four of them, as they could not have acquired the restitutive faculty otherwise. We are thus met at the very beginning of our argument by what must be called a real absurdity, which is hardly lessened by the assumption that regeneration was acquired not by all four legs together, but by one after the other. But it is absolutely inevitable to assume that *all* the ancestors of our *Triton* must have lost one leg, or, more correctly, that only those of them survived which had lost one ! Otherwise not all newts at the present day could possess the faculty of regeneration ! But a second absurdity follows the first one : out of the ancestors of our newt, which survived the others by reason of having lost one of their legs, there were selected only those which showed at least a very small amount of healing of their wound. It must be granted that such a step in the process of selection, taken by itself, would not at all seem to be impossible ; since healing of wounds protects the animals against infection. But the process continues. In every succeeding stage of it there must have survived only those individuals which formed just a little more of granulative tissue than did the rest : though *neither* they themselves *nor* the rest could use the leg, which indeed was not present !

That is the second absurdity we meet in our attempt at a Darwinian explanation of the faculty of regeneration; but I believe the first one alone was sufficient.

If we were to study the "selection" of the faculty of one of the isolated blastomeres of the egg of the sea-urchin to form a whole larva, only of smaller size, the absurdities would increase. At the very beginning we should encounter the absurdity, that of all the individuals there survived only those which were not whole but half; for *all* sea-urchins are capable of the ontogenetical restitution in question, *all* of their ancestors therefore must have acquired it, and they could do that only *if* they became halved at first by some accident during early embryology. But we shall not insist any further on this instance, for it would not be fair to turn into ridicule a theory which bears the name of a man who is not at all responsible for its dogmatic form. Indeed, we are speaking against Darwinism of the most dogmatic form only, not against Darwin himself. He never analysed the phenomena of regeneration or of embryonic restitution—they lay in a field very unfamiliar to him and to his time. I venture to say that if he had taken them into consideration he would have agreed with us in stating that his theory was not at all able to cover them; for he was prepared to make great concessions, to Lamarckism for instance, in other branches of biology, and he did not pretend to know what life itself is.

Darwin was not a decided materialist, though materialism has made great capital out of his doctrines. His book, as is well known, is entitled "The Origin of *Species*," that is of organic *diversities*, and he himself possibly might have regarded all restitution as belonging to the original properties of life, anterior to the originating of diversities. Personally, he might possibly be called even a vitalist. Thus dogmatic "Darwinism" in fact is driven into all the absurdities mentioned above, whilst the "doctrine of Darwin" can only be said to be wrong on account of its failing to explain mutual adaptation, the origin of new organs, and some other features in organic diversities; the original properties of life were left unexplained by it intentionally.

An Important Vitalistic Consequence

It has often been said that orthodox Darwinism is the only possible way to explain the phylogenetic process in the mechanistic sense, all other phylogenetic theories implying some sort of vitalistic agent. This is true; and it is at the same time very important for ourselves. For we are thus entitled to say that our proof of the impossibility of orthodox Darwinism is at the same time a *new and independent proof of the autonomy of life.*

Let me say a few more words on this topic. Be it granted that a good many functional faculties in the organism are due to mechanical arrangements, and that these arrangements are the effect of contingent mutations and natural selection. Even if this were true—it is not proved at all, but is, on the contrary, very improbable—even then the origin of the "faculty" of morphogenetic *restitution* can *not* be explained in the Darwinian manner.

Purely functional performances, such as nervous conduction, secretion, muscular contraction, may be said to be "the same" throughout the whole animal kingdom. But restitution is not "the same" everywhere; for the regeneration of a foot is the regeneration of a foot, the restitution of an eye is the restitution of an eye, etc. Therefore, with regard to restitution, a *particular* apparatus must have been created by contingent mutation and natural selection *in each single case,* according to the Darwinian point of view. And even this is of a degree of improbability that practically equals impossibility—quite apart from the absurdities related to a Darwinian explanation of the origin of restitution mentioned above.

The faculty of restitution *is,* in fact, a *general* organic faculty just like nervous conduction, secretion, contraction, etc. As a *general* faculty, it cannot have originated in the Darwinian way, because it manifests itself specifically in each single case. And with regard to its *specificities,* as we have shown, this is also impossible.

Now, the impossibility of a Darwinian explanation of the origin of any organic institution implies the impossibility of a mechanistic explanation of its origin in general. And therefore refusing Darwinism means proving at the same time the autonomy of life.

4. THE PRINCIPLES OF LAMARCKISM

As the word "Darwinism" does not signify the proper theoretical system of Charles Darwin, so Lamarckism as commonly understood nowadays is a good deal removed from the original views of Jean Baptiste Lamarck. Lamarckism is generally regarded as reducing all organic diversities to differences in the needs of individual life, but Lamarck himself, as must be emphasised from the very beginning, did not at all maintain the opinion that the great characteristics of the types were only due to such accidental factors. He supposed a sort of law of organisation to be at the root of systematics, as developed in history, and the needs of life were only responsible, according to him, for splitting the given types of organisation into their ultimate branches. Thus Lamarck, to a great extent at any rate, belongs to a group of authors that we shall have to study afterwards: authors who regard an unknown law of phylogenetic development as the real basis of transformism. Modern so-called Neo-Lamarckism, on the other hand, has indeed conceded the principle of needs to be the sole principle of transformism. Let us then study Lamarckism in its dogmatic modern form. This, however, may be done very briefly.

All facts of morphological adaptations form the starting-point of this theory, and it must be granted that they form a very solid foundation, for they are facts. The theory only has to enlarge hypothetically the realm of these facts, or rather the realm of the law that governs them. Indeed, it is assumed by Lamarckism that the organism is endowed with the faculty of responding to *any* change of the environment which may change its function by a morphologically expressed alteration of its functional state and form, which is adapted to the state of conditions imposed from without.

It is important to notice that this faculty would imply vitalistic causality when taken in the wide meaning which Lamarckism allows to it : indeed, the power of active adaptation to indefinite changes would imply a sort of causal connection that is nowhere known except in the organism. Lamarck himself is not very clear about this point—he seems to be afraid of certain types of uncritical vitalism in vogue in his days ; but modern writers have most clearly seen what the logical assumptions of pure Lamarckism are. Next to Cope, August Pauly [1] may be said to be the most conscious representative of a sort of so-called psychological vitalism, which indeed Lamarckism as a general and all-embracing theory must have as its basis.

This point will come out more fully if now we turn to study another assumption, upon which dogmatic Lamarckism rests. Accidental variations of form are supposed to occur, and the organism is said to possess the faculty of keeping and storing these variations and of handing them down to the next generation, if they happen to satisfy any of its needs.

But these " needs " are not of the actual type, brought forth by a change of the functional state of the individual, as in the case of adaptations : they are of a somewhat mysterious nature.

In fact, Pauly does not hesitate to attribute " liking " and " judgment ", along with other psychological elements, to the organisms whilst undergoing their transformation. There has been formed, for instance, by accidental variation some pigment which by its chemical nature brings the organism into a closer connection with the light of the medium ; the individual likes that, keeps the pigment for itself and produces it again in the next generation ; and indeed it will safeguard any sort of improvement which chance may effect in this primitive " eye ". Such a view is said to hold well with respect to the origin of every new organ. And this psychological argument is also said to afford the real explanation of adaptation proper. Adaptation also is regarded not as a truly primary faculty of the organism, but as a retention or provoking of metabolic states

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[1] *Darwinismus und Lamarckismus*, München, 1905.

which occurred by accident originally and were then found to be useful ; now they are reproduced either in every single case of individual morphogenesis, without regard to actual requirements, or else only in response to such : in the first case they are "inherited", in the second they only occur as regulations. Thus the process of judgment, together with all the other elemental factors of psychical life concerned in it, has been made to account for adaptation proper. The whole theory has accordingly become very uniform and simple.

But, is it also a probable and satisfying theory ?

The inheritance of acquired adaptations, as we know, is very problematic. This kind of inheritance, however, is not needed, if, with Pauly, we take adaptive characters as contingent mutations, stored and transmitted to the next generation like any other kind of mutation. For mutations, we know, are inheritable.

So far there would be no difficulty, with the exception perhaps that it is rather a strange idea to conceive adaptive characters as mutations.

And yet Lamarckism must break down, and this for the very same reasons which have made Darwinism impossible.

As it is important to understand well the real logical nature of our objections to both of the great transformistic theories, we think it well to interrupt our argument for a moment, in order to consider a certain point which, though very important in itself, seems of only secondary importance to us in our present discussion. Dogmatic Darwinism—I do not say the doctrine of Charles Darwin—is materialistic at bottom, and indeed has been used by many to complete their materialistic view of the universe on its organic side. The word "materialism" must not necessarily be taken here in its metaphysical sense, though most materialists are dogmatic metaphysicians. It also *can* be understood as forming part of a phenomenological point of view. Materialism as a doctrine of science means simply this : that whether "nature" be reality or phenomenon, in any case there is but one ultimate principle at its base, a principle relating to the movements of particles of matter. It is this point of view which dogmatic Darwinism strengthens : on the theory of natural selection and mutations, due to chance, organisms are merely arrangements of particles of matter, nothing else ; and moreover, their kinds of arrangement are understood, at least in principle. Lamarckism, on the other hand, is not materialistic, but most markedly vitalistic—psychistic even.

Now, it is very important, I think, to notice that this difference between the two theories is unable to disguise one main point which is common to both : and it is to this point, and to this point only, that our chief objections against both these theories converge at present.

The *contingency* of the typical organic form is maintained by Darwinism as well as by Lamarckism : both theories, therefore, break down for almost the same reasons. Darwinism dealt with small mutations occurring at random ; the organic form was the result of a fixation of only one kind of such mutations, all others being extinguished by selection. In other terms, the specific organised form, as understood by Darwinism, was a unit only to the extent that all its properties related to one and the same body, but for the rest it was a mere aggregation or summation.

To this sort of contingency, as maintained by Darwinians, criticism has objected, as we know, that it is quite an impossible basis of a theory of descent, since it would explain neither the first origin of an organ, nor any sort of harmony among parts or among whole individuals, nor any sort of restitution processes.

Now, Lamarckism of the dogmatic kind, as will easily be seen, only differs from Darwinism in this respect, that what according to the latter happens to the organism *passively* by means of selection, is according to the former performed *actively* by the organism, by means of a " judgment "—by the retention and handing down of chance variations. But the specificity of the form as a whole is *contingent* also according to Lamarckism. And, indeed, criticism must reject this contingency of being, in exactly the same way as it rejected the contingency of form maintained by Darwinians.

As far as the inheritance of truly adaptive characters comes into account—that is, the inheritance of characters which are due to the active faculty of adaptation possessed by the organism, bearing a vitalistic aspect throughout—hardly anything could be said against Lamarckism, except that inheritance of acquired characters is an hypothesis of small and doubtful value at present. But, that *specific organisation proper* is due to *contingent* variations, which accidentally have been found to satisfy some needs of the individual and therefore have been maintained and handed down, this reasoning is quite an impossibility, of exactly the same kind as the argument of Darwinism.

The process of restitution, perfect the very first time it occurs, if it occurs at all, is again the classical instance against this new sort of contingency, which is assumed to be the basis of transformism. Here we see with our eyes that the organism can do more than simply perpetuate mutations that have occurred at random and bear in themselves no relation whatever to any sort of unit or totality. There *exists* a faculty of a certain higher degree in the organism, and this faculty cannot possibly have originated by the process which Lamarckians assume. But if their principle fails in one instance, it fails as a *general* theory altogether. And now, on the other hand, as we actually see the individual organism endowed with a morphogenetic power, inexplicable by Lamarckism, but far exceeding the organogenetic faculty assumed by that theory, would it not be most reasonable to conclude from such facts, that there exists a certain organising power at the root of the transformism of species also, a power which we do not understand, which we see only partially manifested in the work of restitutions, but which certainly is not even touched by any of the Lamarckian arguments? There does indeed exist what Gustav Wolff has called primary purposefulness (" primäre Zweckmässigkeit "), at least in restitutions, and this is equally unexplainable by Darwinism and by the dogmatism of the Lamarckians.

The whole anti-Darwinistic criticism, therefore, of Gustav Wolff for instance, may also be applied to Lamarckism, with only a few changes of words. How could the origin of so complete an organ as the eye of vertebrates be due to contingent variations? How could that account for the harmony of the different kinds of cells in this very complicated organ with each other and with parts of the brain? And how is it to be understood, on the assumption of contingency, that there are two eyes of almost equal perfection, and that there are two feet, two ears? Islands and mountains do not show such symmetry in *their* structures.

We shall not repeat our deduction of the origin of restitutions, of regeneration for instance, on the dogmatic Lamarckian theory. As we have said already, it would lead to absurdities as great as in the case of dogmatic Darwinism, and indeed we already have mentioned that Lamarckians would hardly even attempt to explain these phenomena. It follows that dogmatic Lamarckism fails as a general theory about form.[1]

There is, finally, one group of facts often brought forward against Lamarckism by Darwinian authors which may be called the logical *experimentum crucis* of this doctrine, an *experimentum* destined to prove fatal. You know that among the polymorphic groups of bees, termites, and ants there exists one type of individuals, or even several types, endowed with some very typical features of organisation, but at the same time absolutely excluded from reproduction: how could those morphological types have originated on the plan allowed by the Lamarckians? Of what use would "judgment" about means that are offered by chance, and happen to satisfy needs, be to individuals which die without offspring? Here Lamarckism becomes a simple absurdity, just as Darwinism resulted in absurdities elsewhere.

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[1] Compare also the excellent criticism of Lamarckism given by G. Wolff, *Die Begründung der Abstammungslehre,* München, 1907.

5. PHYLOGENETIC PROBLEMS

THE two great phylogenetic theories having failed, the question may arise whether the whole theory of descent is not simply a great illusion. But that is very far from being true. We are merely obliged to search for other hypothetical phylogenetic principles.

Lamarck himself, as we have mentioned already, was not blind to the fact that a sort of organisatory law must be at the base of all transformism, and it is well known that hypothetical statements about an original law of phylogeny have been attempted by Nägeli, Kölliker, Wigand, Eimer, and many others. But a full discussion of all these "laws" would hardly help us much in our theoretical endeavour, as all of them, it must be confessed, do little more than state the mere fact that some unknown principle of organisation must have been at work in phylogeny, if we are to accept the theory of descent at all.

We shall ourselves, therefore, attempt nothing more than to establish the chief *phylogenetic problems*.

And in this respect the first question is, no doubt, whether or not organic life in its totality may be regarded as *one great whole* of super-personal character.

And there are four *indexes* of wholeness in organic life, so it seems to me :

First, the fact of propagation, *i.e.* the *active* formation of new starting-points of individual morphogenesis on the part of all organisms.

Secondly : the existence of the organic *system*, *i.e.* the fact that the totality of living forms is not chaotic.

Thirdly : the existence of so-called *analogies*, strongly emphasised by Bergson, *i.e.* of very similar organs in forms which have no systematic relations. Think of the eyes of vertebrates and cuttle-fishes.

Fourthly: all *mutual* adaptedness, as among plants and insects, among gall-forming insects and their hosts.

The second great question is, whether phylogeny is a real *evolution*, and not a mere contingent *cumulation* as the so-called geological "evolution" of the earth certainly is. These concepts will be fully explained in the philosophical part, and we only note in this place that the embryological process is the very prototype of what we mean by "evolution."

The answer may be in the affirmative here also, first, because the contingency theories of Darwin and Lamarck have failed; this, of course, is a negative argument. And, secondly, because a good many palaeontological lines of forms show us something like a specific direction.

But even if, in this way, the process of phylogeny may appear as one great super-embryology, the differences between phylogeny and embryology must not be overlooked.

Embryology ends in the formation of *one thing*. The phylogenetic process manifests itself in *many things*. And the spatial and temporal relations among them, the *hic et nunc* of the individuals, to use the scholastic phrase, is contingent. Only the quality, the *essentia*, is important.

And, further: embryology occurs in *many cases*, whilst there is only *one* phylogeny (of which we ourselves are a part!). This, in fact, is the ultimate reason of our ignorance in phylogenetic questions. We cannot make experiments with "the" phylogeny, and therefore we know nothing of its law. We do not even know what the "end" of phylogeny is, and whether the end has already been reached or not. Simply to say that man is the end, would be very egotistic. There are probably many "ends".

Are the individuals *organs* of a super-person, comparable to the organs of an individual? Then they should accomplish a "function" with regard to that super-person. What function? We are ignorant.

But let us stop here, though the list might easily be continued; and let us, at the end of all, only state two more problems, in the form of questions:

What does it mean to say that a certain species has *died out*, as, *e.g.*, many great reptilia have? Does it mean that they really have died without offspring? Or that they have been transformed into a higher type? Steinmann and Dacqué have raised this question.

And is the polyphyletic or the monophyletic theory true? If the first were true, then the "amoebae," as we may call them, of primordial ages would not all have been real "amoebae"; but some of them would have been *potential* vertebrates, others *potential* arthropods and so on.

What, finally, about the *coexistence* of very highly developed *and* of very primitive creatures in our present days? Why have the latter remained "primitive"?

Again—the list of questions is far from being complete.

But there are no answers.[1]

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[1] We strongly recommend the study of two valuable books: J. A. Thomson, *The System of Animate Nature*, and J. C. Smuts, *Holism*. Lloyd Morgan's *Emergent Evolution* is also very suggestive. Comp. also the discussion on "Emergent Evolution" in *Proc. of Sixth Intern. Congress of Philosophy*, at Cambridge, Mass., 1926 (published in 1927).

PART III

ORGANIC MOVEMENTS

Introductory Remarks

Our study of morphogenesis has led us to a very important result. We have become convinced of the autonomy of life, as far as the origin of the individual living form is concerned. The short surveys that we devoted to the physiology of metabolism and to biological problems of the systematic and historical kind have not proved so successful. Physiology afforded us but few indicia of a future vitalism, and in the large field of phylogeny we found that there was very little known at all.

We now begin the analysis of the physiology of *organic movement*. And this will be as instructive as the study of morphogenesis has been; it will bring us into close contact with philosophical questions again.

The physiology of organic movement may raise the following questions, and, indeed, every text-book of physiology shows us that it actually has raised all of them. All movements, in some way, are reactions to external stimuli, *i.e.* are changes of the organic body in question with regard to its external surroundings. In other words, there is a line of processes, the first of which leads from without to within, whilst the last one leads from within to without; and besides these there are intermediate processes. We now may ask: What happens in the organism when it receives the external stimuli, what is the final effect of these stimuli, and what is there between the stimulus and the final effect?

The physiology of the so-called sense organs would give us the answer to our first question; it would teach us to what sorts of stimuli the organisms are responsive and by what means of their organisation and function they are so. The physiology of locomotory organs takes account of the question about the final acts in the process of movement: the contraction of the muscle is studied, but so is also the ciliary movement in infusoria, or the strange process of secretion and absorption of gases by which the movements of Siphonophora or of Radiolaria are carried out. And all intermediate processes concerned in organic movements would come under the physiology of the nerves and nerve-centres.

Now we should hardly gain very much for our philosophical purposes, if in our analysis of movement we were to follow the lines of ordinary physiology, which we have shortly sketched here. Moreover, there is wanting something very important in our sketch, and when looking back to it we may be reminded of the words of Goethe: " Dann hat er die Teile in seiner Hand, fehlt leider nur das geistige Band." Ordinary physiology indeed does not offer us much more than " die Teile ". But *is* there anything besides them; is a specific motor act of an organism as such anything in itself, is it not merely a sum or aggregate? It seems to me that this is the central *problem* of motor physiology; in other words, it seems to me that the question about the " wholeness " of the act of moving must come up at the beginning of the analysis. It certainly is impossible to neglect this question from the very beginning.

We therefore shall not follow the lines of ordinary physiology in our analytical studies, but shall turn the questions into a somewhat different shape. And, indeed, we know already from our previous researches *how* we may turn them in order to be successful: let the concept of *regulation* again be made the centre of our discussion, though in a slightly different and more complicated sense than when we were speaking of the physiology of morphogenesis and metabolism. There is indeed no properly " normal " state of organisation or function that could be said to be "restored" or "regulated" by organic movements. But, in spite of that, there is something in these movements that bears the character of a *correspondence* to a change or variation of the medium or the organism, just as in the case of regulation proper.

An actual instance will give you perhaps a better idea of what I am thinking than mere abstraction can do. Take a dog and ask what characters resembling regulations, if not regulations themselves, may occur in his movements. The dog is running towards a certain place along the direct line that leads to it, a carriage is crossing this line just when the dog has to pass: the dog will run a little more quickly and will make a curve in order to avoid the carriage. Another dog has undergone an operation involving the loss of a part of one hemisphere of the brain: at first his movements are very defective, but after a certain time, as the experiments of Goltz and others have shown, they become much less so than they were immediately after the operation. And a third dog is injured in one of his legs so that he is forced to run on three legs only: yet he manages to reach the place he wants to get to, by using his three legs in a manner somewhat different from the normal.

Here we have instances of all possible kinds of regulation, or, if you prefer to say so, of the correspondence between the conditions and the effects concerned, which may occur in the field of motor physiology, no matter by what means or organs movement is carried out, be it by cilia, muscles, or threads of protoplasm. In the first instance the dog's goal was reached, in spite of a change in the outer conditions, by means of a change in certain single acts of movement: the dog ran round the carriage instead of following the straight line. In the second instance we do not know very much about the change of function that follows the change effected in the dog's brain, but we may assume hypothetically that other lines of nerves have been used for carrying out what there was to be done. In the third instance the change from without affected the organs which perform the movement itself, and this change was followed by a change in the use of these organs: for it is clear that the work done in walking by every single leg when there are four legs at the disposal of the organism does not remain the same when there are only three.

Reviewing our three instances, we may say that in the first case there was a variation in the totality of the external stimuli, followed by a corresponding variation in the effect, whilst such a corresponding variation followed a change of the intermediate organs in the second case, and a change in the general condition of the proper effectuating organs in the third. We observe, then, a co-ordination of our three instances to the three fundamental branches of ordinary motor physiology already mentioned. It is not this co-ordination, however, but the existence of something like *regulation* in organic movement that interests us chiefly, and here we have the starting-point of our future researches.

All changes, whether in the external conditions, or in the intermediate organs, or in the effectuating organs, may be described as changes of motor stimulation in general, and we may therefore say that *the relation between motor stimuli and movement as such* is in fact our general problem. Are there sums or aggregates on both sides or not? If not, what *is* there? These are the questions we have to answer.

1. Some Remarks on Lower Forms of Animal Movement

This book is not the right place for an enumeration of all the various motor performances that have been discovered and analysed during the last, very active, period of animal physiology.[1]

We will only select a few typical cases of what may be called the lower forms of animal movements, and immediately turn to the higher forms, *i.e.* those forms in which so-called instinct and so-called experience (" memory ") are implied.

J. Loeb has tried to reduce all movement to chains of reflexes and tropisms. But his views have been shown to be far too simple, and Loeb himself has already been forced to introduce all sorts of subsidiary hypotheses as soon as several motor stimuli are in question.

Jennings,[2] in a very valuable series of works, was able to prove that even in protozoa matters are very complicated, and that " tropism " is not more than a word for an effect that is reached in very complicated ways, at least in most cases. He introduced the concepts of a " movement at random " and of a " trial and error ". The first of these concepts was by no means destined to overthrow the concept of causality, but was only to express that the movements are so complicated and irregular that is was impossible to analyse them to the very utmost; whilst the phase " trial and error " had only been used analogically, leaving it an open question whether there was a real " trial " and a real " error " in the psychological sense.

In many of the trial and error movements memory was

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[1] In the first edition of this book a much more detailed account of organic movements is to be found.

[2] *Behaviour of the Lower Organisms*, 1906.

implied—perhaps in all of them. We intentionally leave out this problem at present and give one single instance of Jennings's important discoveries.

The "righting reactions" of the starfish are the case we select (*Univ. Californ. Publ. Zool.* 4, 1907, p. 53). The "righting reaction", *i.e.* the reaction which is performed when the starfish is turned upside-down, may show a great many very different types. In each case the *initial* movement of each single arm is determined *separately* by external stimuli or internal conditions, but as soon as the least result with regard to righting is reached a "*unified impulse*" appears; co-ordination sets in where inco-ordination had been, and by no means can every single motor act now be related to a single stimulus, as was the case at the very beginning of the process; on the contrary, "single" stimuli now cease to have any influence at all; we may say that the animal is not "distracted" by anything. The "unified impulse" may be based upon a great many different constellations of initial movement of the single arms. It is very important to notice well that the righting reactions are not referable to the "normal" position of the animal as such: this hypothesis is refuted by the fact that during the unified period of the reaction the single arms very often perform movements by which they come into "abnormal" positions themselves, or which are indifferent for their own righting: everything occurs in the service of the whole.

It is true, Jennings has shown that the starfish is capable of a good deal of what is popularly called "experience"; therefore the righting reaction and other movements of this animal do not exclusively belong to this chapter. But it seems to me that it was well worth devoting a few words to the discoveries of Jennings at *this* place, as the movements of the starfish have often been looked upon as enormously simple. In any case the reactions of the starfish are not "reflexes", but are in the highest degree what on a later occasion will be called "individualised movements".[1]

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[1] I am very glad to see that Jennings himself insists upon the *unity* of the phenomena observed. He even concedes that my entelechy would explain this unity, though he declines to see here a true "explanation". In this respect I hope that the discussions which are to follow will convince him.

In Vertebrates and Arthropods also almost all of the so-called "reflexes" are *not* reflexes in the old sense of the word, but are motor reactions determined by the stimulus and by all that has happened and that is happening in other parts of the moving body—nay, even by the contingency of the actual general arrangements of the motor organs at a given moment. Sherrington and Uexküll have worked out a complicated system of concepts and laws in order to cover this very important field scientifically.

The "centres", we are told, store and bind and stop stimulations, and set them free at the right time, and so on. But the word "centre" is only a name here for hypothetic anatomical places, where these processes are supposed to occur. Nothing whatever is explained by the use of this ambiguous word.

Let me give one more instance, discovered by Bethe[1] in Arthropods. As soon as he had removed one or other of the motor organs, *i.e.* the legs, of these animals, they at once adjusted themselves to the new conditions, using the legs which were left in a different way—nay, using certain organs, as *e.g.* the so-called mouth legs, which normally never serve for locomotion.

In all these cases we already find what later on we shall call the *Individuality of Correspondence between stimulus and reaction*.

But as this feature will come out very clearly when the higher forms of animal movement are analysed, we say nothing more about the lower forms and proceed to our fundamental investigations.

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[1] *Archiv. für Psychiatrie*, 76, sec. 81. See also Baldus, *Zeitschr. f. vergl. Physiol.* 6, 1927.

2. INSTINCT

IN the former chapters of this book we saw that form evidently depended on the arrangement of certain elements, and that all genesis of form could be reduced to the action of certain factors concerned in it ; but neither was form a mere sum of those elements nor was its origin the result of a mere sum of these factors. Nothing at all is proved about a complex phenomenon being a mere sum or not a mere sum by demonstrating the elements it consists of : this holds for form as well as for movements.

A very intimate analysis is always required in order to decide this question. Let us then try to decide it, and let us begin with the analysis of so-called *instincts*. For *instinct* is one of the higher classes of animal movements.

INSOLUBLE PROBLEMS

The problem of instinct used to be one of the chief points in the fight between Darwinians and Lamarckians. As we cannot accept either of these theories, it follows that we shall not study instinct from the usual points of view. It may suffice to state here that the specific instincts of the worker-bees, which are excluded from propagation, would never be open to any Lamarckian explanation, as Weismann has most clearly demonstrated ; and, on the other hand, every Darwinian explanation fails here for the same general reasons for which it fails in every explanation of combinations that are typical units.

But a second problem appears, round which discussion centres very often. We shall be forced to decline *a limine* this problem also, but a certain justification is required for declining it, and as this justification is to rest on an epistemological basis, which is of first-rate importance for all our studies of animal movements in this chapter and the next, a short excursion into philosophy is necessary.

Are instincts " conscious " or " unconscious " movements? This is the question that has very often been discussed. And yet this problem *cannot* be a problem of " science " proper.

As *naturalists* we study animal movements as movements of bodies in Nature, and we can do no more. But the terms " conscious " and " consciousness " do *not* belong to that part of the Given which we call Nature; they belong to the Ego, to " my " Ego, and to my Ego exclusively. It is not even possible to express with clearness what is meant by saying that there " *is* " consciousness in any material being in Nature. We may only use this word analogically.

Other physiologists also have denied the possibility of really " discovering " consciousness or unconsciousness in the motions of animals. But it almost always was in a practical sense that they spoke of such an impossibility. We understand it in an epistemological sense. There may be feelings quite unknown to us, such authors have said; therefore it would be better not to speak about feelings. But we say: the " being " of " feelings " in Nature is not a problem of natural science. For *natural science* relates to bodily movements and changes exclusively.

It is true: the concept of " being " may be enlarged by an advanced philosophical science; we ourselves have enlarged it, and shall do so further on by introducing potentialities and even entelechy as " being ". But even such factors, if conceived as *natural* agents or factors, would never be " consciousness ". The word " conscious " belongs to introspective psychology exclusively.

THE ACTUAL PROBLEM. DEFINITIONS

But what about instincts? How are we to formulate *our* legitimate and scientific problem? It seems to me that there can be but little doubt how we are to formulate it. Are those animal movements, commonly called instincts, such that they might be founded on a machine, a physico-chemical manifoldness in space, embracing only physico-chemical elemental factors, or are there some features in instincts which forbid us to assume the existence of such a machine even hypothetically?

Let us first try to give a purely verbal definition of the instinctive motions in question. It will prove to be rather difficult to find an under limit of instinct, though it is easy to find an upper one. All instincts are separated from the next higher group of motions, which we propose to call "actions" in the widest sense of the word, by being *complete* in their *specificity* from the *very first time* they occur. There may be some improvement in consequence of their being repeated, but this improvement never affects their specificity as such. Perhaps it will be more correct to say that we shall not apply the term "instinct" to any animal movement that shows an improvement with regard to its specificity.

Instincts are often said to be "purposeful" with regard to their performer. We prefer to say, at present, that they possess some regulative character; that they tend to "normality" with regard to the whole life of the organism which performs them. Here the limit between instincts and the lower classes of motions is not always very clearly marked: almost all typically combined motions are alike in possessing a regulative character. And it is impossible to draw a sharp boundary here, if one has renounced the question of "consciousness" as illegitimate. It is only the degree of combination that comes into account.

THE PROBLEM OF THE STIMULI OF INSTINCTS

J. Loeb has tried to show that all instincts are nothing but "chain-reflexes". If this theory were true, it would follow that it only can be the simple and elemental agents in Nature which can act as *stimuli* to instincts. The stimuli of instinctive movements might be light of different wave-lengths, or heat, or moisture, or chemical compounds, *but never specific typical bodies.*

It will soon appear how important this statement is. If only *simple* stimuli are concerned in instinctive life, the relation between the medium and the instinct may, in fact, easily be explained on the analogy of a machine, at least in principle. But what are we to say if typical complicated stimuli, if "*individualised*" stimuli, as we shall call them, also awaken instinctive movements?

Let us first try to show, by the aid of a simple instance, what is meant by our two contrasted classes of stimuli: Lloyd Morgan[1] performed a series of very fine experiments in order to show whether chickens, just hatched from the egg, react to the specific bodies forming their food or not. Putting them in front of a dish which contained peas and other small bodies of the most different kinds mixed together, he saw them pick up these little bodies most accurately. But they took *all* kinds of them, and experience alone taught them to discriminate between what was food and what was not. On the other hand, it had often been pointed out that young poultry had an instinctive fear of the hawk and the hawk's cry. Lloyd Morgan showed that young poultry are frightened by *any* large body in motion and by *any* very shrill sound. Thus these fine experiments teach us two things: they teach us what simple and what individualised stimuli are, and that, in this case, only simple stimuli are the external stimuli of instincts. Indeed, the few cases of instincts which have been the subject of experimental work hitherto have proved to be due to simple external stimuli exclusively. The instinctive antipathy between dog and cat is probably also the effect of chemical compounds, of a "smell", if we choose to speak a little less accurately, and not of an individualised stimulus, not of the cat or the dog as being "seen".

But the experiments about this important question are not at all numerous, and it can by no means be categorically asserted that instincts, in the true sense of the word, are

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[1] *Habit and Instinct*, London, 1896.

never called forth by a specific body which psychologically would be called a " seen " one,[1] or, speaking more generally, by a stimulus of the individualised type.

Now, it is very important to notice that, *if an actual case of a specific individualised stimulus of an instinct should become known, the limits of the possibility of a mechanical explanation would be exceeded.* They would be exceeded, and an autonomic or vitalistic factor would be at work, because it could by no means be understood how the specifically combined or "individualised" stimulus could be *received* by the organism in such a way as to become the cause of a specific and fixed series of motions in the organism. Supposing that any organism were specifically affected in its instinctive movements by the mere *sight* of any other typical organism, say of the same species, but of the other sex,[2] and that this affection were the same, whether the organism which forms the stimulus were seen from before or from behind, or from the side and at any angle whatever: what would follow from such a fact? A machine could only be fitted to receive the specific complicated stimulus in a few typical positions, but how could a machine be imaginable if an infinite variety of aspects had the same invariable instinctive effect?

We may stop our discussion at this point, as a very similar problem will meet us in our analysis of action, and will be fully discussed on that occasion. Moreover, the whole of our

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[1] Elise Hanel (*Zeitschr. f. allg. Physiol.* iv., 1904) has shown, following the line of certain experiments of Ch. Darwin, that the earthworm reacts specifically to the specific form of leaves or pieces of paper, always trying to draw them into its tube-like cave by their most pointed edge; the earthworm, in fact, can be stimulated by a typical sequence of different singularities, which are only relatively determined, and its reaction is perfect for the very first time, that is, instinctive. New researches are required to clear up the facts that come into account here.

Chickens are well known to peck their peas or corn with a right calculation concerning the dimension of depth the very first time they do peck. Speaking psychologically: the right idea of space is innate in them not only "*a priori*", in the sense of Kant, but strictly "before" all experience in the temporal sense of the word "before".

Are these facts of use in our present problem?

[2] As regards sexuality the existence of " individualised " stimuli of instincts seems indeed highly probable. Male moths deprived of their wings were found by Mayer-Soule (*Journ. Exp. Zool.* 3, 1906) not to be admitted to copulation by the females; but only if the females were not deprived of their sight!

present analysis rests on a *problematic* basis: for nothing is *known* at present with absolute certainty about individualised stimuli of instinctive motions. But it seems to me highly probable that future investigation will discover such cases, and the present discussion is written particularly in order to encourage research in this direction. Bees and ants especially, but vertebrates too, it seems to me, would have to be studied with respect to the question whether there are cases in which specific complicated bodies that are " seen " may be the stimuli of real instincts.

If we like to give up for a moment our strictly scientific language and allow ourselves the use of the common pseudo-psychological terminology, we may say that all cases in which individualised stimuli were at work would require the assumption of a something that would be nearly related to the " innate ideas " refuted by Locke in another sense. Physiologists of the old school of the German " Natur-philosophie " often have spoken of a sort of dreaming as being the foundation of instinctive life. It would be this sort of dreaming that we should meet here, and the only difference between the old investigators and ourselves would be one of terminology: we should not speak of dreaming or of innate ideas, but, as naturalists, we should say that an autonomic, an entelechian natural factor was found to be at work in instinctive life, as far as the reception of stimuli is concerned.

THE PROBLEM OF THE REGULABILITY OF INSTINCTS

Our mention of the old physiologists may serve us as a stepping-stone to the analysis of the second chief problem which instincts offer to theoretical biology. Here also the main point must remain problematic, as facts are too scanty at present for a definite statement. But here also the analysis of possibilities may serve to give an impulse to future research.

The old physiologists, such as Treviranus and Johannes Mueller, often compared morphogenesis with instinctive life, and it is to Schopenhauer that the most thorough comparison between the phenomena of instinctive movements and embryological processes is due. Instincts are regarded by this school as being in some way the *continuation of morphogenesis*, as growing upon the same ground, as governed by the same reason, viz. the vital principle.

As we have said already, we do not know at present whether such a view is fully legitimate or not; further investigation will determine that. But we can make use of the comparison between morphogenesis and instinct to raise another question, besides the problem of the nature of the instinctive stimuli, the answer to which may one day enable us either to admit the autonomic nature of instincts or to deny it.

Certainly instincts are comparable with morphogenetic phenomena for the simple and descriptive reason that they occur completely and purposefully the very first time they go on in the individual. Might not there be another point of similarity? Morphogenetic processes, as we know, are liable to be regulated on the largest scale: disturbances of the organisation or of the morphogenetic process itself are followed by atypical processes leading again to the typical result. Are there any true *regulations* known among instincts?

Regulations in instincts, of course, would hardly be accessible to observation if there were not any visible effects of the instinctive activity. But that happens in all cases of so-called technical or artistic instincts, as known among birds, among spiders, and among bees, ants, and some other insects. The instinctive activity of these animals ends in a certain specific state of the medium. Let us disturb the state, say of a nest or a bees' hive, let us change the material offered to a bird for its nest, and let us see what will happen.

Unfortunately, very few experiments have been carried out with the special purpose of determining the kind and degree of regulability of instinctive movements as such. Such knowledge as we have has been gained almost entirely in the field of so-called natural history, and without a full analytical discussion.

It is important to notice once more, at the very beginning, that we are not dealing here with the possibility of a modification of instinctive life by so-called "experience". Our question is this: Are instinctive acts liable to regulative modifications in the same manner, complete and purposeful from the beginning, as are embryological processes?

Bees are known to repair the cells of their honeycomb after disturbances; they, moreover, may change the style of building them, to suit the requirements of space, and they also may build their house in an abnormal direction with respect to gravity, should circumstances require it: instead of building from above to below, they may also build from below to above, and also sideways. The silkworm is said not to form its web of silk if it is cultivated in a box containing tulle, and some species of bees which normally construct tunnels do not do so if they find one ready-made in the ground; they then only perform their second instinctive act—separating the tunnel into single cells.

In all of these cases, except the one relating to gravity, the state of affairs seems to be the following: What has been changed from without is either the perfect result of the full sequence of instinctive acts, or it is what might be called an embryological state somewhere in this sequence, that is, some state in the sequence that leads to the perfect result. And the artificial change of the second class may again be of two kinds: either something may be taken away from what the animal had accomplished already, or something may be added to the result of its activity—something, of course, that would occur in the process of normal construction. In all these cases the animal will adjust its instinctive movements to the *actual* state of matters, no matter whether it has to do more or less than normally—more, if parts of its own construction are taken away; less, if parts are added to it artificially.

There can be no doubt that the term "regulation" is justified in these cases. What then does this mean, and what can it teach us as to our question about the autonomic character of instincts?

Of course, the *actual* state of affairs, artificially modified from what had been performed by the organism, must be *transmitted* in some way to the latter, in order that its future behaviour may correspond to this actual state. Now, it is from the possible or probable nature of this transmission that an analytical discussion of our problem must start. The instinctive motions concerned in all sorts of constructions form a consecutive chain of single performances, which normally seem to be called forth one by the other, but which, as experiments show, *may* also be called forth independently. So we again meet the problematic question as to the " calling forth " of instinctive motions, as to the instinctive stimulus. Normally the whole sequence of a constructive instinct *may* go on as follows: The elemental act *a* results in the state of construction *A* ; the next state of construction is *B* ; *B* is due to an instinctive process *b* ; *b may* be set going only because *a* is finished, but it also *may* be called forth by the existence of *A*, which, of course, is something very different. The mere fact of regulation, as we have described it, now seems to show that the second alternative meets the case: that it is the existence of *A*, the constructive result of the first elemental instinctive act, that is the stimulus of *b*. For, in the case of regulation, *b* goes on without *a* or after *b* itself has already once taken place: *without a*, if the result of the instinctive act was changed by the adding, and *after* a previous *b*, if it was changed by the removing of anything. It is here that we meet the problem of how the state of *A as such* may be transmitted to the organism in order to determine what is to go on, and it is clear that this is precisely the problem of the *nature of the stimulus* calling forth *b*, regarded as an independent instinctive phase. *Is this stimulus simple or is it individualised,* that is to say, specifically combined of elements ?

It is not very pleasant to be again obliged to leave our question unsolved, but nothing has been done in an exact manner towards answering it. It may seem, of course, as if only typically combined or " individualised " stimuli could suffice to explain the modification of the instinctive acts in exact correspondence with what is required ; but this is only probable, nothing more.

I once more feel obliged to say that the evidence of the mere *fact* of regulation among instincts is very scanty at present.

Indeed, even what we have mentioned about observations of this kind is hardly as well established as it ought to be, and I freely confess that I have treated so-called "facts" here as if they were a little better established than they probably are, simply in order to get a basis for our analytical discussion. It remains, however, a mere discussion of possibilities. For not one of the observations which we have mentioned, regarding the regulability of instincts, has been made with the special purpose of studying that particular point.

Let us shortly mention the only experimental case in which our problem has been studied with full and careful attention. The entomologist Ch. F. Schroeder,[1] in studying the behaviour of certain caterpillars by the aid of experiments, has found that these animals are able to adapt their instinctive acts of spinning most accurately to the real state of the product formed so far; he not only saw them repairing their weaving, after it had been disturbed intentionally, but his caterpillars also formed typical tissues by using leaves of abnormal forms intentionally prepared, or by using leaves of plants that are not normally employed.

It is to be hoped that future research will follow in the track of the one last mentioned, that is to say, that entomologists will observe the behaviour of their insects with the full appreciation of the bearing of the study upon the problems of theoretical biology, and not only in the interests of natural science proper.[2]

Here, then, we may close our discussion of instinctive movements. It has yielded some indications of vital autonomy in the field of instinctive life, but no real, absolute proofs.

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[1] *Verhandl. D. Zool. Ges.*, 1903, p. 158.

[2] Once more I call attention to the "turning over" of animals when put into an abnormal position, though we are not accustomed to speak of instincts proper in these cases (see page 190). No doubt, the process of turning in its single phases is exclusively made up of "regulations". Are they of such a type that the "whole" of the actual abnormal state enters in some way, or are they mere sums of single acts, purposeful only on account of their performer's general organisation? Certain experiments of Preyer's seem to me to deserve more attention with regard to our question than they have generally received (*Mitt. Zool. Station Neapel*, vii., 1886. See also Jennings, *Behaviour of the Lower Organisms*).

3. ACTION

a. PRELIMINARIES

THE way generally taken by science is from the simple to the complicated phenomena, and therefore when turning to the analysis of those organic movements which are called "actions", we might probably be expected to follow this ordinary and well-established route. But we shall not do so, and we have good reasons for so choosing our path. It might seem most natural, after having discussed the main points of the theory of instincts, to proceed to analyse first the most simple cases of what might for any reason whatever be called "action", and, after surveying the whole series of animal organisms, to end by analysing the action of man. But there is one special point which renders a totally different arrangement of materials far more suitable and convenient. On account of a very strange feature, which, in spite of its strangeness may be pronounced the most universally known in theoretical biology, we prefer to begin our analysis of action with those cases where action is of the most complicated nature, and only to add certain remarks about its simpler forms at the very end. *The reasoning and analysing naturalist is an acting organism himself*—that is the strange though universally known fact spoken of. One of our final chapters will try to deal with the most central problem, both of philosophy and of biology proper, that is established by this fact ; at present we make use of it in a purely practical manner. In observing the actions of animals and men, many more differences are revealed to us in the men than in the animals, because we *understand* the former and not the latter. Psychology thus, though not our aim, is becoming our means of investigation.

" Behaviourism "

By no means, of course, do we intend by our appeal to psychology to introduce that sort of pseudo-psychology which we excluded from natural science when we were studying instincts. All acting organisms, including acting men, are to us simply *natural bodies in motion* ; at least they are *immediately* presented to us as such, though analysis in its progress may introduce natural agents which would represent not motion only but also the possibility of movement. These agents or factors, however, would by no means be psychological in the introspective sense—the only sense which the word " psychological " may legitimately possess.

We only deal with such phenomena as occur on *bodies in nature,* called organisms, and it will be our purpose to discover the laws according to which the motions of these bodies occur. We may end in vitalism again in this chapter ; but certainly we shall avoid pseudo-psychology.

So far we agree with modern *behaviourism.* We, in fact, fully appreciate the work done by Watson and his followers, so long as it is a *method* of research. We reject, however, behaviourism, if it is to imply a mechanistic conception of life *a priori.*

General Definition of Action. Classes of Movements which are not Actions

A few remarks about the most general definition of action, in both a positive and a negative form, seem desirable by way of preliminary.

An " action " is every animal movement which depends for its specificity on the individual life-history of its performer, in such a manner that this specificity depends not only, as will be seen later on, on the specificity of the actual stimulus, but also on the specificity of all stimuli in the *past,* and on their effect. No animal movement is to be called an action in which this criterion is not present at least in a certain degree. In the language of subjective psychology this criterion is called " experience ". We shall presently introduce a more suitable name for it, but in this short survey the word " experience " may be used.

There is no experience, and therefore no " action ", when simply the final physiological elemental process in the motor organs, *i.e.* the process of contraction, goes on quicker the second or third than it did the first time : we speak of " functional adaptation " of the nervous system in this case. Nor is there " action " in the case of so-called muscular " fatigue ".

But both these phenomena, especially functional adaptation, that is, an improvement of functioning by functioning itself, may be combined with real acting, and, indeed, there is one group of facts in which this combination is very important. You all know the process which is commonly called the *mechanisation* of acting ; the piano-player offers a good instance of it, but anyone going down a staircase is also an example. Popular psychology says that here we see complicated motions, which, though under the control of consciousness when first learned, are freed from this control later on. Science has to say that one and the same action-effect, repeated very many times, may combine with functional adaptation of some unknown part of the nervous system in such a way as to acquire almost the character of a typical reflex. This process of what is called " *exercise* " is by no means identical with the process of acting as such, and we have devoted these few words to it in this place in order that we may exclude it from our studies later on.

Moreover, we are not entitled to speak of an " action ", if one and the same stimulus has different motor effects according to the variation of certain physiological conditions which are not concerned in the specificity of anything motorial. Such cases are well known among lower animals, as *e.g.* in the discoveries of Jennings we have already mentioned. In such cases there is nothing like an individual history of the performer, certainly nothing like history with regard to the particular stimulus then at work.

But then, historical elements of *this* sort are entirely absent in another group of phenomena, where at first glance it might possibly seem that they were present. Let us begin with an instance discovered by Jennings in studying the Protozoon *Stentor*. To one and the same mechanical stimulus *Stentor* first reacted by a simple turning aside, but this reaction did not bring it out of reach of the stimulus ; it then reversed the direction of its ciliary movement, and after that contracted itself into its tube, but without success ; the stimulus, a falling of powder, continued ; then, finally, the *Stentor* swam away. We here see three or more different reactions following each other in correspondence to one stimulus. We may say, perhaps, that the following reactions occurred *because* the first one was not successful, and certainly there is something of an individual historical element in this behaviour ; but, in spite of that, we should prefer not to speak of an action. It is *one series* of events that occurs here, not one reaction at one time and another reaction, modified by " experience ", at another ; there is " trial " perhaps, but no " experience ".[1]

But there is " experience ", and therefore action, though in its most primordial form, when *Stentor*, the experiment with the powder being repeated after a short time, reacts from the very beginning with its fourth kind of reaction instead of with the first one. This example, besides excluding a whole group of motor phenomena from our future discussion, may well serve at the same time to illustrate provisionally what really will be called " action " by ourselves.

The Distribution of Acting

True actions, though, as will be stated later on, of a less high degree of complication than actions in man, are most clearly exhibited in the following classes of the animal kingdom : in all, even in the lowest classes of vertebrates, in bees, ants, and some beetles, in crabs, cuttle-fishes, Actinia, and some Protozoa.

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[1] The same holds for the movements of Ophiurids, according to von Uexküll and Glaser (*Journ. Exp. Zool.* 4, 1907). There is a great variety of reactions, but no " experience ". Preyer was right in his description of facts, but not in his interpretation. But in Asterids there exists " experience ", besides a great variability of reacting (see the memoir of Jennings cited on page 189).

One point has always to be kept well in mind in all investigations about so-called animal "intelligence". All organisms, of course, can acquire "experience" only about what *is* "experienced" by them: in other terms, only about that which stimulates them to motor reactions. Now it is clear that it always must remain doubtful in lower organisms what sort of sense organs—to use the common expression at this stage of our argument—they possess; their "medium" will only be the sum of the factors to which they are accessible. How, for instance, could we expect individualised stimuli to act upon organisms possessing no organ like the eye or the ear? Perhaps it is for this one reason that so little is exactly known about real acting in Protozoa. There are many observations about them—those about their hunting, for instance—which seem to prove that a rather high degree of experience may exist in infusoria; but who can feel able to give any fairly correct answer about the stimuli—of a chemical nature perhaps—which are able to reach such minute organisms?

And on the other hand, there may be spheres of experience —in the higher classes of the Invertebrates, for instance— which are almost unintelligible to ourselves in a subjective way. Bees seem to remember the absolute amount of their change of place in space. Even if they have been transported passively, and not on a direct line, they always reach their hive again. And similar facts occur in birds.

The very important facts recently discovered by Pawlow and his followers also belong here, as it seems to me, though they do so in a different way. "Association" may relate not only to phenomena of the sensorial or motor class, generally spoken of as "conscious" ones, but to processes of secretion also. Secretion, on the part of the salivary glands, for instance, may be called forth by any stimulus that has ever been contemporary with the original stimulus of the *purely physiological* process of secretion in any way.

A few words on the distribution of experience, not in the animal kingdom, but among the *parts* of one organism, may close these preliminaries. A little more on the same subject is to follow in another connection. It has been shown by the experiments of Goltz, Schrader, and others that it is not only the so-called hemispheres of the brain of vertebrates that are related to experience. Frogs and pigeons at least, and probably dogs also, may acquire new experience, or may at least make use of older experience, even after the total extirpation of those hemispheres. No doubt there is less experience shown after the extirpation than before it ; but experience is by no means lost. Thus we see that other parts of the central nervous system besides the hemispheres may also be in relation to experience. This holds for all so-called lower brain centres, and perhaps for the spinal cord also.

What the real meaning of these facts is, must also be reserved for a future discussion. And now we are prepared to enter minutely into an analysis of the process of acting itself. We take *man* as our example, but *behaviouristically* : *i.e.* we look upon an " acting man " as upon a *material system in motion*, excluding all psychology most decidedly.

β. THE FIRST CRITERION OF ACTING. THE HISTORICAL BASIS OF REACTING

The phonograph is a well-known machine the reactions of which depend on its individual history in their utmost specificity : the phonograph may give forth what it has received in the past. Now, we have said already provisionally that the individual history is one of the most important features concerned in the characteristics of acting. Is, for this reason, acting in any way comparable to the reactions of a machine such as the phonograph ? With this question we may fitly begin our analysis of the process of " action ".

If we at first consider the acting organism as a whole, without laying any special stress on what is called its nervous system or its brain, we may say that the specificity of every one of its actions depends on the specificity of all stimuli relating to sensation and movement which have encountered it in the past, and on all the specific effects of those stimuli. This character we have already tried to describe briefly by saying that acting depends on the " individual history " of the organism, and we shall now describe it technically by saying that an "*historical basis of reacting*" is one of the chief components of which the specificity of every action is a function (in psychological terms we are accustomed to speak of "memory").

Without any difficulty you will become convinced, I suppose, that this "historical basis of reacting" of men, being one of the foundations of action, is something different from the "history" of a phonograph. Therefore the *technical* term "historical basis of reacting" requires a precise *technical* definition: it is to mean more than the mere verbal expression states. The phonograph, though determined in the specificity of its reactions by the specificity of its history, is not able to change in any way the specificity of what it has received. It might, rather vaguely, be compared to a schoolboy reciting a poem, or to an actor on the stage. The organism has the faculty of profiting from the specific combinations received in order to form other combined specificities. It changes, so we may say, the specificities it has encountered into other specificities, which it forms on the foundation of their elements. Here we find what we are in search of: the historical basis of acting is "historical" only in a most general, not in a specific meaning; specificities, it is true, have made up the "history" that is commonly called "experience", but the basis of reacting, as a basis of action created historically, is not in any way specified in detail, but consists of the *elements* of the experienced specificities. The second half of our analysis of action will have to show us how new combined specificities may be formed on the foundation of the elements of the historically received ones.

But a second fundamental difference between the "historical basis of reacting" of a phonograph and of an organism may at once be discovered as easily as the first difference was. The phonograph receives vibrations of the air and gives off vibrations of the air; in other terms, previous stimulus and later reaction are of the *same* nature. The organism receives impressions on its sensory organs whilst acquiring "experience", and gives off movements. That is to say, the events which have created the organism's history, and the events which occur on the basis of this history, belong to two absolutely *different* classes of phenomena.

We now must insist more fully on the analysis of our " historical basis ", and shall in the first place justify a certain phrase that we have used in our definition. We have said that actions not only depend on all the stimuli received in the past but also on the *effects* of those stimuli. The word " stimuli " is to include here everything that has affected the sense organs of the acting subject in any form whatever ; the word " effects " is to embrace the final consequences of any previous moving that had been caused by any stimulus. The second half of this explanation now may seem to want some further interpretation, and this interpretation may advantageously be founded upon a short discussion of a fundamental problem, very often discussed by philosophical psychologists, the problem of the so-called *origin of the act of volition* in the child. It will hardly be avoidable to use a few psychological expressions in the following analysis, but we repeat that we use them only for the sake of brevity, and it would be better could every one of them possess its proper phenomenological correlate ; for it is with moving bodies in nature that we are dealing.

The Origin of the Acts of Volition

Movements without any specific regularity, called forth by unknown general causes from without and within, are considered to be the real starting-point of acting in the child ; a supposition that agrees very well with the discoveries of Jennings. The child notes the effect of every one of those movements and its share in bringing pleasure or pain—these words taken in their broadest meaning—and afterwards it " desires " and carries out certain possible effects of its movements, and others it does not " desire " and carry out. The possible effects, of course, as the age of the child advances, may relate to any change of the medium in the widest sense, as far as the medium may be the subject of experience. It belongs to Psychology to make out what elemental psychical functions are concerned in this "desiring" and "liking": of course the rudiments of judging are concerned in it, and a fuller analysis would probably reveal that volition, reasoning, and liking are at work here as a whole, inseparable in fact and separated only by analytical science.

In this way, then, the *contents* of "willing" are specified by experience, as time proceeds. Willing itself, of course, is a primordial fact.

But let us turn back to our proper problem, which is a problem not of psychology but of natural science. The discussion of the genesis of the volitional act has shown us most clearly that the *effects* of motor stimuli *may* form part of the historical basis of reacting. It was the *effects* of random movements that became liked by the child, and this liking of the effects enters into the historical basis of his future actions, just as do all sorts of stimulations themselves. In a certain sense we may say that the effects of motor stimuli become new stimuli on their own account, at least as far as they are a something presented to the organism and "experienced" by it, and in this way the whole analysis of the "historical basis" might seem to become more simple and uniform. But nevertheless, it is worth while to maintain the distinction between two different types of historical bases of acting, and to study them as they actually occur in special cases.

The Different Types of Historical Bases

Acting based upon the experienced final *effects* of previous motor stimuli always starts from "chance", and it is in so-called "trying" that it gains its highest importance. Imagine you have got a new portmanteau without knowing how to open it. You first try all sorts of manipulations familiar to you from your experience about the effects of moving your hands with regard to opening other trunks, but no success attends this "trying". At last by chance you press a certain plain knob, and the opening of the box is the "effect". The second time you will press the knob at once; there is no "trying" any more, but the new experience assists you in "trials" in the future. The whole process has a great similarity to what we know already from the analysis of the first actions in the child, though, of course, differences must not be overlooked.

Experience based upon *stimuli* alone is no less familiar to all of you than our last instance. The learning of languages and all cases of imitation are typical instances of this class. The general scheme of this type of "historical basis of reacting" is this: you learn by experience that a certain simple secondary phenomenon always accompanies the primary one which is the proper motor stimulus of your acting, and you then, in response to that secondary or indicating phenomenon, perform the same action that at first only followed the primary stimulus. In this way you learn to identify different tramway lines by the coloured boards or coloured lights they bear.

This is what the psychologist calls *association.*

A good popular illustration of the difference between an "historical basis" concerned with previous stimuli and effects and one concerned with stimuli alone is given by the two following instances. If in a strange town you want to reach a certain place, of which you only know the general position, you will probably go wrong very often the first time, but will "learn" to go right by the "effects" of your walking. If, however, you are accompanied the first time by a friend who knows the town, and give good heed to what you "see" on your way, you may find the place the next time without any "error".

One of the most important features, we said, of the historical basis of reacting is that its specificities may be resolved into their elements. We must not, however, forget that, in spite of this possibility of being resolved, a *certain* conservation of the combination of the specificities received is the *conditio sine qua non* in the process of acting: otherwise there would be no "association". Psychology, as you know, speaks of two kinds of "association", one dependent on contiguity, the other on similarity or contrast. Now, all association by contiguity is to be regarded as in some sort the conservation of at least a part of the original specificity of combination in the stimuli forming the historical basis of acting. The mere fact on the other hand that, psychologically, association alone is quite unable to explain the totality of psychical life, shows that conservation of a portion of the specificities originally present cannot play more than a subordinate part in acting: conservation does indeed play a part, but there would be none but very primitive forms of acting, if conservation were not accompanied by separation and new combination of what had been received originally, and if there were no such thing as the remarkable phenomenon of association based upon contrast and similarity. But these processes, and in particular the process of resolving given complex peculiarities into other peculiarities, can hardly be properly understood without a discussion of the second fundamental characteristic of action.

In proceeding to discuss this second characteristic, we do not bid farewell to the first. On the contrary, as the first proved to be incomplete in itself without the second, so the second will prove to be inseparable from the first.

The Historical Basis a Proof of Vitalism

But a mechanistic interpretation of action may already be refuted on the foundation of the first characteristic taken in itself.

The first type of the historical basis, *i.e.* "learning" by trial, means ultimately this:

A material system M is affected by a stimulus S, and reacts by a series of reactions R_1, R_2, R_3 . . . Rn until a specific state of material constellation is reacted. If M is affected by S a *second* time, it reacts at once with the reaction Rn.

The second type of the historical basis, *i.e.* "learning" by association, means what follows:

A material system M is affected by a stimulus S, and reacts in a particular way. Together with S there occurred another event in nature, T, which also affected the system M, but without provoking any reaction. Later on T, when affecting the system alone, will provoke the same reaction, which originally had been the effect of S.

There is *nothing* like this in the inorganic world. All comparisons of these facts with the elastic after-effect, magnetic hysteresis, etc., are a mere playing with words; for only quantitative changes come into account here. The phenomena just named might be an analogy to fatigue. But fatigue is not—" memory ".

So vitalism has been established on the foundation of the first characteristics of action exclusively.[1] And we have not even spoken of what Bergson calls *pure* memory (*souvenir pur*), *i.e.* of our faculty of remembering past events with their specific dates. This topic belongs to psychophysics proper.

And now we proceed to an analysis of the second characteristics.

γ. THE SECOND CRITERION OF ACTING. " INDIVIDUALITY OF CORRESPONDENCE "

We have already explained, whilst dealing with the theory of instincts, what is meant by a " simple " and an " individualised " stimulus. A stimulus is individualised if it consists of a specific combination, specifically arranged, of single elements; the arrangement may be one of space as well as one of time.

Now, the second of the two main characteristics of action, considered as a problem of natural science, is *that action always is a reaction corresponding to an individualised stimulus.* I need only remind you that the sight of a specific person or a specific house may influence your behaviour in a specific manner, and that a melody or a specific phrase you hear may do the same, in order to give you a concrete instance of what our analysis expresses more abstractly.

And then the individualised stimulus of actions has an *effect that is individualised also.* There are many cases in the inorganic world where the same thing happens, and yet in spite of that there is a great difference at the first glance

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[1] A full discussion is given in *Sitzungsberichte Akad. Heidelberg.*, 1927–28, No. 1.

between the Inorganic and the Organic in this field. A seal with specific initials may also be called an individualised stimulus, or at least cause, and if it is pressed into hot sealing-wax the effect will be individualised also: but the two individualisations are of exactly the same kind in this case. That is not true in the individualisations of cause and effect appearing in action: the one is individualised in a specific manner, but the other is individualised quite differently.

In more technical language we may state the result of our provisional analysis as follows: Besides the principle of the " historical basis of reacting ", there is another fundamental principle concerned in actions, when considered as bodily processes in nature; this second fundamental principle may appropriately be called the principle of " *individuality of correspondence* " between stimulus and effect.

We now in the first place have to study more fully in what the individuality of correspondence in acting really consists.

As every problem of a complicated nature is easier understood when at first demonstrated in a concrete instance, I prefer to begin our discussion with a concrete fact.

We all experience a hundred times a day what a conversation between two human beings is. Let us try to analyse what a conversation would mean from the behaviouristic point of view taken by natural science. Two friends meet in the street, and one of them, A, says to the other, B, " My brother is seriously ill ". There will be a very specific effect caused in B by the stimulus that went out from A. Let us imagine that the brother is in America: B then would talk about the difficulty of his coming home, or of visiting him, and very many other things, all of them of a very definite and specific character. But what would have happened if instead of the word " brother " the word " mother " had been used? Certainly something very different, and certainly something very specific also. The mother may be living in the town where the friends meet: then B might ask whether he could do anything for her, he might remark that the illness must be attended with some danger at her age, and he would say very many other things, all very specific.

Taken as stimuli from the point of view of natural science, *i.e.* as a sequence of air waves or as a mechanical "resultant", the phrases "my brother is seriously ill" and "my mother is seriously ill" differ only in a point of utmost unimportance: *br* is pronounced in one case where *m* is pronounced in the other. In spite of this *minute* difference, the effects of the stimuli are *totally* different.

And now let us assume that the two friends are of different nationalities, the one being German, the other French, but that the town where they are staying and where they meet is an English town, and that both friends talk English, French, and German equally well, and that they are accustomed to use all three in their conversations. Then A, instead of saying "My brother is seriously ill", might also have said "Mon frère est sévèrement malade", or "Mein Bruder ist ernstlich erkrankt". What would have been the effect of these variations, which from the physical point of view are enormous? Certainly the same as that of the phrase spoken in English.[1]

This example shows us, that in acting the effect may remain unchanged in spite of a most fundamental change in the stimulus: this second result of our analysis is the exact counterpart to the first.

In acting, then, there may be no change in the specificity of the reaction when the stimulus is altered fundamentally, and again, there may be the most fundamental difference in the reaction when there is almost no change in the stimulus. This is a very strange result to have reached by our analysis.

Let us now try to state our result in more abstract form. This will bring us face to face with our central problem: Is acting explainable on the hypothesis of a specific physico-chemical arrangement, say a machine, or is it not?

The individualised stimulus in acting, represented in our instance by the phrase "my brother is seriously ill", may be

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[1] It has been said that in these instances it is not the phrases "my brother is ill", etc., that constitute the real stimulus of action, but the general "mental" condition of the person addressed. But, beyond doubt, these phrases *are* real stimuli in the true physical meaning of the word, and, moreover, the general "mental" condition, *i.e.* what we call the "historical basis" in all its essentials, could never account for these particular and specific reactions at this particular place and time.

expressed analytically as being a specific arrangement of the specific elements $a, b, c, d, e, f, g, h, i$, and so on. The specific effect which the stimulus has upon the acting person, say the friend B in our example, may be figured as being a typical combination of $a_1, b_1, c_1, d_1, e_1, f_1, g_1, h_1, i_1$, and so on. The question then is: How is the series a, b, c, etc., connected with the series a_1, b_1, c_1, etc., and is there any way of explaining a_1, b_1, c_1, etc., by a, b, c, etc., with the aid of the given organisation, with the aid of the brain in particular, or at least with the aid of *any* kind of machine, in the broadest sense of the word, in general?

Matters would be easy if to each element of the stimulus there corresponded an element of the effect, if a_1 were the effect of a, b_1 of b, c_1 of c, and so on. That is so in the phonograph, but by no means in acting. How then may our observations of what happens in ordinary conversation be formulated analytically? It seems to me that our particular result may be generalised in the following manner:

Firstly, change the stimulus from $a, b, c, d, e, f, g, h, i$ into $a, b, \gamma, d, e, f, g, h, i$, and the effect may be transformed from $a_1, b_1, c_1, d_1, e_1, f_1, g_1, h_1, i_1$ into m, n, o, p, q, r, s, t.

And secondly, change the stimulus from $a, b, c, d, e, f, g, h, i$ into $\alpha, \beta, \gamma, \delta, \epsilon, \zeta, \eta, \theta, \iota, \kappa$, and the effect may *remain* $a_1, b_1, c_1, d_1, e_1, f_1, g_1, h_1, i_1$, in spite of that change.

There can hardly be a clearer expression of the fact that it is the *totality in its specificity*, both of the stimulus and of the effect, that comes into account in acting, and nothing else. But what is the meaning of this totality?

Here we have used the word that embraces our problem, almost unwillingly; we may say that it came upon us unawares: the word "meaning". The totalities of stimulus and effect have a "meaning", and their meanings do not at all depend on one another piece by piece.

We meet a psychological term here, though we know that we are not allowed to enter the field of psychology: at any rate we have found something very strange. And we must always remember that the "totality" or "individuality" of the stimulus is *not* a "resultant" in the sense of physics.

δ. A NEW PROOF OF THE AUTONOMY OF LIFE

We now ask the important question : Is there anything like this in inorganic nature ? If not, one of our principles concerned in acting, the principle of the *individuality of correspondence*, would form a new and independent proof of the autonomy of the phenomena of life, of vitalism, just as the principle of the *historical basis* has done already.

Is it possible to imagine a machine, or rather, to conceive the brain as a machine, the reactions of which, being individualised combinations of a high degree of complexity, change correspondingly with any sort of a stimulus which is also itself individualised ? Or does it contradict the concept of a machine to assume that a typical arrangement of physico-chemical elements might respond to typically combined stimuli with always a typically combined effect, though the single elements of the one do *not* stand in causal relation to the single elements of the other, and though also the physical " resultants " of the stimuli do not play any rôle ?

In the former part of this book, when dealing with the physiology of metabolism and of immunity in particular, we said already that the indefiniteness of correspondence between specific cause and specific effect, always following the principle of adaptive regulation, may be taken as indicating at least the autonomy of life-processes. It was of " simple " stimuli that we were then speaking ; but now we have to do with " individualised " stimuli, and it seems to me that a *proof* of vitalism is now possible instead of a mere indication of it, on account of the intimate nature of the correspondence between the individualised stimulus and the individualised effect, both of which are totalities.

Goltz,[1] when analysing the movements of frogs deprived of their hemispheres, introduced the term " answering reaction " (" Antwortsreaktion ") in order to state what happened in his experiments. He did not altogether avoid pseudo-psychology in his discussions, but, in spite of that, his concept seems to me

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[1] *Beiträge zur Lehre von den Functionen der Nervencentren des Frosches*, Berlin, 1869.

to be as valuable as his experiments were. Indeed, we may say that it is because they are *answering reactions*, or still better, individualised answering reactions, that actions seem to be beyond the reach of mechanical explanation.

A few words may not be out of place with regard to the different possible kinds of " individuality " that stimuli and effects in acting may acquire. The individualised effects of action, as will easily be understood, may be composed according to order in time exclusively, like a phrase in a conversation or a melody, or according to time and space, like all objects of art or handicraft. The individualised stimuli may belong to the two classes just mentioned, but there is also a third class which is composed specifically only with regard to space : the perfect object of art or handicraft as a stimulus belongs here, and so does *any* typical object. Also this last class of stimuli possesses an individual *wholeness*, as a table or a dog, for instance. We meet here the problem we met already when dealing with the problematic stimuli of instincts. The dog, " this dog ", " my dog " is " the same " stimulus, seen from any side or at any angle whatever : it always is recognised as " the same ", though the actual retina image differs in every case. It is absolutely impossible to understand this fact on the assumption of any kind of preformed material recipient in the brain, corresponding to the stimulus in question, even if we intentionally neglect the fact that the material recipient would have been created *by* the stimulus in the individual's life : a recipient for the dog seen from the side would not suffice for identifying the dog from behind ! In fact—to speak psychologically—identification or simple remembrance of sameness depends only in part on stimulation, and is in the main an active trying on the part of the Ego.

So much, for the present, about the " individuality of correspondence " in its bearing on vitalism.

It always is an agreeable occurrence when two investigators in the same scientific field independently arrive at almost the same results. It was in the spring of 1903 that I first published the argument forming a new and independent proof of vitalism, which I just have explained, and it was at about the same time that the late philosopher Busse, in his book, *Geist und Körper*, *Seele und Leib*, brought forward an argument against so-called psycho-physical parallelism, which is almost identical with my analysis down to the smallest details ; and we knew nothing at all about one another. Busse uses a telegram as his instance, where I use a conversation, but that is the only difference. Later on we shall see that proving the autonomy of life, as revealed in acting, is indeed the same as defeating the parallelism theory.

But there is still another case of independent argument to be mentioned. Henri Bergson, in his profound analysis of the relation between *Matière et Mémoire*, had, as early as 1896, established what I should call the autonomy of acting, by a discussion which, though confined to Psychology, and therefore different from my own analysis *in verbis*, is very similar to it *in re*. I most strongly recommend Bergson's book to all who take a deeper interest in our subject.

Let us call those arguments in favour of the autonomy of life which were gained from the analysis of the differentiation of the harmonious-equipotential systems as concerned in morphogenesis the first proof of vitalism. Let us call the evidence obtained from the discussion of the genesis of the complex-equipotential systems, which are the foundation of heredity and of many morphological regulations, the second proof. Then we may see a *third proof of vitalism* in our analysis of action. This proof is as independent and self-contained as the first two proofs; nothing but the general logical scheme is the same, viz. a machine of whatever kind or degree of complication is not imaginable.

A few words may still be devoted to the union of the two chief characteristics of acting.

The principle of the individuality of correspondence, as we know, does *not* mean that there is a *statical* or fixed something, through which that correspondence passes, and the real nature of which—whether machine or not—is in question. The reacting something has been created in its specificity, has been made such as it is *by* its history. Thus both our principles of action are united inseparably.

And the same is true of the vitalistic arguments derived from them. Each of the principles leads to a separate vitalistic proof. The more so, of course, does their union.

Let us then try to formulate in a definite manner our third proof of the autonomy of life, founded upon the analysis of acting as a phenomenon in objectified nature.

All acting is correspondence between individualised stimuli and individualised effects occurring on a basis of reaction that has been created historically from without.

Acting defies explanation of any kind on the basis of physico-chemical tectonics of any sort, for the following reasons.

It is impossible to imagine a machine—in the widest sense of the word—such as to allow of even the individuality of correspondence in acting, taken alone. For it can be shown that it is neither the single constituents of the stimulus nor their physical resultant on which the single constituents of the effect depend, but one whole depends on the other whole, both " wholes " being conceivable in a logical sense exclusively.

But to this first general impossibility is added a second, still more important, by an analysis of the character of the historical basis. That the individualised correspondence in acting takes place upon a *historical* basis, that its basis is made from *without* by *chance*, is a very strange feature in itself—but here we have the phonograph as an analogue. The historical basis of acting —the " prospective potency " for acting, if you care to say so by analogy—differs in two fundamental respects from the phonograph, or from *any* sort of machine imaginable in physics and chemistry. Firstly, the effects that are given off in acting occur in a field of natural events very different from that of the stimuli received historically : sensations belong to one, movements to another field. Secondly, the historical basis serves only as a general reservoir of faculties, the specific combinations of the stimuli received historically being preserved by no means in their specificity, but being resolvable into elements ; these elements then—transferred, however, to another sphere of happening—are rearranged into other specificities, according to the individuality of the actual stimulus in question.

The " something " that " acts " has the innate faculty of producing some specific combination of muscular movements ; the combination it produces in a special case depends on the individuality of the stimulus present in that case, and on the whole of past sensations in the widest sense.

This is the result of an analysis of action unbiassed by dogmatism.

ε. THE " PSYCHOID "

This seems to be just the right place in our discussion to give a *name* to the " acting something " which we have discovered not to be a machine. We might speak of " entelechy " again, as we did in the theory of morphogenesis, but it appears better to distinguish also in terminology the natural agent which *forms* the body from the elemental agent which *directs* it. The words " soul ", " mind ", or " psyche " present themselves, but one of them would lead us into what we have so carefully avoided all along, viz. pseudo-psychology. I may speak of *my* " psyche " —which is more than saying " Ego " [1]—but there " are " no souls in this sense in the phenomenon called *nature in space.* I therefore propose the very neutral name of " Psychoid " for the elemental agent discovered in action. " Psychoid "—that is, a something which though not a " psyche " can only be described in terms analogous to those of psychology. In fact, there can be no doubt that only the processes called " abstraction ", " thinking ", and so on, will enable us to *understand* the correspondence of the two individualities in our important principle : and it is these processes which cannot be described in mechanical terms. That is our justification of the name " Psychoid ".

If the analysis of instincts should help us some day to a true proof of vitalism, instead of offering only some indications towards it, it might also be said that a " psychoid " is the basis of instinctive phenomena. The usual difference between the " Conscious " and the " Unconscious " would then have to be brought to its legitimate and truly philosophical expression by distinguishing between two different kinds of psychoids.

There certainly is a difference, expressed already by the want of experience in instincts. But there is a difference

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[1] Compare my *Crisis in Psychology*, Princeton, 1925.

between the instinctive psychoid and morphogenetic entelechy also. In a later chapter we shall see whether or not all " kinds " of entelechy are ultimately the same.

The first systematic vitalist we know, Aristotle, saw these analytical differences very clearly and gave a very adequate denomination to them. Calling the spiritual principle, which he regarded as the real foundation of life, ψυχή in general, he carefully discriminated between three kinds of it. The lowest of all is the ψυχὴ θρεπτική, the soul of metabolism, which, together with its modifications, called αὐξητική and γεννητική, that is, the soul of growth and of propagation, may be said to represent our " Entelechy " as concerned in morphogenesis ; it is possessed by all organisms, plants as well as animals. The next higher class of souls is represented by the ψυχὴ αἰσθητική, the soul of sensation as well as of volition ; it belongs to animals only, and to some extent may properly be called the soul of instincts. It is only to men, according to Aristotle, that the highest soul, the νοῦς, is given, that is, the faculty of reasoning, corresponding to what we have called the " psychoid " as regulating action.

Indeed, it seems to me that the general classification of Aristotle may be accepted even nowadays, at least with a few modifications, if we give up his restriction of νοῦς as being only possessed by man. Certainly there is more than mere instinct in animals, at least if the word instinct is used in its original meaning, that is, in the sense of perfection in reacting *without* any experience or anything similar to experience in any way. We do not intend to deny by this statement the great differences that exist between acting in man and acting in even the highest animals ; later on we shall learn a little more about these problems. But there certainly *is* " experience " in the proper sense of the word in many animals.

We now have completed the outlines of our analytical study of action as such, and have given a provisional name to its results. But we must not yet leave our present studies : the part which the brain and nervous system play in acting is not yet clear from what we have said, and a few words about the real differences in acting between man and animals may also seem to be required.

ζ. THE "SPECIFIC ENERGY" OF THE SENSORY NERVES

According to our analytical researches so far it might seem as if the brain were almost unnecessary in acting; but, of course, such an opinion would be very far from the truth.

Let us then try to connect our analysis with certain problems of the physiology of the nervous system. And in the first place let me refer to the problem of the so-called "specific energy" of the sensory nerves as established by Johannes Mueller.

According to Mueller, the meaning of this principle was that the specificity of sensation, say of red or green, or heat, or a musical tone, was in some way a "property" of the single nerve fibre under stimulation, and that it was quite indifferent by what sort of an occurrence the stimulation had happened. Later science has transferred the specificity from the nerve fibres to specific localities of the brain, but the general view has remained almost the same.

Intentionally we shall put aside the whole epistemological part of the question concerned here, which is by no means an easy problem, and take up the position of naïve realism in the short discussion that is to follow.

We simply ask, is it true that the process of nervous conduction is always the same, and that specific qualities reach the brain only because specific parts of it have been stimulated, without any relation to the nature of the stimulus? Certainly there is not a single instance brought forward in favour of Mueller's principle that can be said to be above all doubt. The often discussed fact, for instance, that cutting the optic nerve gives the sensation of light proves nothing, since, as all modern authors agree, this operation is not possible without stimulating the retina to a certain extent before the nerve has been cut quite through. The electrical phenomena, on the other hand, that are exhibited equally well in any stimulation of nerves whatever, are only secondary phenomena, and prove nothing either for or against the problem of qualitative differences in nervous conduction. There remain only the facts—strange as they are—of a localised feeling of, say, the hand or the fingers after the amputation of the whole arm; but not a single one of these amputations has been performed on an individual who had not already received the specific sensations in question in the normal manner during his previous life. There always had been many normal stimulations before the operation, and who is able to say whether the different localities of the brain may not have become specific *by having been stimulated specifically*? We shall come back to this question on another occasion.

Now, on the other hand, the experiments made with the aid of an extirpation of parts of the brain, as carried out by Goltz and many others, have positively shown that there may be a certain functional regulation in those parts, at least to a certain extent. Of course, there probably will be a difference in regulation according to whether the single parts of one and the same sensory sphere, or whether parts belonging to different "senses", are in question. There may be a regulability in the first case and not in the latter. But even then, the principle of "specific energy" would be broken as far as the single elements of one nerve or the single parts of one so-called "centre" are concerned: one and the same element of the brain would be related to *various* qualities of sensation—at least with regard to one and the same sensory sphere—and, on the other hand, we could hardly escape the hypothetic assumption that one and the same fibre of a nerve is able to transmit stimulations that are different with regard to sensory "quality". This view was held by Hering,[1] while Wundt[2] seems to go still farther in assuming what might be called the original equipotentiality of the brain.

Thus, the principle of Mueller might be half true, half false, as far as the adult is concerned, though it is perhaps quite false for the child. We soon shall enter once more into these questions.

But the most important point for ourselves—strange to say—is not the question about the adequacy or inadequacy of the theory of "specific energies", but the simple fact *that this*

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[1] *Zur Theorie der Nerventätigkeit*, Leipzig, 1899.

[2] *Physiologische Psychologie*, 5. Aufl., Leipzig, 1903.

whole problem does not touch at all our principle of the " individuality of correspondence". It was only to make this clear that our short remarks about the present state of the problem of specific energy have been made here.

In fact, if any kind of equipotentiality of the brain were positively established, a *new* and independent proof of vitalism might be gained from that fact alone. But even if Mueller's law held good, *nothing* would be affected in our *previous* discussion. For the principle of the "individuality of correspondence", one of the two foundations of our third proof of life-autonomy, only deals with the *unity* and *individuality* of a totality which is constituted by single elements, *without asking in any way by what sort of processes the elements of the external " individualised " stimulus may be offered to the " something " that is reacting.* That this " something " cannot *be* a machine, though it may *use* a machine, *i.e.* the brain, remains equally true both if different processes of conduction may occur in the same nerve fibre and if it is different localities of the brain which, when irritated, represent the different elements of the " individualised stimulus ". In neither case is this stimulus a mere sum ; and the fact that there *is* more than a sum proves in *any* case that there is more than a machine at work.

Thus we understand that our analysis of action is independent of the problem whether the doctrine of " specific energy " be right or wrong.

η. SOME DATA FROM CEREBRAL PHYSIOLOGY [1]

But now let us try to ascertain positively what may be the part played by the brain in acting.

At the beginning of the present part of our book we observed that we should study organic motions especially under the aspect of regulations, and we mentioned briefly that regulations may enter into these motions in three different

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[1] Compare besides the text-books of Physiology: Lewandowsky, *Die Funktionen des centralen Nervensystems*, 1907. A very good historical and critical review of the whole subject will be found in C. Hauptmann, *Die Metaphysik in der modernen Physiologie*, 1893, and in E. Becher, *Gehirn und Seele*.

ways. The specificity of movement may be determined, firstly, by the specificity of the stimuli coming from without; secondly, by the specificity of the variable state of the motor organs; and thirdly, by the specificity of the variable state of the central organs (page 187).

Hitherto we have been studying only the first class of these regulations. Our analysis, leading to a new proof of vitalism, has started almost exclusively from the stimuli.

Let us now say a few words about regulability of the brain functions themselves. This subject has just been touched in our remarks on the doctrine of specific energy. There exists anything but unanimity and agreement in this field of physiology, and to form a proper judgment is very difficult for one who, like myself, has no personal experience of the matters in question and is obliged to rely on the literature. On the one hand, the parts of the brain are regarded as almost completely equal in function, whilst, on the other hand, the utmost functional specificity even of the individual cell has been insisted on.

As far as I am capable of judging, it seems to me that *two different* fundamental factors are to be distinguished relating to the organisation of the brain and of the so-called cerebral hemispheres in particular, and each accounting for different results among the experimental and pathological facts.

In fact, there is an interesting parallelism between the brain and the youngest germ, inasmuch as they are constructed according to two different types of complexity. In the mature germ[1] we had the intimate structure of mere direction, more or less regulable according to the state of the protoplasm, and the true material structure showing scarcely any regulability at all. In the brain of the adult we find the two features—a simple structure for conduction and then some higher sort of tectonics; and here again only one of them seems to be regulable to any great extent. The hypothetic differences between the young and the adult brain with regard to regulability are paralleled, on the other hand, by the differences of the germ before and after fertilisation and maturation.

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[1] See pages 44-48.

In the first place, the brain is a system of nervous connections of almost inconceivable complexity for the work of *conduction.* I think we shall not be very wrong in saying that not only is every part of the brain connected in some way with every other, but also almost every part of the surface of the body is by the aid of the brain connected in some way with every other part.[1] It is to these features that the functional regulability of the brain relates. It is a known fact that defects in the brain, caused by a localised operation or a wound, are followed by sensorial and motorial defects, but that these defects become smaller and smaller as time advances,[2] until a certain maximum of regulation is reached. It is highly probable that this regulation, in part at least, is due to the fact that some typical nervous connections in the brain, which had been destroyed by the apoplexy or by the operation, are restored after a while: not, of course, morphologically, for there is no actual restitution or regeneration of any sort in the brain of vertebrates, but physiologically, in the sense that the functional connection between the parts A and B is now, after the destruction of the shortest route, accomplished by some other of the many possible routes.

These facts, when more accurately and minutely established, might furnish a sort of new and independent proof of vitalism, by showing the brain to be what might be called a "functional harmonious-equipotential system". The specificity of a motory reaction is not dependent on the specificity of the brain as such, but the organisation of the brain is only *used* in order to perform a specific reaction, and its different parts may be used differently in such a manner that harmony, *i.e.* the specificity of the individualised effect in question, is never altered.

By no means do we wish these words to be understood as if the possible harmony of the parts of the brain in use were perfect

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[1] For man this statement can be proved as follows: You are able to decide voluntarily that when a certain point of your skin is touched you will touch with your finger another certain point of it; the two points may be any you please.

[2] As a rule this diminishing of functional defects is attributed to the ceasing of the "shock". Most recent authors, however, agree that use has been made a little too freely of "shocks". There can be little doubt that this favourite term has often blinded us to the existence of true regulation.

in every case. On the contrary, in spite of the enormous manifoldness of cerebral connections it can very well be imagined that *certain* apoplectical or experimental disturbances will render functional reparation impossible. In such cases there is no longer any connection between the points A and B, and clinical or experimental defects are permanent.

But the permanency of such defects generally seems to have other reasons, and I hope we shall learn to understand them, if we now turn to study the second fundamental feature concerned in cerebral organisation. The brain is *not only* a system of connections: it is something more. The specific differences of sensations, to speak psychologically, seem to require some specific arrangement in organisation, specifically localised, which renders the brain *in*equipotential to a certain extent.

And these arrangements are really found to exist. Certain specific parts of the brain seem to have a specific functional value that is more than a mere locality of specific connection, at least in the adult. Disturbances of these " spheres ", as they are called, by disease or experiment are to a great extent irreparable. These cerebral specificities would seem to be responsible for the specificity of " sensation ", and to justify as much of the old law of Johannes Mueller as will stand criticism, at least with regard to the adult. But they are not the only factors concerned in specific sensation: the specificity of the process of centripetal nervous conduction is another factor of importance. It is now granted by the first authorities in this field that at least in one and the same sensorial sphere, such as sight, for instance, one nerve element may transmit different " qualities " in their specificity; and as far as the sense of smell is concerned I do not see any possibility of escaping this conclusion. The peripheral organs, being the seat of the real stimulation of the organism, in this way become responsible for the specificity of sensation to a very high extent, though not, of course, on account of the nature of the stimulating external agent alone, but also on account of their own (chemical ?) specificity.

Thus it is by the co-operation of both parts, the specific centres as well as the specific reception organs, that specificity of sensation occurs. The specific centres are not liable to regulation.

But this is only true for the adult. Bechterew[1] remarks that extirpation of the so-called motor spheres carried out in the *newly born* dog or cat has no effect whatever on its future motions. Moreover, it is a well established fact that aphasia may be almost completely cured by re-learning to speak. These facts seem to prove that " spheres " are not innate but created *during life,* and that even " spheres " are liable to regulation, at least in some cases. That would allow us to call the brain an organ which possesses *originally* the same functional " prospective potency " in all its parts, these parts obtaining their specific " prospective value " secondarily, and being able to modify it to a certain extent under certain conditions. It is true, nothing has been actually ascertained here at present, so far as *sensorial* nerves and centres are in question. Might we expect that specificity of " centres " in the adult is *completely* a *product* of specificity of previous centripetal conductions ?—that by interchanging the connection of the optic and acoustic nerves to their respective sensory organs in the newly born, the optic brain-centre of the adult would be transferred to the place where the acoustic centre normally is, and *vice versa* ?

Enough of such hypothetic discussions : the cerebral physiology of the *adult* certainly *does* reveal certain specificities in the brain which are not liable to regulation.

But, most important of all, the very factor that ultimately *determines* the *specificity* of any cerebral or rather motor reaction is not a material " sphere " in any sense ; we have proved that this factor is not physico-chemical in character at all. So we may say, there is something more concerned in reactions starting from the brain or passing through the brain than mere localities of connection, and something more also than localities of specific function ; but this " more " is not a " sphere " or " centre " in the sense of something material *in* the brain. This " more ", our Psychoid or Entelechy, *uses* the conductive and specific faculties of the brain as a piano-player uses the piano.

In these words is included what we are *not* entitled to attri-

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[1] *Bewusstsein und Hirnlokalisation,* Leipzig, 1898, p. 48.

bute to brain-functions proper. "Memory" and "Understanding of *meanings*" are the two main features in action which cannot be attributed to the material brain in any sense whatever. For a purely *material* system is only what it is at a given moment, namely, a particular constellation of electrons and protons. It does *not* carry its history on itself, and it is *not* able to "understand". For this reason the material brain may be *related,* in an unknown way, with certain particulars in the sphere of memory and understanding, but it certainly is *not* their foundation *qua* material brain.

θ. REGULABILITY OF MOVEMENT WITH REGARD TO THE MOTOR ORGANS

We have finished our discussion of the regulations occurring in the brain and of all that is connected with them, and therewith have closed at the same time the study of the second type of the possible regulations concerned in movement, those relating to the intermediate organs, at least as far as the "hemispheres" come into account. Certain remarks, now, seem to be required about the third possible kind of regulation of movement, that is, about regulations regarding the motor organs as such. This may be done rather shortly, for facts may suitably be reduced here to the two other types of regulation.

The dog who is wounded in one of his legs, and therefore is forced to walk on three legs only, is a good instance of what we mean: regulations are going on here in the use of the three legs left; these three legs are used otherwise than they would have been used if there were still all four of them. It seems to me that all instances of this kind[1] may without difficulty be subsumed under our first class of regulations in motion, those starting from the specificity of motor stimuli, and therefore a full discussion is not required. Indeed, the fact that there are but three sound legs is an item in the sum of the motor stimuli and conditions just as a carriage crossing the path of our dog would be; it forms part of the "individualised

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[1] Compare also the cases mentioned on pages 189-191.

stimulus", according to which the individuality of the action is determined. But any one who prefers it might also gain an independent proof of autonomy from this kind of motor regulation, by saying that, besides the individual correspondence between the stimulus proper and the action, a correspondence of an individualised type is also going on between the specified state of the motor organs and the specified use of them. In some way, of course, it is to the brain again that this regulation relates; other centrifugal nerves are used for one and the same action, according to what kind of abnormal state the motor organs are in.[1]

A very interesting clinical experiment, carried out by Vulpius,[2] deserves mention in this connection. The tendon of a flexor muscle of the foot was split and one of its halves was made to heal in such a way that it could perform the function of stretching—the extensor muscle being paralysed. After a certain time, in fact, the flexor muscle was "split" also physiologically: part of it was used for bending, part for stretching, as circumstances required. In a very strange and perfect manner the "acting principle" had succeeded here in using quite an abnormal centrifugal nerve, and, of course, quite abnormal central parts also, in the service of certain "individualised" reactions that were needed. One could hardly imagine a better illustration of the rôle of the nervous system as a mere instrument for acting; of course, in the light of this discovery the so-called "motor spheres" also appear as anything but absolutely fixed;[3] in any case, the organism may learn to use *abnormal* centripetal nerves for its *normal* performances.

It may be added to what we have said that not only a functional partition of a tendon is possible, but also the transportation of a particular function from one tendon upon

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[1] Ophiurids deprived of one or more arms also show good instances of this class of regulability in movement. Compare Preyer's experiments, which I have most completely confirmed myself.

[2] *Die Sehnenüberpflanzung*, 1902, p. 88 f.

[3] Flourens knew as early as 1842 that fowls use their wings in the right way if the two main nerves of the plexus brachialis are crossed by a complicated operation. See also Spitzy, *Zeitschr. f. orthopäd. Chir.*, 1904, vol. xiii.; and Bethe, *Münchener med. Wochenschrift*, 1905, No. 25.

another one by transplantation. In this case the *flexor* must be innervated when *stretching* is intended.

The performance of the new function must always be "learned", and everything is very similar to the origin of volitional acts in the child (page 209); it is first "by chance" that the tendon (or part of a tendon) performs its new function. This then becomes "noted" and is afterwards "willed".

What the patients themselves have said, according to Vulpius, is very interesting. "My hand, at first, did not will what 'I' was willing," or "It was not really 'I' who was stretching," etc.

Things are different when irregularities or disturbances of nervous connection as such are in question, without any alteration in the conditions of tendons or muscles.

The experiments of Boeke, Detwiler, and others have shown that, in embryology as well as in regeneration, the growth of the nerve fibres from the centre to the peripheral organs occurs quite at random, the (chemotactic ?) attraction on the part of these organs being by no means specific (page 71). And yet muscular contraction does always occur in a typically co-ordinated way. In other words: there is a typically combined central stimulus, and there is a typically combined reaction on the part of the muscles, but that which is *between* the one and the other, viz. the system of nervous connections, is by no means typical, but may be in a great disorder. How is this possible ?

Weiss, on the basis of transplantation experiments, has worked out a very suggestive hypothesis in order to explain these strange phenomena. He gives up the orthodox theory that the process of nervous conduction is always of the same kind, and that a muscle *must* contract if the nerve which connects it with the centre is stimulated. There are specific differences in the *quality* and *intensity* of nervous conduction, so he says; and, besides, there is a sort of fixed harmony between the specific quality of a nervous stimulation and the contraction of a particular muscle, each muscle giving a reaction, in the form of contraction, only if it receives a stimulation which corresponds to its immanent nature ("Resonanztheorie "). In this way the disorder that prevails in the system of nervous connections between centre and muscles becomes irrelevant. But no " learning ", as in the experiments of Vulpius, is required.

The *new* feature, introduced by Weiss,[1] consists in the hypothesis that motor nervous conduction is *specific* with regard to quality and intensity, and that there is a sort of harmony between the specificity of stimulation and the specificity of receiving it. All *regulation* in nervous conduction would, thus, be of the *primary* type (page 121), if I may use our own terminology, whilst in the experiments of Vulpius it would be *secondary*, combined with " learning ".

It seems to me that the hypothesis of Weiss is at any rate possible. If we reject it, we are forced to assume that, the central impulse being given, the *psychoid* determines at each bifurcation of a nerve fibre which way the stimulation must take. This theory, of course, is possible also, but the hypothesis of Weiss is more simple.

The principle of the *individuality* of the stimulus (page 213 f.) would be maintained under both aspects, just as it has been indifferent, with regard to this principle, whether Mueller's theory of " specific energy " was right or not (page 225).

ι. THE LOWER BRAIN-CENTRES IN VERTEBRATES

To the whole of our discussion about the rôle of the brain in acting in general a few remarks must be added concerning the physiological importance of the so-called lower brain-centres in vertebrates. Pflüger was the first to speak of a " Rückenmarksseele ", that is, of the faculty of the spinal cord of frogs that had been deprived of their whole brain to react to stimuli in a manner which resembles action. But later researches have left it doubtful whether these reactions of the spinal cord really deserve the name of acting, it being perhaps more probable that there occurs nothing but a consecutive line of different single motions in correspondence to

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[1] Weiss, " Erregungsspezifität und Erregungsresonanz ", *Ergebn. d. Biol.* iii., 1928.

a permanent stimulation which has not been removed by the first or second of them. We have seen already that Jennings has found such a sort of behaviour—besides real acting—in the infusorium *Stentor*, and that there is no reason for speaking of actions in such cases.

It was Goltz who showed for the first time that frogs deprived of the hemispheres, but possessing more of their central system than the mere spinal cord, are capable of reactions which —to speak in our own terminology—show most clearly the two fundamental characters of action: the "historical basis" and the "individuality of correspondence". Schrader afterwards proved the same to hold for the nervous system of birds, and finally we have the experiments carried out by Goltz on a dog with no hemispheres at all.[1]

What these animals performed was indeed much less than what they would have done with the use of the parts removed. But, after all, they *did* "act" in the true sense of the word: obstacles were avoided, even if one of the legs was made helpless; there were reactions to specific optic sensations; dogs (but not pigeons) ate and drank spontaneously, frogs caught flies, pigeons flew with an absolutely right calculation of distance. The "memory" of these animals, it is true, for the greater part related to experience gained before the operation, but to a certain extent they also were able to acquire new experience even in their defective state. In other words, on the basis of a general "prospective potency" the lower parts of the brain acquired a definite "prospective value", which otherwise they would not have acquired.[2] It therefore cannot be denied that acting in some measure is possible even without the main part of the brain, though the degree of this acting is of a much lower kind.

The term "Antwortsreaktion", which we have already made use of elsewhere, was invented by Goltz to describe what he had

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[1] Pflüger, *Die sensorischen Funktionen des Rückenmarks*, 1853; Goltz, *Beiträge zur Lehre von den Funktionen der Nervencentren des Frosches*, 1869; and Pflüger's *Archiv*, 51, 1892. Schrader, *ibid.* 41, 1887, and 44, 1889.

[2] Therefore, as Lewandowsky also well observes, operative experiments are not able to teach us the "normal" performances of the parts left by them. But they demonstrate what I call the "prospective potency", and that is more valuable.

discovered in his frog deprived of the hemispheres. He himself speaks of the impossibility of imagining a machine as the basis of the phenomena, and then tries to introduce a psychological terminology. It is strange that he did not notice that it was vitalism, the autonomy of vital processes, that had been proved by his discoveries. But Goltz does not stand alone here: many authors agree that the so-called " soul " plays a positive and causal rôle in acting, without noticing that a natural factor which is neither chemical nor physical is thus introduced into the argument.

That real acting may go on in animals deprived of the hemispheres is of great importance, of course, for the theory of life-autonomy in general: it shows that the " psychoid " is not only related to the cerebrum, but may also use the lower parts of the brain. One might say that a higher sort of psychoid governs the main brain, a lower one the thalamus opticus, the cerebellum, the medulla, and so on, and this would correspond, in some way, with the discrimination between consciousness and " subconsciousness " that is made by modern psychologists. But it may well be true, in spite of our statement, that all motor entelechy is one and the same in one individual, and that it is only on account of the primitive state of their organisation that it can do less with the lower parts of the brain than with the hemispheres. In any case there must remain an open question.

κ. DIFFERENT DEGREES OF ACTING IN DIFFERENT ANIMALS

Human acting was the starting-point and centre of our analysis of acting; but our discussion would be incomplete if we said nothing about the different kinds and degrees of acting in the other parts of the animal kingdom.

Apes and dogs learn a good deal; apes have even made use of " instruments " in Koehler's famous experiments. There is an " historical basis " to their acting of a very complicated character indeed, but their acting lacks all that we call " abstraction". In logical terms we may say that they *act* according to the principles of contradiction and of causality without *con-*

sciously possessing these principles. This would seem to be the chief reason why they invent nothing, and have nothing resembling language except quite superficially. Wundt has well said somewhere that animals have no language not for any reason of their organisation, but because they have nothing to talk about. It is very strange indeed how restricted the inventive or imitative faculty is even in the highest apes. Thorndike observed some apes kept in a sort of stable with several doors that might easily be opened; he opened a door several times very carefully and distinctly in order to show the apes the mechanism of opening, but not one of them followed his manipulations. Only after one of the animals had succeeded in opening the door by chance did it notice what opening was, and thus "learn" opening. Even then his fellows did not profit by their companion's experience: each animal had to learn by personal experience, realising absolutely by chance what opening was.

Certainly, then, there exists that which our term "historical basis of reacting" expresses. The specificity of their behaviour is determined by their individual history, *i.e.* by the specificity of the stimuli that occurred to them, and by the effects of these stimuli. But the dissolution and re-combination of the elements of their historical basis is far less complicated and far less variable than it is in man.

It seems to me that analysis must keep especially to this point of the characteristics of acting in order to state well in what the differences in behaviour between man and higher animals have their foundations. We have said on another occasion that the term "element" as a part of the analysis of action means something relative. Everything in the stimuli and effects concerned in the creation of the historical basis *may* be regarded as an "element" in some way. Single words *or* letters may be the elements of a phrase; in a landscape the elements may be whole parts of it, or the individual bodies in it, or some parts of the individual bodies, or anything else. Now, I think a fair description of the behaviour even of higher animals would be, that they are far less capable than man of resolving data into elements. They cling to the combinations in the form in which they have occurred—at any rate they do not go farther than to resolve what is given into individual bodies ; a stick and a bone are as it were the very letters of a dog's alphabet. The lack of abstraction may depend on this.

And from all this follows the comparatively small range of their power of combination, though this power is by no means absent.

Thus the lack of the power of resolving data seems to be the reason of the rather low mental state of animals ; all the other differences between the acting of men and the acting of animals are consequences of this fundamental diversity.

Acting of the type found in apes and in dogs seems by no means restricted to the higher vertebrates only : many insects, not only ants and bees but also beetles, are capable of actions of almost the same degree of complexity. Many of you know, I suppose, that Lord Avebury carried out numerous beautiful experiments about the experience of ants. I need only remind you of his " bridge-experiment ", for instance.

In recent times it is *v. Frisch* to whom the most important results about the behaviour of insects are due, and I strongly recommend my readers to study his works very thoroughly.[1]

Let us close our present discussions with a few words about the most inferior kinds of experience.

American authors[2] especially have studied the most simple types of acting in lower animals, in particular in Infusoria, Actiniae, worms, and crayfishes. We have stated on another occasion already, when trying to define the concept of acting in its contrast to other kinds of changeable motor reactions, that a mere consecutive line of changes of reactions in response to one and the same often-repeated stimulus, as discovered by Jennings in the Protozoon *Stentor* and in the earthworm, never deserves the name of real acting, but may be due either to fatigue or to some unknown conditions of the physiological state of the organism. But there is acting, if the first time the reactions A, B, and C have answered

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[1] *Sinnesphysiologie und " Sprache " der Bienen*, Berlin, 1924.

[2] For literature see the work of Jennings referred to at page 189, note 2.

to the stimulus a one after the other, and if the second time C answers to it without any delay, it being understood of course that it was C that had produced a "liking" or had overcome a "disliking" on the part of the organism: that is what actually happens in *Stentor,* and is very important as being a case of experience in a *simple* motor act. Primitive forms of experience relating to motorial *combinations* can be studied most advantageously in Crustacea. In Yerkes's "labyrinth" experiment a crab was placed in a box containing two different tracks, only one of which led to the water. The crab ran at random for a while, until at the end of many "trials" it found the entrance to the water; the second time the path to the water was taken with much fewer mistakes, and at the end of a set of experiments, the crab ran to the water directly without going wrong. Here we have a most typical case of "experience" in which the "effect" of previous motor stimuli is concerned, and it hardly matters at all whether we assume that the crab was guided by sight or that it was guided by some spatial memory, unknown to us, such as we have supposed to exist in some insects. Experience here consisted in the omission of a set of previous reactions in favour of the last effective one occurring in a series of consecutive stimulations. In another set of experiments carried out by Spaulding, the facts lay a little differently. A hermit crab was fed with pieces of fish placed under a green screen, and after a certain number of experiments it ran beneath the green screen even if no piece was there. Similar experiments have been carried out by the pupils of the Russian physiologist Pawlow with dogs.[1] In all these cases a certain reaction, originally caused by the stimulus A, is in the end called forth by a stimulus B that always was united with A. Whilst in the instance with the crab shortening its way to the water there was a very clear kind of trial, there is not trial in the second experiment. Both experiments offer good instances of the two fundamental characters of our historical basis (page 210): in the first it is not only former stimuli but former

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[1] But here the process influenced by association is not movement but secretion of the salivary glands.

effects also that are responsible for the specificity of the reaction; in the second it is former stimuli only.

But the scheme is always the same.

And now let us close our long discussions of animal motions, and let us close at the same time the first part of this book, the one which has had to deal with the *Science* of the organism.

SECTION B

THE PHILOSOPHY OF THE ORGANISM

SOME INTRODUCTORY REMARKS ON ENTELECHY

1. The Concept of "Teleology"

We begin our philosophical analysis by mentioning a concept which has often been applied to the phenomena of life, but has not once been used by ourselves.

"Teleology" is the concept I am thinking of; the words "teleological" or "purposeful" have, in fact, not once been used; and in spite of that we have almost always dealt with phenomena which were teleological or "purposeful" in the popular sense.

What has been the reason of our avoiding this term?

Nothing but its psychological aspect. *My willing* is "purposeful". But this term has nothing to do in *science* and will be replaced by a true term of natural science later on.

This term can only *analogically* be applied to organic phenomena. But the analogy is rather vague, and must be applied very carefully. And this for the following reasons.

Whilst studying the processes going on in an engine constructed by man, we understand with absolute clearness and distinctness that a process in nature may be teleological or purposeful in the popular sense, and that it may be *at the same time* of a purely mechanical or physico-chemical order; indeed all processes going on in human-built machines are of that class, no matter what the machine. We know that in these cases, every single process of the whole of the engine's function goes on in its singularity, and that its purposefulness or teleology is due only to its place and combination in the whole: it only is purposeful *because* it stands in this special *relation* to other single processes, and for no other reason at all.

Let us speak of a *statical teleology* in such cases, or of a *teleology of constellation*, if we wish to apply such concepts at all.

Now at once the question arises: Are all teleological processes in nature of the statical type, and what would follow if they were not? Of course, the name *dynamical teleology* might be given analogically to all kinds of natural processes which are purposeful without being the mere outcome of the constellation of a machine.

We have proved by three independent lines of argument that such processes do exist in organisms. From our analysis of the differentiation of harmonious-equipotential systems and of the genesis of complex-equipotential systems, and from our intimate study of the process of acting, going on upon an historically created basis and with the criterion of an individualised correspondence between cause and effect, we have learnt that no machine, of whatever kind and whatever degree of combination, can afford us the means of understanding what happens here in the organism. There was a natural factor at work, *autonomic* and *not* resulting from a combination of other agents, but elemental in itself; this factor, then, may be called a factor of dynamical teleology—on analogy. There is something teleological *within* its acting.

If now, once in the (dangerous) fields of analogy, we allow ourselves still a little more of it, we may say that it is *as if* our entelechy is endowed with *knowing* and *willing*. But only the *psychoid* possesses these faculties in the form in which "I" am in possession of them. For only the psychoid "knows" and "wills" on the foundation of experience. Instructive and morphogenetic entelechies know and will in another form. We may call this form *primary* knowing and willing, whilst "my" knowing and willing and, on analogy, that of the psychoid are of the *secondary* type. The words primordial and acquired might also be applied here.

But enough of analogies.

2. The Characteristics of Entelechy

EXTENSIVE AND INTENSIVE MANIFOLDNESS

ENTELECHY either underlies the origin of an organic body, typically built up of typical elements, or it underlies an action, *i.e.* a typical combination of typical movements. Thus we see: entelechy always results in a manifoldness of a typical kind, the single elements of which are beside each other in *space*, or one after the other in time, or both, always in a typical order. Let us call such a manifoldness as is the result of the manifestation of entelechy an *extensive manifoldness*, and let us not forget to notice that all sorts of engines or machines are also extensive manifoldnesses in this meaning of the word.

Now we believe we have proved that entelechy, *i.e.* the foundation of the extensive manifoldnesses just mentioned, whether organisms or machines, is not in its turn an extensive manifoldness of the type of any machine whatever. In other words, the actual organism, as it offers itself to observation, is certainly a combination of singularities, each of which may be described in terms of physics and chemistry, like a machine, and also all changes in these singularities lead to results which may be so described; but the reason of the *origin* of the combination and of all its changes is not a law or any combination of laws taught us by physics and chemistry, but rests upon entelechy, as does the reason of the origin of any kind of machine that results from acting. We therefore propose to give the name *intensive manifoldness* to all kinds of entelechies or psychoids: there is, in fact, something "manifold" in them, but the elements of the manifoldness are neither one beside the other in space nor one after the other in time. We may say that entelechy is manifold in thought but simple as a natural agent.

THE ORDER OF ENTELECHIES. ENTELECHY AND MACHINE-WORK

We know already that not every event that takes place during morphogenesis and metabolism is the direct outcome of entelechian acts, and it seems worth while to say a few more words about this point. And first let us remark once more that, provisionally at least, different kinds of entelechies may be said to be at work in the organism. There is first the entelechia morphogenetica, and after that the entelechia psychoidea, and the latter may be discriminated as governing instincts and actions separately. Furthermore, the different parts of the brain, such as the hemispheres and the cerebellum in vertebrates, may be said to possess their different kinds of entelechy. In fact, we may speak of an order concerning the rank or dignity of entelechies, comparable with the order of ranks or dignities in an army or administration. But all entelechies have originated from the primordial one.

Now, the primordial entelechy of the egg not only creates derived entelechies but also builds up all sorts of arrangements of a truly mechanical character : the eye, in a great part of its functioning, is nothing but a camera obscura, and the skeleton obeys the laws of inorganic statics. Every part of these organic systems has been placed by entelechy where it must be placed to act well in the service of the whole, but the part itself acts like a part of a machine.

So we see finally that the different forms of harmony in the origin and function of parts that are not immediately dependent on one another (page 76 f.), are in the last resort the consequence of entelechian acts. The entelechy that created them all was harmonious in its intensive manifoldness : the extensive structures which are produced by it are *therefore* harmonious too. In other words, there are many processes in the organism which are of the statical-teleological type, which go on teleologically or purposefully on a fixed machine-like basis ; but entelechy has created this basis, and so statical teleology has its source in dynamical teleology—if again we care to speak in analogical terms.

We now see the full meaning of the statement that entelechy is an " intensive manifoldness " realising itself extensively ; in other words, we know what it means to say that a body in nature is a living organism ; we have given a full descriptive definition of this concept.

CONCLUSIONS AND NEW PROBLEMS

But how can an " intensive manifoldness " be an elemental factor in nature ? The answer to this question will depend, of course, on what is understood by the expression " elemental factor in nature ". In other words, a detailed analysis of this concept will serve to show us the circumstances under which it is legitimate or illegitimate to speak of a factor of nature as elemental.

Materialistic dogmatism would reply here that the concepts of mechanics or energetics are the only legitimate elementalities of all science—but we have nothing to do with dogmatism of *any* kind.

The principle of so-called "economics of thinking", as prevalent nowadays, might say, on the other hand, that every elemental natural factor is legitimate by being necessary. Whenever analysis shows that there is something hitherto unrecognised in nature that is not to be expressed in terms of natural factors already known to science, then " economy " would allow us to create a new elementality just as we like, and would only want to find out whether this new factor is to be regarded as a " constant ", or a " force ", or a sort of " energy ", or what not.

We are not partisans of this purely economic view, which, in our opinion, is a little too simple.

We believe that we must *justify* the new concepts we have introduced into science. And this justification, we think, must proceed along two different lines. In the first place we have to show that our vitalism, though not a part of inorganic science, may yet be put into clear relations with its fundamental principles. And in the second place a purely logical justification of *entelechy* as a concept seems necessary.

We begin the first kind of justification forthwith.

PART I

ENTELECHY AND PHYSICS

A. ENTELECHY AND UNIVOCAL DETERMINATION

THE concept of the *univocal determination* of being and becoming may be called the very starting-point of physics, if by this word we understand the science of inorganic nature in its entirety. No states and no events are without a sufficient reason for their being such as they are at such a place and time, and the same thing always is or happens under the same conditions. These are the most general expressions of the principle of determinism. Of course, nothing in the doctrine of entelechy is opposed to them ; given certain circumstances, and given a certain entelechy in a certain state of manifestation, there will always be or go on only one specifically determined event and no other.

I do *not* give the name of "causality" to this principle of natural necessity or determination. Causality relates to a particular kind of changes exclusively, and the relation entelechy bears to it will be discussed later on. Our principle of necessity or univocal determination relates to *everything* that may be or happen in the universe, without any reference to the character and nature of the changes in the case of things that happen. Of course, this principle holds, whether entelechy plays its part in a series of events or not. The facts in the universe that originate in entelechy will be univocally determined as such whenever entelechy is such as it is, and entelechy is either of this or of that determined kind. And, moreover, any *single* spatial occurrence induced or modified by entelechy has its previous *single* correlate in a certain *single* feature of entelechy, as far as it is an intensive manifoldness.

Determinism, then, is a postulate of vitalism, considered as a *scientific* theory ; and vitalism is by no means equivalent to indeterminism.

A *supreme* mind, conversant with all the inorganic facts of nature and knowing all the intensive manifoldness of all entelechies and psychoids, including the individual history of the latter, would be able at once to predict the actions of any psychoid with absolute certainty. Such prediction is just as possible as it would be in pure mechanics, as stated in the fiction of the " Laplacian mind ".

Human mind, on the other hand, is not able to " predict " in this way, as it does not know entelechy before its manifestation, and as the material conditions of life, which alone the mind of man *can* know—(not " does " know !)—in its completeness, are not the only conditions responsible for organic phenomena. It is true, we may predict, in so far as we may say that an egg that comes from a hen will give us a chick. But this is a very rough sort of prediction, which does not even hold good whenever there is a phylogenetic step.

B. ENTELECHY AND CAUSALITY

General Introduction

Entelechy may be aroused to manifestation by a change in bodily nature, such as is effected by fertilisation or by some operation, or by some motor stimulus ; and, on the other hand, entelechy may on its own part lead to changes in bodily nature.

All this is very general ; it asserts that entelechy may be *related to* causality, *i.e.* to the principle of connection of changes in spatial nature. But it does not make the smallest assertion about the most important question : " Is entelechy by itself a specific form of causal connection, or is it not ? " This question must, however, be answered.

DIFFICULTIES

Now let us recollect that not every single event in space resulting from the manifestation of entelechy has its own single *external* cause. It was precisely on account of the impossibility of this being the case that our concept of entelechy was created. We should not need this concept if there were to be found a single external cause of every single step in the differentiation of an harmonious-equipotential system, and we should not need the psychoid were it not that action is a whole and not a sum. The single steps in the manifestation of entelechy are, as we know, univocally determined, but they are so by their being united in the intensive manifoldness of their realiser. In other words, it is the essence of an entelechy to manifest itself in an extensive manifoldness : all the details of this extensive manifoldness depend upon the intensive manifoldness of the entelechy, but not upon different spatial "causes". Thus the problem of the relation between causality and entelechy seems by no means simple, and therefore we shall best approach our subject by a rather lengthy series of analytical considerations.

First let us analyse a little more deeply the pure concept of causality, as understood in organic sciences.

DIFFERENT FORMS OF THE PRINCIPLE OF CAUSALITY

A complete system of natural ontology, whilst dealing with causality, would have to develop more specified principles regarding it. The principle of "phases" and the principle of the "least action" are cases in point. We shall not make use of these principles in our discussion; but we shall apply and therefore shall insist more fully upon the analysis of two specific causal principles which have played a great rôle in the history of inorganic sciences: I refer to the two so-called "principles of energy"

It seems to me that these principles, generally spoken of as the "conservation of energy" and the "augmentation of entropy", have their logical sources in the different aspects which causality offers to a thorough analysis.

The "cause" of an effect in spatial nature is that change in spatial nature which is invariably and "necessarily" followed by the effect. We now may consider this relation of "causality" in a more general and more specified manner.

We first imagine the totality of a "system", that is, a limited part of space including all the natural realities embraced in it. We study the states of the system as a whole at the different moments t_1 and t_2, all causal relation between it and its surroundings being excluded. Then we assure ourselves that the causality of the system with regard to its surroundings has remained unaltered in *amount* in spite of all internal changes. The system's state at t_1 as a whole has been the "cause" of its state at t_2; but as a causal system with regard to its surroundings it has remained the same. This, at least, is a postulate on the foundation of the general principle of univocal determination.

Let us now study two systems in the sense described, and let us assume that there are causal processes going on between these two systems, but in no other way or direction. Then we call the whole of the change of the totality of the one the cause of the whole of the change of the other, and are convinced that both changes are equal in *amount*.

It is upon these two fictions that the principle of the *conservation of energy* rests, and from these two fictions it derives its two fundamental modern formulations: "the energy of an isolated system is constant", and, "any loss of energy in one isolated system corresponds to an equivalent gain in another one", and *vice versa*. Robert Mayer was well aware that his principle was based upon an aprioristic foundation, and he did well to place in the beginning of his discussion the two phrases: "causa aequat effectum" and "nihil fit ex nihilo aut ad nihilum". In fact, it is upon a combination of the categories of *causality* and of *quantity* that the aprioristic part of the principle of the conservation of energy rests: *energy*, in the logical sense, *is causality in space quantitatively determined*.

But causality may also be conceived in a very different fashion, which enables thus the foundations of the second so-called principle of energetics to be laid. In this case we may speak of *specified* causality. We imagine a limited system again, but it is the singular diversity of all sorts of physical and chemical agents concerned in it that we consider. We then find that *diversities* in the different single parts of the system are the necessary condition that anything may happen in it at all; that nothing can happen unless there are original diversities. For the sufficient reason of happening would be wanting in a system which was uniform throughout, wanting at least so far as the system was uniform. Only if an element or any part of a system is different from others can something happen on that particular element or part. Such, at least, is the most general ontological source of the second principle of energetics, the *principle of becoming*, as Ostwald has called it. It relates to specificities in causation, just as the first principle related to generalities.

So much for the *logical* sources of the two great principles of energetics. In *physics* proper, they assume a particular form, which we have still to explain.

1. ENTELECHY AND THE PRINCIPLE OF THE CONSERVATION OF ENERGY

α. THE PRINCIPLE

" ENERGY " in the sense of physics is also a measurement and nothing else ; it measures in a particular form the amount of causality given off or received by a limited system in no other sense than the kilogramme or the pound measures the amount of gravitating matter. The physical unit of this measurement is the unit of " work ", in the terminology of mechanics.

" Conservation " of energy in the sense of physics, then, means that an isolated material system retains its faculty of doing *work* irrespective of all events occurring in its interior, and that, if there is an interaction between two systems, one of these systems gains as much of that faculty as the other has lost.

There are various forms of energy : mechanic, thermic, electric, etc. But their units stand in fixed relations to one another, and thus the principle of conservation may easily be maintained. Mechanical energy, *e.g.*, may be " transformed " into heat in this way, in a fixed quantitative relation.

But things become a little more complicated under certain conditions. The law of the conservation of energy is far from being empirically true if only those natural agents which are actually measurable as performing work are taken into consideration. But the truth of our principle is postulated, and therefore the empirical incorrectness of the principle is corrected in a very interesting way. Whenever the principle fails to hold at the first glance, so-called " potential energies " are postulated, into which actual energy may disappear or from which it may originate. Such potential energies play their rôle in the theories of gravitation, of electricity, elasticity, and some other branches of physics, and also in chemistry. There is nothing actually stated or measured in the case of all these potential energies: it is simply assumed that there *must* be a something representative of quite a definite amount of the faculty to do *work*, in order that actual energy may not seem to arise out of nothing. We therefore may properly call all sorts of potential energies *subsidiary*: they are "real", so far as possibilities can be regarded as real in ontology, but they never are immediately real in any sense—they represent mere potentialities. In this meaning there "is" a certain amount of potential energy whenever a pendulum reaches one of its highest points. This amount is regarded as equal in quantity to the "work" performed by the pendulum whilst overcoming gravity, which "work" again is equal to the kinetic energy of the pendulum at its lowest point.

β. THE PRINCIPLE IN ITS RELATION TO ENTELECHY

After these preparatory discussions we now may ask: firstly, how stands entelechy to the principle of the conservation of energy; and secondly, how stands entelechy to the concept of energy itself?

We *might*, of course, assume that the principle of conservation is broken by entelechy; in other terms, that entelechy creates energy *de novo*. This is imaginable, for the principle of conservation is only valid if causality of the spatial or material kind is in question. But entelechy is acting *into* space, as will be clearly seen later on. We should, however, be more satisfied if we might keep to the conservation principle, in spite of our vitalism. And it seems to me that such a view is not impossible.

Let us remember once more that the principle of conservation is merely quantitative, that it says nothing at all about the quality or direction of events. How *could* the principle be kept valid in its relation to processes of life in which entelechy is at work? It seems to me that *two* different answers to this question are *a priori* possible. Take an organism in the midst of a given limited medium, and imagine that we know, on the one side, the energetic value of any possible event leading from the medium to the organism, and, on the other side, the energetic value of any possible event leading from the organism to the medium. Then it is possible that the sum of the energetic values of both kinds of events is the same, or that there is a difference, either in one sense or in the other. In the first case, we should say that in passing through processes of life energy is not changed in its quantity at all; in the latter case energy would seem to be changed by passing through an organism—it would either be partly stored in some unknown form, or be awaked into actuality from some unknown form of storage. Whatever might happen, we should find a way to unite it with the general principle. The unknown energy spoken of in the case of a difference of the amounts of energy entering and leaving the organism would be of the potential or subsidiary kind; and we should know nothing more about it, except that it must exist in some form.

Certain Facts

Before going on in our analysis, let us appeal to certain facts regarding the actual relation between the inorganic forms of energy and vitality. Very important researches carried out most carefully, especially by Rubner and Atwater, have shown that there is no difference at all between the sums of energy leaving and entering the organism, as far as the adult organism is considered, in which metabolism is almost completely functional and not morphogenetic. Considering the heat of combustion of the food, and comparing it with the heat of combustion of all excreta, added to the thermodynamical equivalent of the actual work performed, the two values are found to be equal within the limits of error.[1] Such a result greatly simplifies the problem of energy: subsidiary energies are unnecessary for understanding functioning energetically. The results would be different, probably, if in the place of the adult the developing organism were the subject of study; but it seems to me that even in this case

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[1] A good summary is given by Zwaardemaker, *Ergebnisse d. Physiol.* 5, 1906.

a real equation between the energy taken in and the energy given out might be gained, if all substances which are chemically stored during ontogeny, or, rather, which are stored as chemical ones, were considered as given out, and were measured according to their heat of combustion also.

Thus we see that the principle of the conservation of energy is actually or probably demonstrated by the organism in the clearest form ; but, what is still more important, we also have seen that it might " hold " for the organism, even if the forms of energy known to us should not appear sufficient to form a complete equation of the organism's economy. In this case also, it would not be absolutely necessary to give up the principle of conservation in the realm of vitalistic biology.

On a Supposed Vital Energy

But what about the rôle of entelechy, and what about its relation to energy ? Ostwald, and many others following him, have admitted that, in cases of morphogenesis, and probably in nervous phenomena too, some unknown potential forms of energy may be at work, and that the specificity of vital phenomena and their autonomy is due to the peculiarities which that unknown energy possesses, just as mechanical energy has its peculiarities regarding direction in space, and radiating energy regarding periodicity. In other words : that entelechy is *itself* a peculiar form of energy.

That the energy in question would be a subsidiary one, would not in itself be an objection to such a view. So-called chemical energy is of that kind : it is always the mere difference between two amounts of thermic energy that is *called* chemical potential energy—that is all.

There exists, however, one objection to regarding entelechy as being of the type of an energy itself that seems to me to be absolute. All " energies ", actually known to exist or invented to complete the general energetical scheme, are *quantities*, and relate to phenomena which have *quantity* among their characteristics. In asserting these phenomena to be of the energetical order, we state that there can be a *more or less* of them, and that this more or less possesses most distinctly the faculty of being *measurable*, as being equivalent to a more or less of actual "work".

But entelechy lacks all the characteristics of quantity: entelechy is *order* of relation and absolutely *nothing* else; all the quantities concerned in its manifestation in every case being due to means which are used by entelechy, or to conditions which cannot be avoided.

It therefore seems to me that it is not only rather imaginative to speak of an entelechial kind of energy, but that it is absolutely wrong and contrary to the fundamental principles of definition and terminology. It is not legitimate to subsume a something under a general concept as one of its species, if this something differs from the general term just in that property which is the most important and essential. Science does better *not* to classify after the principle "lucus a non lucendo."

Therefore entelechy is *not* a kind of energy, but in spite of that it *does not disturb* the validity of the first principle of energetics. This principle would hold in life, even if an equation of economy were impossible. New subsidiary energies would then have to be created in fact; but these new subsidiary energies would have nothing to do with entelechy and vitalism. Whether they exist or not is a question by itself, which certainly cannot be answered without actual empirical research.

Thus I decline most decidedly any kind of "energetical" vitalism whatever, *i.e.* any form of vitalism which regards entelechy as a kind of energy.

2. ENTELECHY AND THE "PRINCIPLE OF BECOMING"

THE study of the second principle of energetics is to be our next problem. It will bring us to the intimate relation between the non-energetical entelechy and the energetical factors of the Inorganic.

a. THE "PRINCIPLE OF BECOMING"

The *proper* principle of becoming is but a specified physical formulation of the aprioristic phrase, belonging to the realm of general ontology, that nothing can happen without diversities, and that the originating of diversities demands pre-existing diversities. This principle is of an equal logical value with the logical basis of the principle of conservation ; like the latter, it is empirical only as far as it applies to real nature. That the *intensities*, and these only, must be different, and that an *intensity* can only be raised by another *intensity* falling and becoming able to "do work", is the empirical part of it ; but that a "something" must be different was prior to all experience. As an illustration of this *true second* principle of energetics,[1] we may remark that in the very largest quantity of water, say the ocean, nothing at all would happen "by itself" if the temperature were the same throughout, or if the surface level were the same everywhere, though the absolute amount of "energy" contained in the water is enormous. There would be no differences of the intensity either of thermic or of potential mechanical energy in these cases. And on the other hand, it is on account

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[1] The principle of the augmentation of entropy is purely empirical, and has no logical foundation. It simply states that, in a given system, the total amount of the diversities of intensity is decreasing. Or, in short, an ideal pendulum does not *exist*. This principle may also be called the principle of the dissipation of energy.

of such differences alone that a steam-engine does mechanical work, or that a waterfall can produce electric potentials.

There exists a specific equivalence between the factors of intensity of different energies, just as there was such an equivalence between the amounts of energy as such. The increasing of the intensity of any one energy stands in fixed relations to the decreasing of the intensity of the others, in such a manner that there is fixed not only what has been called the " coupling " of one energy A to the energies B, C, and so on, but also the amount of this coupling. By this fact of coupling the concept of the diversity of intensities is enlarged in a very important way : it becomes relative. There may be " equilibrium " if there is so much of the intensity of one energy and so much of the intensity of the other, and there may be a disturbance of equilibrium if the relation of the two intensities is changed.

It is at this point that potentialities regarded as realities enter the field of the second principle of energetics in the same manner as they did that of the first. Intensities can be actually measured only in very few cases; in all other cases they are imaginary and subsidiary. All reasoning proceeds in a circle here. If, for instance, nothing is happening in a system of chemical compounds or of different states of aggregation, we say that " equilibrium " exists ; if anything happens, then there were " diversities of potentials ". But all this is known only *post factum* ; in other words, the potentials and their diversities are created only *after* we know what happens and in what amount. And the leading principle of such creations is always the aprioristic conviction that there *must* have been diversities — of intensities—in order that anything *could* happen.

β. THE PRINCIPLE OF BECOMING IN ITS RELATION TO ENTELECHY

Let us now study the relation of vital phenomena to the true second principle of energetics.

That an " equilibrium " of some sort must have been disturbed if, for instance, a process of regeneration is going on, is absolutely self-evident, and does not throw any light on the problem whatever. To say " there is no equilibrium ", and to say " there is happening ", are identical phrases in the logical sense. Strange to say, there have been certain biological authors who have thought they were uttering profoundest wisdom in saying that vital phenomena, such as restitution, are due to a " disturbance of equilibrium " !

The true problem is: " *By what single acts* does the restoration of ' equilibrium ' take place here, especially in those cases in which it is proved that entelechy is at work, and that physico-chemical diversities and potentials of themselves are not able to offer a sufficient explanation of what happens ? "

As entelechy is not a kind of energy it cannot have an " intensity " itself.

But in spite of that, our study of the true second principle of energetics has been of some use to us. Even though it be not comparable to an energy in any sense, entelechy, as far as it comes into connection with the energies of inorganic nature, can do so only through the aid of those factors which are concerned in any kind of connection of the inorganic energies with one another. The *intensities* of inorganic energies, therefore, are the point at which any possible relation between the living and the non-living must be set up, for upon the intensities depends all material becoming exclusively.

Now, intensities of inorganic energies, as we know, if standing in any sort of possible exchange at all, stand either in the relative state of equilibrium or compensation, or in the state of mutual appearing and disappearing. It is clear from what we have said that entelechy also can act only upon the state of compensation or non-compensation of the inorganic intensities.

Let us try to fix this fundamental relation in a more concrete manner, which will illustrate at the same time, in the clearest way, how we wish the differences between the vital and the inorganic to be understood. Imagine a non-living system of a specific number of specific chemical compounds in specific states of aggregation and in a specific arrangement ; then it is absolutely determined, by the differences of intensity among these constituents, what is to happen until equilibrium is reached. We have chosen a chemical and aggregative system as our instance, because in the organism the *single* phenomena of becoming that can actually be observed are such as to consist in chemical and aggregative specificities. Let us now study the behaviour of a system consisting of chemical and aggregative constituents, as before, but forming at the same time part of a living organism. Our doctrine of entelechy teaches us that the behaviour of this system is *not* exclusively dependent on the differences of intensity among the constituents, but on something further. In what possible relation is this something able to stand with regard to the potentials of the constituents of the system? *It is of the greatest importance to find an adequate answer to this question,* and I hope to be able to give at least the beginning of such an answer in what follows.

The Action of Entelechy in "suspending" possible Becoming

Let us assume that entelechy is *not* able to change the chemical nature of the elemental constituents of the system in a qualitative way. For we have no grounds for such an assumption, which would imply, for instance, that entelechy could make sulphuric acid (H_2SO_4) if it had only the chlorides of sodium and potassium at its disposal. Entelechy, as far as we know at least, is limited in its acting by many specificities of inorganic nature, among which are the specificities included under the phrase "chemical element". Entelechy is also *unable* to cause reactions between chemical compounds which never are known to react in the inorganic world. In short, entelechy is altogether *unable* to *create* differences of intensity of any kind.

But entelechy *is* able, so far as we know from the facts concerned in restitution and adaptation, to *suspend* for as long a period as it wants any one of all the reactions which are *possible* with such compounds as are present, and which would happen without entelechy. And entelechy may *regulate* this suspending of reactions now in one direction and now in the other, suspending and permitting possible becoming whenever required for its purposes. Now, after all we have said, this suspending of affinity, so to say, is to be considered as a *temporary compensation* of factors of "intensity" which would otherwise be uncompensated and would lead to immediate becoming. This faculty of a temporary suspension of inorganic becoming is to be regarded as the most essential ontological characteristic of entelechy. Because it possesses this faculty *without* being of the nature of an energy at the same time, entelechy is *the* non-physico-chemical agent.

Let it be well understood: we do *not* admit that entelechy may transform potentials into actual happening by means of a so-called "Auslösung" in any sense. Entelechy, according to our view, is quite unable to remove any kind of an "obstacle" to happening, such as is removed in catalysis; for such a removal would require energy, and entelechy is non-energetical. We only admit that entelechy may set free into actuality what it has *itself* prevented from actuality, what it has suspended hitherto.

The Rôle of Entelechy in the Continuity of Life

This statement implies a very important consequence. If entelechy always must *have done* something in order that it may do anything in the present and future, there can, of course, never be any real beginning of its acting, but this acting must be continuous. And this is what the fact of inheritance teaches us. Life *is* indeed continuous: a certain portion of matter that stands under the control of entelechy is handed down from generation to generation. And thus entelechy always *has* already[1] acted!

Unfortunately, as will be seen later on, we are unable

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[1] It might be objected here that the continuity of entelechian control would imply a decrease of the amount of possible becoming, according to the principle of dissipation; and that for this reason life, *i.e.* the suspending action of entelechy, would soon come to an end. But the principle of dissipation is a purely empirical principle of inorganic science, and nobody is able to say *a priori* that the regulating acts of entelechy in relaxing suspension must be subject to it. Decrease and increase between coupled intensities, therefore, may amount to the same value in the sphere of vitalistic happening.

to escape this *regressus ad infinitum* in any way; at least, we know nothing about a "first" and really primordial act of suspension of inorganic becoming on the part of entelechy.

Entelechy and Chemism

Of course, we can only affirm the possibility of a temporary suspending of reactions on the part of entelechy in those cases where there is an empirical reason for doing so; and that is only the case at present in the spheres of chemical and of aggregative events. It is probably in the formation of so-called enzymes or ferments that entelechy manifests itself, not really creating them, but permitting them to appear, whenever required, on the foundation of an enormous amount of possibilities. The ferments, when once in existence, of course, do their work along purely chemical lines.

In the chemical and aggregative sphere, then, there is indeed a sort of "overcoming" of inorganic nature by the Organic, an overcoming that is no more strange, of course, than is, for instance, the overcoming of gravity by electricity, when small balls of elder pith are attracted by a rubbed glass rod—though, of course, in the latter case two real "energetical" intensities are in action against each other.

A Practical Application of the "Suspension" Theory

At the end of this chapter, we shall try to apply our hypothesis of the suspending effect of entelechy upon the results of our analysis of the harmonious-equipotential system.

This will render our theory a little less abstract, and will show at the same time that the theory is applicable to observable phenomena.

The different sections of Fig. 15 may represent some of the cells of an harmonious-equipotential system. All these cells have the same prospective potency. We now assume that this potency has a chemical foundation in so far as there exist the same chemical compounds, *a b c d e f g h i*, in each cell. Every kind of compound *may* react with every other in each cell. But it *does* not. Entelechy suspends *all* possible reactions at first, and then, if differentiation sets in, allows only *one* particular reaction in each cell to occur, according to its plan, so to speak.

In this way, a *sum of possibilities* is transformed into an *ordered whole of actualities*, as it is characteristic of harmonious differentiation. We may also say that, though " numerical manifoldness " has not been increased, " manifoldness of relation " has been increased enormously (page 31).

And all these features may be reduced to entelechy's work, relating to the suspension of differences of intensity, *i.e.* of possible becoming.

But does it not seem as if our statements were in contradiction to what we have called the logical foundation of the second principle of energetics, viz. that a something that is homogeneous cannot become heterogeneous " by itself " ? There is no contradiction at all, for the harmonious-equipotential system, though in the beginning homogeneous with regard to its material side, is not homogeneous at bottom: being controlled by the intensive manifoldness " entelechy ".

Intensive manifoldness is transformed into an extensive one ; that is all. And this leads, with regard to the distribution of particles of matter, to an increase in *manifoldness of relation*.

a b *c*	*a b* **c**	*a* **b** *c*	*a b c*	*a b* **c**	**a** *b c*	*a b c*	*a* **b** *c*	*a b* **c**	*a b c*
d e f	*d e f*	*d e f*	*d* **e** *f*	*d e* **f**	*d e f*	*d* **e** *f*	*d* **e** *f*	*d e f*	*d e* **f**
g h i	*g h* **i**	**g** *h i*	*g* **h** *i*	*g h i*	*g h* **i**	*g* **h** *i*	*g h i*	*g* **h** *i*	**g** *h i*

FIG. 15.

Ten cells of an harmonious-equipotential system, each of them containing the chemical compounds *a*, *b*, *c*, *d*, *e*, *f*, *g*, *h*, *i*, of which every one may react with every other one. Entelechy " suspends " at first, and then, if development begins, it allows the reactions *ab*, *ci*, *bg*, *eh*, *cf*, *ai*, *eh*, *be*, *ch*, *fg*, respectively.

An Explanation of the Limits of Regulability and of Life in General

If we understand that the action of entelechy is only an action of suspending that which, but for this, would happen —an action of regulating by suspending—we at once understand two very important features which appear in all phenomena of life: the dependence of life on the conditions of the medium, and the *limits of its regulability.*

We know that life is impossible without food and oxygen, without a certain amount of heat, and without a specific composition of the medium—all within rather narrow limits. We have frequently remarked, moreover, in our purely biological discussions, that there exist great differences in the faculty both of restitution and of adaptation. One plant is able to live in water as well as in the open air, whilst another one is killed if submerged under the surface of water; the newt regenerates the foot with the utmost perfection, whilst mammals are only capable of healing up their wounds.

Even these facts, it seems to me, are understood without difficulty, if we assume that entelechy can only suspend the compensation of differences of energetical intensities or potentials which *exist* already, but that it is not able to create such differences. The acting of entelechy thus becomes dependent on the potentials of the single parts of the body, which are themselves of an inorganic character, and on the potentials of the surrounding medium.

Now, somebody might say that the medium always contains potentials of the highest possible value, as exhibited, for instance, in the temperature of the medium and in the intensity of the rays emanating from the sun. These potentials certainly are of the greatest importance for the permanence of life, because, thanks to them, life is not exclusively dependent on the internal potentials of the material the organisms consist of. But we know, on the other hand, that there must be not only " differences " of potentials as such, in order that becoming may be possible, but also differences in potentials of energy which are " coupled " with each other, which may be transformed one into the other. It is, moreover, a well-known fact that most chemical and aggregative processes are almost absolutely beyond the influence of radiant energy of even the strongest intensity.

Entelechy then is limited in its operation by the differences of potentials already existing, so far as the organism is at the same time an inorganic system surrounded by an energetical medium. This limitation will explain not only the limits of regulability, but also disease and death, at least in part. The limits of regulability may be founded upon some rather insignificant feature, and may be, in spite of that, very marked in their effects. The fragmental development of the isolated blastomeres of some sorts of eggs is a good example of what I have said. It may depend on some very unimportant peculiarity in the consistency of the protoplasm that the isolated blastomere of the Ctenophore egg is not able to restitute its simple intimate protoplasmatic structure into a small new whole. From the impossibility of performing this rather simple regulation it follows that not a whole but a half animal develops from the isolated cell.

All cases of " wrong " regeneration probably also belong here. There may be so-called double regeneration, or an organ may become "re"-generated without having been taken away,[1] only in consequence of the infliction of a wound. Entelechy seems to be wrongly " informed " in such cases, or to be " stupid ". But, as E. Becher has well said : to be " stupid " does not mean to be deprived of intelligence.

Entelechy burdened with as Little as Possible

We have tried to formulate the relation between entelechy and inorganic elemental agents in such a manner that nothing may seem to be postulated which is not founded on experimental facts, and that at the same time the amount of specific performance burdened upon entelechy may appear as small as possible. Our *personal* belief is that we have charged it with *too little,* that future experience will enlarge the sphere of its acting. But it always is the best scientific method not to assume more of the new than is absolutely necessary.

In attributing to entelechy the suspending of possible becoming exclusively, though in a changeable and regulable way, we at the same time, I believe, have avoided one mistake that has been very often a reproach to vitalists. We have not imputed any action to entelechy that might seem to represent

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[1] See page 83.

any amount of energy in itself, and in fact we could not do so, as we had most strictly refuted any kind of theory regarding entelechy itself as a sort of energy. Suspending the compensation of uncompensated differences of intensities among coupled kinds of energies and relaxing that suspension are, in fact, not acts that would require any amount of energy. For, we repeat, our hypothetic act of suspending and setting free actually uncompensated potentials by no means relates to a removal of obstacles, such as occurs in catalysis, for example.

We must always very carefully discriminate between creating differences of potential and suspending the compensation of existing differences. The former can only happen by an actual transfer of energy, whereas for suspending and for relaxing of suspension no transfer of energy is required, but simply a transformation of energy from actuality into a potential form, and *vice versa*.

Conclusions

We now have said, it seems to me, all that can be said at present about the relations of entelechy to the true second principle of energetics, which deals with diversities of intensities and the coupling of them, and which is aprioristic in its foundations. This principle is *fully observed* in life processes, and because it is observed we see that life depends on inorganic processes.

But have we really solved the problem of the relation of entelechy to *causality* ? What sort of natural factor then is entelechy, after all ?

We know already that it is *not* energy and *not* intensity, since quantity is not one of its characteristics. For the same reason it cannot be a " force " in any of the very ambiguous meanings of that word. Could it be called a " constant " ? I thought so once myself ; [1] I thought it possible to speak of the entelechy of an organic system as its " constant " in the sense of its permanent property ; the word property meaning the same

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[1] *Die organischen Regulationen*, Leipzig, 1901.

as it does in the Inorganic, where it is to signify nothing but the possibility of becoming that would be actual with regard to immediate perception. But it now seems to me that the word " constant " can be applied to an entelechian system only in a very metaphorical meaning, if at all : for a constant always is the property of a *body*, always is a something that is really possessed by the body. Only by help of the categories of substance and inherence can the real relation of a constant to its bearer be properly understood. Our next chapter will show that we are not at all able thus to regard the relation of entelechies to the material systems upon which they act. So then it must be sufficient to state it here in a more provisionary and apodictic way : *entelechy is not a constant.* We may only say that in this specific harmonious system or in this acting system we are studying there is something which is constant, viz. its prospective potency, which comes into all its reactions in the same manner. But this something which is constant is not " a constant " in the sense of physics.

What then is our elemental vital factor in nature ?

Let us only say in this place that entelechy remains " elemental " also with regard to its true ontological character, just as it was elemental with regard to the law it obeys. Entelechy is *not* energy, *not* force, *not* intensity, and *not* constant, but—entelechy.

Entelechy, as we know, is a factor in nature which acts " teleologically ". It is an intensive manifoldness, and on account of its inherent diversities it is able to augment the amount of manifoldness in the inorganic world as far as relations are concerned. It acts by suspending and setting free reactions based upon potential differences regulatively. There is nothing like it in inorganic nature.

And yet entelechy seems to be a *causal* agent. But in which sense ? It will be the aim of the logical part of this book to decide this question in a final way.

3. Entelechy and Mechanics

α. MECHANICAL PHYSICS

We now leave the realm of energetics, with all its consequences, and turn our attention to the mechanical interpretation of nature.

The meaning of the word " mechanics " is very ambiguous, particularly in our days. And yet there is one point which is common to all " mechanistic " theories in physics and chemistry. All of them intend to reduce the great variety of inorganic phenomena to a *something* that may *move* in space.

This " something " is called *matter*, in the most general sense of the word.

There may be various kinds of this primordial matter. Science hopes, however, to discover ultimately only one kind. At present the proton, the electron, and the ether are practically regarded as being the three primordial material species, though many authors, theoretically, take the protons and electrons as mere etherial states.

All this is indifferent for our chief intentions, and, in spite of Maxwell and Einstein, we may even make the classical mechanics of Newton the foundation of our arguments, *i.e.* that mechanical theory which knows solid atoms and nothing but two forms of mechanical energy—the actual form, expressed by the formula $\frac{m}{2}v^2$, and the potential form, expressed by Newton's law of attraction.

For, whatever form our physicists may give to " mechanics ", they all agree that *inorganic* nature may be understood as a material system — in the sense defined — in which all future states may be mathematically derived from the present state, if, with regard to this present state, three things are known :

The momentaneous situation of each ultimate part of matter.

The momentaneous velocity of each part.

The law of interaction among two such parts.

All events in inorganic nature are the *geometrical sum* of all single movements and forces of the material ultimate elements.

It is with " mechanics " in this very general form [1] that our vitalism must harmonise itself.

I say " must ". For the problem that enters the scene here *cannot* be neglected ; and I dare to say that any sort of " vitalism " which does not clearly face this problem, but tries to avoid its discussion, is without value from the very beginning.

Of course, nothing but a discussion of possibilities is allowed us in this field, and it is for this very reason that it is a matter of indifference which actual form of mechanics we take as our basis. But mechanics in general *must* be confronted with vitalism, as the theory of the autonomy of life claims to interfere with the laws of inorganic nature in some way.

What vitalism proclaims is this : the parts of a material system move in a *various* way, *i.e.* subjected to *different* elemental laws, according to whether they are constituents of an inorganic body or of an organic one.

What, then, is the difference expressed on the grounds of mechanical physics, the word " mechanical " taken in the widest sense ? For simplicity only, we shall take mechanics in the Newtonian form ; but our arguments are of very general validity and may easily be transformed into any other mechanistic language.

Now we might say, in the first place, that entelechy creates velocity within material nature, *i.e.* that it is able to give an impetus to particles of matter. But this kind of action on the part of entelechy would come into conflict with the principle of the conservation of energy, and we have said that, as far as we know, vitalism *must not* necessarily overthrow this principle—

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[1] We need not even consider the question whether the " prima materia ", *i.e.* ether, is discontinuous or not.

(though, of course, it *might* do so, for the principle of conservation is a postulate only, so far as causality within space, and not " into " space, is concerned).[1]

Let us try, then, to find out how vitalism might interfere with mechanics within the sphere of the conservation principle.

β. ENTELECHY AND MECHANICS

Entelechy in its Relation to the two Forms of Mechanical Energy

I am thinking in the first place of entelechy as *suspending* the becoming that otherwise would happen. The process of compensation of potentials, in the most general meaning of the word, such as differences of coupled intensities, could as we know (page 261 f.) be suspended by entelechy. Does anything similar happen in pure mechanics with its two and only two kinds of energy? Kinetic energy and potential mechanical energy, of course, would be the only fields accessible to the action of entelechy. Now it would certainly not be a legitimate hypothesis to assume that entelechy is able to transform any potential energy into the kinetic form by removing some kind of obstacle that has hitherto impeded this transformation, for this process of so-called " Auslösung "—to use the untranslatable German word—requires a certain finite amount of energy in any case, and entelechy is not energy. But the problem acquires a very different aspect as soon as we assume that kinetic energy, *i.e.* " happening ", is always the given material entelechy has to work with, but that entelechy is able to transform actual happening into a state of mere potentiality by suspension, and that it can only set free such " potentials " as it has itself created by its suspension of happening. A combination of processes of the following kind, it seems to me, is well able to explain what I suppose to be the work of entelechy. An element of mass m moves with velocity v, until it comes within range of a repulsive force; its velocity then decreases constantly until it becomes zero. That point will be reached when the amount of its

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[1] Compare page 254.

original kinetic energy $\frac{m}{2}v^2$ has been equalled by the potential energy derived from the repulsive agent. Finally, the element m receives an impulse in a direction opposite to the original one, and this impulse—decreasing from moment to moment, as velocity increases—will last until the element has reached its original velocity, and also its original kinetic energy $\frac{m}{2}v^2$, taken in the opposite sense. Now imagine that the process of constantly decreasing motion just described is *suspended* by entelechy at some stage or other—say at the moment in which the velocity is v_1—in such a form that the amount of $\frac{m}{2}v_1^2$ is transformed into an equivalent amount of "potential" energy, localised at the place of m and kept there until it is set free, that is, transformed into the actual kinetic energy $\frac{m}{2}v_1^2$ again. Could not such a thing happen without any relation to questions of energetics? Certainly it could, for the process of suspending would not touch the amount of energy in any way, though it would interfere with inertia, and the process of relaxing suspension would be in no sense equivalent to an "Auslösung" or removing of obstacles. The mechanical process we have imagined is represented very clearly by an inelastic body moving with the velocity v and entering during its motion into an elastic ball. It will move into this ball for a certain time with decreasing velocity, come to rest for a moment, and then move in the opposite direction with increasing velocity again: let this process be stopped at the moment when the inelastic body has traversed say one-third of the path into the elastic mass. There is no contradiction to energetics in such an event, *provided, of course, that after the suspension has ceased the mechanical and energetic events continue their course from the point where it was broken.*[1]

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[1] Our hypothesis, of course, implies that a movement like that of a pendulum, which changes its direction periodically, passing through states of mere potential energy at the point of change, may be suspended in this point of change, in which there is *no* movement. This case, of course, is more simple than ours, and would not charge entelechy with an actual stopping of kinetic energy. But our more general hypothesis seems to me to be legitimate as well.

So I think that even in mechanics proper we have the possibility of formulating in a strict logical sense what is done by entelechy.[1]

Entelechy, *by its very nature,* may suspend movement, transforming kinetic energy into potential energy, and it may set free suspended movement as circumstances require.

Of course, as we saw with regard to general energetics, entelechy can only be regarded as able to set free those potentials which it has *made* " potentials " by its own suspending action, but not potentials that owe their existence to any inorganic cause. This important feature would lead us to a discussion of the continuity of suspension by entelechy, as seen in inheritance, but we regard our previous remarks on this point of the theory as sufficient (see page 262).

Entelechy as Transporting Mechanical Energy

Before discussing our result any further, let us turn to the second possible way in which entelechy may influence mechanical systems. The discovery of this possible rôle of the Non-mechanical in mechanics goes back to Descartes. In our own days Eduard von Hartmann in particular has investigated more carefully what is supposed to happen here. Descartes, strictly speaking, was not trying to study the influence of entelechy as a natural factor on mechanical mass and motion, but to fix the interaction of " mind " and body. But Descartes' analysis holds well on a different basis in the form that *any* non-mechanical agent, though not able to change in any way the amount of energy in any dynamical system,[2] has the faculty of reversing any mass-element it likes, and of thereby changing the *direction*

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[1] A similar view, with regard to " psycho-physical " interaction, has been urged by Wentscher and others ; but as a rule " suspending " and " Auslösung " have not been distinguished clearly enough.

[2] Descartes, strictly speaking, according to his theory of the continuity of matter, knew only kinetic energy ; the so-called " quantity of motion " (*mv*), therefore, was the mechanical quantity he would not allow to be altered by mind. For this reason our first hypothesis about the relation between entelechy and mechanics would have been impossible for him. Even his own statement about this relation—or rather about the relation between " mind " and matter—does not acquire any very clear meaning on the kinetic theory.

of forces and motions. It might be objected that a certain amount of energy would be necessary for any " turning " of a mass-element, there being required a certain force, or rather pair of forces, from the side on account of inertia. Where is the necessary energy to come from, since entelechy itself is regarded as non-energetical ? Hartmann tries to avoid this difficulty by assuming that entelechy—or, as he calls it, the " Unconscious " —may transport energy from one axis of space into the other. The energy it needs for the process of turning as such is taken from the one axis and placed at the other : the sum of all the energies remains unaltered, there only are energetical changes with regard to the three chief co-ordinates x, y, and z, and thus the action of the vital principle would pass the boundaries of mechanics, *i.e.* of inertia, but not of energetics in general. But I can hardly agree that this complication is necessary. Entelechy *is* a natural agent *per se* ; why not assume that its action in changing the direction of force and energy is an action " *per se* " that is implied in its intensive manifoldness ? The laws of pure mechanics are broken in *any* case, and entelechy must by no means be imagined as a mechanical apparatus : it is just the negation of that. We must free ourselves from all the conventional images as completely as possible. You may say, if you like, that entelechy, when turning a mass particle, acts upon it at right-angles to its path—this kind of action requiring no energy—but even thus there would only be a pseudo-obedience to the laws of real mechanics, since entelechy must be regarded here as non-energetical, and as interfering with inertia at the same time.

The Suspending and the Transporting Action of Entelechy Discussed Together

If now we consider the theoretical probability of the two possible ways in which entelechy or anything non-mechanical whatever *may* influence mechanical systems, it seems to me that our first hypothetic statement dealing with the possibility of a suspension of becoming in mechanical systems offers several advantages which are not afforded by the doctrine of a changing of the direction of forces. According to the latter theory, entelechy would seem to be limited by practically nothing except the amount of existing energy, whilst, according to the former, it would be limited not only by energy as such but also by pre-existing differences with regard to velocities and potentials. And we do, in fact, see that entelechy *is* limited and restricted in its actions to a rather high degree. But I confess that the theory of " turning " and thus changing the direction of forces and energies must also be regarded as a possible solution of our problem. In any case, it would assume less than any hypothesis about the real creation of energy by entelechy.

The Hypothesis of Immaterial Resistance

But still a third form of interference on the part of entelechy with mechanics is imaginable, and this I shall call the *hypothesis of immaterial resistance.*

Think of walking in a large park in which it is " prohibited " to walk on the grass. The distribution of the people walking in the park will be a very specific one in this case, all of them using the roads.

Now let us imagine that entelechy also " prohibits " certain paths of motion to the elements of a material system, according to a particular design, as it were. In this case, all matter would move collectively on the territories of the system which are not " forbidden ", and in this negative way the plans of entelechy would be carried out. Matter would not be positively directed, it would be left to itself to a great extent ; but on certain points it would be rejected, just as rays of light are by the surface of a mirror, and perhaps even also according to the law of equal angles. That which " rejects " would be an *invisible immaterial resistance,* put by entelechy into the material system and comparable to an absolutely elastic material wall.

It seems to me that this view resembles certain hypotheses advocated by Noll about twenty years ago, and that it also resembles the theory of the *morphe* or the *morphogenetic field* as established by a modern Russian biological writer, A. Gurwitsch, a most careful study of whose important papers I strongly recommend.

CONCLUSIONS

If now, finally, we ask which of our three theories about the problem *entelechy and mechanics* is right, we simply confess that we do not know. We have had to deal with *imaginable possibilities* exclusively. But such a discussion has not been without value; on the contrary, as we have already said, it forms a necessary part of every vitalistic system that claims to be complete.

Let me only mention further that, in one respect, our third hypothesis about the relations between entelechy and matter has a certain advantage which we do not find in the two others: our third hypothesis would explain the *dualistic* character of the organism. The problem of dualism in general will be discussed in a later chapter; but what is meant by "organic" dualism may be easily understood even here. By this word we intend to denote the *fact* that entelechy only controls the *general* features of morphogenesis, but not the individual peculiarities, these peculiarities depending on the position of the single cells which are contingent. It is this *contingency* of the position of the single cells which our theory of immaterial resistance would explain.

Let us look back to the people walking in a park in which it is "prohibited" to leave the roads: nothing but the most general distribution of the individuals is fixed by this regulation. The same is true when a house is built: the architect does not prescribe where each single brick or stone is to be set. And, in the same way, the immaterial resistances, leaving matter to its own laws, with certain exceptions only, would explain that the general features of the organisation are guaranteed in their typical form and position, whilst the very *haecceïtas* of each individual, to use the scholastic phrase, is not.

Is there any "contradiction" to mechanics in our three hypothetic statements? Certainly, as far as the *exclusiveness* of mechanics is concerned. Wherever there is life in the universe something happens that is not present in the given mechanical constellations as such: something is introduced, not changing the quantitative side but changing the *actuality* and *direction* of mechanical events. But I should prefer to speak of a "contrast" instead of a "contradiction".

And, of course, there must be *some* such contrast—otherwise life would not be autonomous. And its autonomy has been proved.

4. HOW ENTELECHY IS AFFECTED

WE have discussed at full length how entelechy may possibly act with regard to an energetical or a mechanical inorganic system, or, in other words, what it may change in any way in such a system. But we have not even mentioned so far the corresponding question: how may changes in any inorganic system affect entelechy? But this problem, of course, needs at least to be mentioned as well as the other.

α. THE PRINCIPLE OF ACTION AND REACTION AS RELATED TO ENTELECHY

In the first place we are, I think, obliged to inquire whether in the work of entelechy there may occur anything comparable with the Newtonian principle of action and reaction, this principle, of course, being understood in the widest possible ontological sense. Of course, since, according to our theory, entelechy is neither an energy nor any factor of the mechanical type, the principle of reaction cannot apply to it in any physico-chemical or mechanical sense. But, even then, entelechy is an " agent " or a " factor " in nature, entelechy is a something acting univocally with regard to the inorganic, as we know, and therefore there must be something in this relation that is comparable with the principle of reaction in a general logical sense, though beyond inorganic causality. For all becoming—not inorganic causality alone—must always be conceived under the form of a mutual interaction. Whenever a factor A affects B, not only is B affected but so is also A. I believe now that we can easily find out how to relate the concept of a " reaction " to entelechy. Entelechy when performing any act in a system becomes changed with regard to its intensive actuality by this act itself; the "having done" changes its "doing", for doing is no longer necessary after having done. Thus entelechy is affected by the accomplishment of its own performance, in acting as well as in morphogenesis. We here meet the first case in which any kind of affection of entelechy occurs.

β. THE TYPES OF AFFECTION OF ENTELECHY

We now turn to a short survey of the possible ways in which entelechy may be affected by a mere change in inorganic nature as such.

Morphogenetic Entelechy

The organism, we know, is a system the single constituents of which are inorganic in themselves; only the whole constituted by them in their typical order or arrangement owes its specificity to entelechy. Therefore the single constituents of an organism also stand in energetical or mechanical possible relations to many external constituents of the inorganic universe. These possible relations may disturb the whole as governed by entelechy: by some such disturbance entelechy, in the first place, may be possibly affected—may be called into activity, so to say.

We here meet the problem of the stimuli of restitution and adaptation again.

In order that adaptation may happen, the functional state of the organism must be disturbed in its normality: this fact affects or calls forth entelechy.

In cases of restitution we were not able to state anything in detail about the precise stimulus that sets this process going: but, since in all restitutions the morphogenetic performance, though occurring on the basis of indefinite possibilities, was always in the most typical and specific relation to what had been disturbed, we were able to say that the stimulus of restitutions is most probably something connected with the *specificity* of the disturbance of the normal whole (page 84). This "something" must be regarded as affecting entelechy.

Let us not forget in this connection that we know a good many cases, where entelechy works, so to speak, *in vain*, where it seems to be "stupid" (page 266). And this may occur in two different forms. In Roux's experiment on the frog's egg, *e.g.*, the forming of half an embryo was going on whilst there was no possibility of forming the other half, and in the sea-urchin, as we know, the ectoderm with all its derivates may be fully built up whilst there is no endoderm. All cases of "self-differentiation" (page 77) may lead entelechy to such "stupid" acts. And, on the other hand, there is super-regeneration in many cases: an organ is "re"-generated though it was not missing at all; but, to speak in anthropomorphic terms, entelechy "thought" it was.

It is as if entelechy as a whole were split up into subentelechies, and as if these subentelechies, each for itself, received a certain message in the form of affection which they would also have received if their work had been really required. Thus they become "misled" and "mistaken". They know what they have to do upon a specific signal; but they don't supervise the whole. There are many human analogies—during a war, for example.

To sum up: morphogenetic entelechy in cases of adaptation or restitution is affected whenever the state of normality is changed by the effect of external becoming. Entelechy then at least tries to modify its suspension in such a way as to reduce that external becoming to normality.

But such a view fails in the face of *normal* development. Here, we know, fertilisation or some substitute for it is necessary in order that entelechy may come into action. What does that mean? It seems to me that we shall meet the point if we assume that fertilisation or its substitute affords here some necessary means, some necessary specific potential differences, as it were, without which entelechy is condemned to inactivity, just as it is in the absence of oxygen. Artificial parthenogenesis, as analysed by Loeb, lends strong support to such an hypothesis. But this would mean that even in the case of normal development entelechy is called into activity in the proper sense *by missing its normal result where it might exist* *potentially*, and thus normal development would be regarded as a mere example of all restitution. Fertilisation or its substitute would thus play a rather secondary part. It would not call forth entelechy by itself, but would only allow entelechy to act after it *had* been called into activity already by the mere existence of a living fragment of an organism.

Of course, this is no answer to the problem why the organism *does* actively form " fragments " in the service of " reproduction " ; but this problem leads beyond the theory of " personal " entelechy as the subject of embryology, and has already been mentioned on a former occasion.

Any restitution, like normal morphogenesis, is accomplished by a great number of consecutive single performances,[1] or, in other words, single stages. What about the manifestation of *each stage* by entelechy ? We may say here briefly, I believe, that the spatial existence of, say, the stage A affects entelechy with respect to its performance of the next act leading to stage B. Thus morphogenesis becomes a *series* of events that occur between matter and entelechy, and *vice versa*. New experiments are required in order to discover the details of this mutual connection, in which, of course, the "stupidity" of entelechy may play its rôle again.

The Affection of the Psychoid

As to the affection of the psychoid or the entelechy of real acting by external inorganic events, we must not forget that the concept of " normality " comes in here only so far as a certain actual liking and willing takes the place of normality ; to will a certain thing at a certain time is " normal " for the psychoid at that time.

If we restrict our analysis to such acting as ends in a distinctly visible result, say an object of art or of handicraft, we may say : the psychoid, its specific willing being given, is affected by the very *specificity* of combination of what there is, compared with what there ought to be according to its willing. In this way a printer or a painter will always take up his work at

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[1] Comp. the chapter on morphogenesis and time ; page 74 f.

the point where he left it the day before. A similar view would hold with respect to acting in general.

Psychologically all passivity, or rather receptivity of entelechy with regard to external changes, is expressed by the words sensation and sensibility. We can hardly avoid describing, at least analogically, what *must* happen in the affection of entelechy in general by words similar to these, just as we have spoken of a primary knowing and willing of entelechy. But, of course, our postulate that an affection of all entelechy by external changes *must* exist and that this affection relates to specificities of order or combination is more important than mere terminology.

As in discussing the affection of morphogenetic entelechy we came back to the stimuli of restitution, so here we could analyse again what we called " individualised stimuli " when we were discussing action. Both times the analysis of the type of affection of the vital " something " itself constitutes a proof of vitalism and forces us to call this " something " entelechy.

γ. THE CONTRAST BETWEEN AFFECTION IN THE ORGANIC AND THE INORGANIC

To sum up: Entelechy is *affected* and thus called into activity by *changes of any normality* governed by it which are due to external causes, and these changes *do not affect entelechy as a mere sum of changed singularities but as changes of normality as a whole.*

This point is very important, for, on the other hand, our careful analysis of the relation of entelechy to energetics and mechanics has taught us that the activity of entelechy relates immediately to *single* inorganic events, though in the service of normality.

The fundamental contrast between the affection of entelechy from without and any kind of affection in the Inorganic is well illustrated by the mere fact that in the case of entelechy the affecting inorganic combinations act as totalities. It was for this reason that we said that the " analysis of the type of affection " by itself forms here a proof of the " autonomy " of what happens; whilst in our discussion of the active rôle of entelechy, with regard to energetics and mechanics, we had to start from the autonomy of life as proved, and had to study what might follow from such autonomy with regard to *single* effects in inorganic nature.

All changes of normality that affect entelechy are "causes", of course, in so far as they are changes of given realities in space, though their effect is not an immediate spatial effect but one that has passed through entelechy. *Qua* causes, they are as specific as is their final spatial effect induced by entelechy. Thus we meet the strange fact here that, as regards biology, first cause and final effect are in the most intimate relation to one another with regard to *specificity*, though not in an immediate relation. This sort of relation between cause and effect occurs nowhere in the inorganic except in *pure* mechanics, and there in quite another form. A general ontological theory of relation—I do *not* say of " causality "—might take advantage of this most important logical fact.

GENERAL CONCLUSIONS

The contrast between the Non-living and the Living has appeared in all the discussions of this long part.

But the contrast always was a contrast with regard to nature, or rather *in* nature as the " Given " in space. We have at no time lost sight of nature by what we have said.

This contrast is indeed of a most fundamental character : there is quite a new type of natural becoming revealed to us, whenever entelechy is at work, actively increasing in a regulatory way the manifoldness of relation (p. 31) of a given material system on account of its intensive manifoldness after it has been affected by individualised stimuli. Inorganic becoming relates to extensities and is measured by energy ; we may say that energy measures the amount of causality which is spatial in itself. Entelechy is a diversity or a manifoldness in itself but not in the sense of spatial extensities ; therefore it has nothing to do with the amount of spatial causality as such, though it relates to events in space ; and therefore it is not measured by energy. In fact, entelechy is affected by and acts upon spatial causality as if it came out of an ultra-spatial dimension; *it does not act in space, it acts into space*; it is not in space, it only has points of manifestation in space.

But, after all, how does entelechy stand to causality? Is it a special type of causality itself?

I am sorry to say that the ultimate answer to this problem must once more be put off until considerations of another kind have been weighed.

We have charged entelechy with the minimum amount of non-physicochemical performing that is possible in regard to its dealing passively and actively with inorganic causality. Perhaps we have charged entelechy with too little, though what we have done stands in harmony with our actual knowledge, which has shown us *limits* of regulability at many points. Let us not forget that there may exist many realities which we do not know yet and possibly shall not know for some hundred years, on account of their minuteness perhaps—the word "realities" to be understood here in the sense of "possible objects of experience", as long as metaphysics is excluded. Let us not forget how recently the phenomena of radio-activity have become known to us. In other words: there may be still more fundamental actions done by entelechy than those which we at present know of and therefore admit. May not entelechy have an individualising action upon electrons directly? And what about the first origin of life? But here we are already touching some problems which belong to the next chapter.

Perhaps it will really become necessary some day to admit that entelechy not only suspends potentials, but that it creates potentials—perhaps by coupling or chaining uncoupled differences of intensity—and thereby creates energy; something similar would be expressible in purely dynamical terms. We have no reason to deal more fully here with such an assumption, which, of course, would have to consider the problem of the finiteness or infiniteness of the universe; for it was our endeavour in this chapter to draw only such theoretical conclusions as are nearly related to well-known facts.

At the end of this chapter, I should like to emphasise one particular topic.

We have *not* said that every single movement of an electron or proton within an organism is under the control of entelechy. Entelechy only interferes at certain points and at certain moments, and then leaves matter to itself; so it is in the realm of all three of our theories of entelechial interference. We are not going wrong, I believe, in saying that it is in particular the formation of enzymes or the activation of zymogens that is under the control of entelechy, in morphogenesis as well as in physiology. Entelechy acts, localising in space and in time, and then machine-work sets in—until entelechy interferes *de novo*.

C. ENTELECHY AND SUBSTANCE

a. INORGANIC SUBSTANCE

By the word "substance" philosophy means that which does not change during the change of its "properties", or, in short, *the unchangeable.*

Metaphysics centres in the problem of the real, the ultimate substance. But our present problem is not of so high a rank, and in this chapter we shall only deal with the concept of substance as used with regard to the non-living world, and we shall try to bring entelechy into relation with this concept.

In the realm of inorganic nature, substance is the same as *matter*, in the most general sense of the word (page 269), and therefore the relation between entelechy and matter is to be our first problem. Only occasionally shall we raise the question whether entelechy itself may deserve the name of a substance, the full discussion of this problem being reserved for the last part of the book, as is the discussion of the corresponding problem regarding causality.

In what follows we shall only use one fundamental result, common to all the different theories of substance relating to the Inorganic. Inorganic substance is a something consisting of single elements which are one beside the other *in extensity.* All particular extensities in the Inorganic are built up out of such substantial elements. That the substantial elements of inorganic nature relate to extensities and to extensities alone also holds good, if the substantial elements themselves are understood dynamically, that is, if they are regarded as certain elemental "spheres" in space which are each the seat of forces going out from a centre. Even in this case, though the centre of the force is a point and is not extensive in itself, the substantial element in space as such is an extensity. We have no desire to advocate the dynamical atomistic theory by what we have said, at least not without restrictions. We only wish to emphasise the fact that inorganic substance in *any* possible form relates to extensities; and that if it relates to varieties and manifoldnesses, it does so with regard to *extensive* ones and to nothing else.

We now turn to our proper field of research—biological philosophy in its relations to the category of substance.

β. ORGANIC "ASSIMILATION"

In the first place we shall have to deal with some characteristics of life which are by no means philosophical by themselves. These introductory remarks will serve at the same time to fill a certain gap in our survey of life phenomena.

RESPIRATION

Respiration and assimilation are generally regarded as the most fundamental functions of organic life—as the very foundations, indeed, of all physiology.

Respiration in its scientific meaning is the oxidation of any chemical compound of the body, that is, its combination with oxygen, in order, as text-books tell us, to provide a source of energy for functional performances. The compounds to be oxidised may be split into simpler ones before oxidation or they may not. The last result of the process of oxidation is the production of carbonic acid, uric acid, urea, and some other compounds, which are poisonous to the organism if care is not taken for their removal.

As we have said already, oxidation is generally regarded as a source of energy exclusively; or, better, as a source of so-called free energy, that is, energy that may do work on account of differences of coupled potentials. But this rôle of oxidation would never explain its absolute necessity. If such a doctrine were the whole truth, the stopping of oxidation would only stop the functioning of the organism; but the organism is not only damaged, it *dies* if oxidation is not allowed, and death is well known here *not* to be due merely to a poisoning by the final products of oxidation, such as carbonic acid, for the removing of which the most elaborate arrangements exist in the organism. Therefore, there must be yet another part played by oxidation. We should not be wrong, I suppose, to formulate this rôle in the following way:—The organism by its merely synthetic or analytic metabolism seems to produce some substances which are poisonous to it, *i.e.* which disturb the order of its metabolism in an irreparable manner if they are not converted into an innoxious form: *this conversion into an innoxious form is done by oxidation.*

For a long time, the foundations of organic oxidation were an absolute enigma to biology, and all sorts of theories were invented to solve it. All these theories, as, for instance, the one which utilises the effect of oxygen in its so-called active state (O_3), have become antiquated owing to the discoveries of the last decades. It was the mistake of all former theories of oxidation to look upon respiration as a process in which the organism plays an almost passive rôle. Either some compounds of the organism were regarded as attracting the oxygen of the medium by their own affinity, or oxygen itself was regarded as attracting parts of the organism. Modern biology has shown that oxidation is an *active* function on the part of the organism for the benefit of the whole. Wherever it is necessary either to destroy noxious compounds or to gain energetical potentials, the organism forms catalysers or calls into activity so-called zymogens, which set up oxidation that would otherwise not have taken place. The fuel consumed for the *supply of energy* consists generally of those constituents that are derived from the food—though hardly without some intermediate change first taking place—but it also may be more important constituents of the tissues themselves, as we have learnt in our analysis of the metabolism of fasting. Oxidation, as a mere *process of anti-poisoning,* attacks all the so-called by-products of metabolism in general.

Thus the most general result gained by modern biological research is the knowledge that oxidation is like all the other processes of metabolism ; that it is as regulable and as limited in its regulability as they ; that it only seems to be more important on account of its universal presence in all forms of life.

We therefore leave the theory of oxidation and approach the general subject of metabolism ; of this general subject oxidation has proved to be but a part.

" ASSIMILATION " AND " DISSIMILATION "

Metabolism, *i.e.* the change of chemical specificities during the differentiation, growth, and functioning of the organism, is generally considered under the two headings of " assimilation " and " dissimilation ". Few terms in science are more ambiguous and problematic in meaning, and few terms are used so freely and recklessly. Of course, nobody would mind if they were only used to signify that some of the processes in the organism which lead to chemical results proceed from the simpler to more complicated chemical compounds, while the rest proceed in the opposite direction. In that case one could only object that the words synthetic and analytic, as commonly used by chemists, would suffice for the needs of physiology also. But, as a rule, something else and something more is meant whenever the words " assimilation " and " dissimilation " are used — and this " something more " is extremely problematic.

We here must enter the realm of so-called physiological chemistry.

Whenever the words " assimilation " and " dissimilation " are to signify anything specifically determined — that is, something other than what chemists call " synthesis " and " analysis "—and whenever at the same time they claim to be used in any strict meaning at all, they *can* only mean that there is a something of a specific chemical nature, yet intimately bound up with life itself, which has the power of making other less complicated chemical materials *like itself* or of producing *from itself* less complicated materials by an analytical process.

Let it be clearly understood: the word "assimilation", as applied by certain authors, does not mean that there is a fundamental material *A* of given quantity, to which *external* means and forces add a further quantity, but it expresses that the material *A* increases by its *own* action at the cost of the components of the medium in the broadest sense.

Taking the word assimilation in this sense, the question of course would arise as to the kind of forces "assimilating", that is, equalising foreign materials to the material *A* and seated in *A* at the same time. But it seems to me that another question should be settled first, which is perhaps of a still deeper importance, though it does not sound so theoretical.

The "Living Substance" in the Chemical Sense

I am thinking of the very simple but very fundamental question: Does assimilation in the sense we have indicated really take place? Does the chemically distinctive substance *A*, the so-called "living substance", exist at all? Are there any criteria of its existence? There are in fact many theoretical authors who have answered these two questions affirmatively; and they have almost always been of the materialistic school. But is it not remarkable that the positive investigators of physiological chemistry never say one single word about the problematic material *A* and the problematic process of real "assimilation"?

What then does physiological chemistry really teach as the result of its experiments?

There are many specific chemical compounds present in the organism, belonging to different classes of the chemical system, and partly known in their constitution, partly unknown. But those that are not yet known will probably be known some day in the near future, and certainly there is no theoretical impossibility about discovering the constitution of albumen and how to "make" it. All the substances present in the organism have a definite range of possibilities regarding their physiological origin and their physiological destruction. They may originate in a certain number of different ways, and may be destroyed in a certain number of ways. Organisms behave differently in this respect. Fungi, for instance, are able to build up all the chief classes of their constituents—fats, carbohydrates, and albumen—out of one organic compound of rather variable constitution, while all animals require constituents of all three classes in their food, or, at least, are not able to live without receiving albumen. The modes of constructing and destroying the constituents of the organism almost always differ to a great extent from those used in the laboratory: to mention but one difference, what is done by heat in the laboratory is generally done by ferments in the organism. And, finally, upon this use of ferments by the organism depends the most remarkable feature of organic metabolism. Metabolism occurs in a regulatory manner which is to the benefit of the whole: at one moment one chemical construction goes on here and at another moment another chemical destruction occurs there, according as the need exists in those places; all the regulations, of course, being confined within certain limits presented by the fact that a certain sum of specific compounds forms the absolutely necessary food of the organism.

In these chief results of metabolistic physiology not a word has been said about our special living substance *A* and its "assimilation". In fact, the specific constituents of the organism may be said to be "assimilated" in so far as they are liable to an increase of their amount; but this pseudo-assimilation is always due to the action of some *other* constituent of the organism, never to themselves. Thus the word "assimilation" seems justifiable only so far as the organism as a whole is considered. In that sense, however, it would mean nothing of importance.

What then is gained by our discussion of the most general results of physiological chemistry for the central problem of this chapter, the problem of the relation of entelechy to substantiality? The facts suggest no reason for assuming that a "living substance", assimilating and dissimilating in the strict sense, is the real base and foundation of life. On the contrary, physiological chemistry knows nothing about a living substance and nothing about " assimilation " and " dissimilation ". The facts revealed by this science, though not amounting to a real proof of the operation of an autonomic factor in life, such as our entelechy, are certainly very easily reconcilable with its existence.

A chemical " living substance " has never been found.

γ. ENTELECHY INCOMPATIBLE WITH A " LIVING " CHEMICAL SUBSTANCE

We shall now regard our problem from its other side. We *know* that the facts show no indication of a " living substance " in the chemical sense, we further *know* that an autonomic regulatory factor is at work in organic processes. What then, let us ask, follows from the concept of this factor or agent itself with regard to the existence of a living substance of a specific chemical constitution, as the foundation of vitality ? Does an analysis of the concept of entelechy lead to the admission of a " living " chemical substance in spite of the negative facts of physiological chemistry, or do the results of such an analysis stand in harmony with our actual present knowledge of metabolism ? In the first case science would have to go and search for the " living substance " until it found it and could show it in a test-tube ; in the second case its main work might be said to be completed in this field.

I now hope to be able to show you from the meaning of the concept of entelechy—that being a well-established elemental agent in nature—that entelechy can be neither the consequence of any sort of specific chemical compound—when it might be represented by such a compound as " living substance "—nor the outcome or consequence of any constellation of different specific chemical compounds of any sort, which might otherwise perhaps be regarded as the *materia viva*.

Entelechy, we know, is an intensive manifoldness, *i.e.* it is an agent acting manifoldly without being in itself manifold in space or extensity. Entelechy therefore is only an agent that arranges, but not an agent that possesses quantity.

What then would be the significance of saying that a specific chemical substance is the bearer of entelechy ? To say so would be to attribute the property of extensity to a something that has nothing to do with extensity at all, to a something which in a certain respect may be said to be the negation of extensity.

It gives a good idea of the strange consequences to which the doctrine of a " living substance " as the bearer of autonomic entelechy would lead, to recall the fact that, of course, a living substance in the sense of a specific chemical compound would be measurable by weight like any other chemical compound. We should have to speak of, say, six pounds of lion-substance, or a pound and a half of eagle-substance, or three ounces of earthworm-substance ; and all these chemical compounds would some day be sold in the market perhaps. We here see most clearly that it is quite impossible to assign the characteristic of extensity to an agent which is simply a determinant of *order in* extensities ; for our lion-substance, of course, would not signify so much of the actual substance of a given lion, but would mean so many pounds of that *homogeneous* chemical material which is supposed to represent the " being-a-lion ".

Of course nothing is said by our remarks against the hypothesis that there may exist real chemical compounds which are characteristic of organic specificity in the sense of being necessary means of morphogenesis, and which perhaps play their rôle in the process of inheritance as far as its material side is concerned. In fact, the discoveries in hybridisation, as we know, seem to advocate such a view to a certain extent. These substances, however, are by no means identical with entelechy, but are used by entelechy.

There is still another very grave objection against the material character of entelechy : if it were material it would be subject to energetical changes, for it would be energetical itself ; but that we have seen is an impossibility. And, moreover, to assume that the disintegration of a certain amount of chemical material, homogeneous in itself, could explain real differentiation during ontogeny, would clearly contradict the principle of univocal determination (page 248).

But now you might reply to our discussion : " Good, a specific chemical compound cannot be the basis of entelechy in the sense that entelechy always appears whenever this compound is formed, by the very fact of its formation. But could not entelechy be a consequence of a specific relative constellation of different chemical compounds of specific states of aggregation ? Could there not appear a new and elemental factor owing to the constellation of some other factors already known ? Do we not see such an event happen whenever electricity is generated by rubbing a glass rod ? "

Let us try to answer this objection at first in a narrower sense. If the typical constellation of the inorganic agents *A*, *B*, *C*, and *D* is to originate a new sort of activity, which does not come to them from without, but is regarded as their true and real consequence, how would it be conceivable at all unless you imagine that one of the four constituents, *A*, *B*, *C*, and *D*, possessed the new agent in question already in a state of potentiality, comparable to the state of a so-called zymogen in fermentation, which is waiting to be transformed into a ferment ? But, if it gives this turn to the problem, the constellation-theory represents no great advance on the purely chemical theory of entelechy already refuted. One of the four elements of the hypothetic constellation creating entelechy would have to perform almost the same rôle that is performed by the specific compound of the chemical doctrine.

But to pass to more general considerations : is it at all possible that new elemental kinds of natural changes can be created by the mere constellation of agents already known ? Can such a constellation possibly be followed by more than a mere resultant action of the sum of the elemental actions of its constituents ?

It has been said occasionally by modern writers that a system, by the mere increase of its amount of material, may begin to exhibit marked differences in its behaviour. Take for instance a homogeneous sphere in rotation. It will simply be flattened at its poles if it is small ; but a large sphere of the same material and moving with the same angular velocity will throw off its equatorial substance in the form of a ring, and a satellite may be formed out of it ; for the absolute amount of peripheral velocity increases enormously with the increase of the total amount of substance. So there *may* result very different definitive forms from systems which differed only in size at the outset.

But, of course, it is clear from the very beginning that the origin of new *elemental* factors is not touched at all in this example.

But how about the relation of rubbing a glass rod to electricity; how about the rise of the electric current from chemical potentials, as we see in the familiar galvanic cell ?

It is true that at the first glance there may seem to be a real creation of something fundamentally new by a mere constellation : phenomenalism in its purest form, in fact, would advocate such a view. But the history of physics shows that it is impossible for human reason to rest content with such a conception. Science always has been in search of some pre-existence of what seemed to be new, and, in fact, science has always managed to find this pre-existence in some way. Either it has attributed the new thing that arose to what existed already, endowing the latter with it in the form of a potentiality, expressed under the name of a so-called " constant ", or it has gone further and has tried to conceive the possibility under the form of a substantiality. Mathematical phenomenalism takes the first line, the modern theory of electricity follows the second ; the mere E of the first, marking the " being potentially electric " as an irreducibility, becomes the electron of the second, in the sense of the elemental quantity of the new phenomenality in question. In some respect our mind is satisfied by both methods, though more by the second. For our present purpose it is enough to know that there exists in our mind a demand for some such satisfaction : newly arising elemental agents must be conceived as already pre-existing in some way.

It will have become quite clear, I hope, from our discussion, that any theory which tries to make entelechy arise as a new elemental consequence of some constellation must result in taking one of the constituents in the real sense of a " living-substance ". But the living-substance theory has been already refuted.

Thus "hylozoïsm", of whatever a form, has been disproved.

The *existence* of entelechy, then, depends in no form whatever on anything that is material, though its *activity* may be related to material conditions. But this is something very different. The activity of an architect depends on the existence of stones. But would you care to say that the architect's existence depends on—stones? A heap of stones without an architect is a heap of stones, and the matter of an organism without entelechy is an amount of matter.

I even dare to say that, if it were possible to construct artificially the material constellation of an egg in all its details, you would have constructed—not an egg in the beginning of its development, *but an egg at the moment of death.*

Entelechy cannot be regarded as arising from material conditions of any sort. What follows from this result for the facts of physiological chemistry, which formed one of the earlier parts of this chapter? It follows, so it seems to me, that what physiological chemistry studies is only *results that are chemically characterised*—not results of processes that are *chemical processes.* It is very important to understand well what this means. Of course, chemical potentials have formed the general basis of all physiological chemical results, but these results, as we know, are not due to the mere play of these potentials as such, but to the intervention of entelechy; therefore something purely chemical is found in the results only, but not in the processes. Without entelechy there would be other chemical results.

Entelechy controls not only oxidation but "assimilation" and "dissimilation" also; without it a chaos of chemical processes would occur, and would soon disturb organisation and functioning. Previous analytical work has taught us that entelechy may act by means of setting free pre-existing potentials the compensation of which it has suspended before; this applies also to its work in the fundamental phenomena of all physiology. It probably is the production and actuation of ferments that is immediately controlled here, oxidation or any kind of chemical synthesis or analysis thus being purely chemical processes that *follow* the fundamental vital act.

Thus metabolism is not the " foundation " of life, but its *effect*.

In a certain respect the problem dealt with in our present considerations is identical with the famous Aristotelian question whether the concept of a house be subordinated—in more than a formal manner—to the concepts of wood or stone as its higher classes. Aristotle answers the question negatively, as we should do also. But it is exactly the same thing, only in a still more general form, to deny that entelechy itself is connected with or dependent on chemical substances.

And still another famous problem has been solved by us implicitly : the " enigma " *how* it might be possible for matter to " think ", a question which plays a great part in one of the well-known addresses of Emil du Bois-Reymond. The answer is simple, for the problem is a pseudo-problem : " matter " not only does *not* " think ", but " matter " is not even the foundation of life in *any* sense. And, therefore, the question of " how " matter thinks does not even arise.

δ. SUBSTANCE AS A CATEGORY IN ITS RELATION TO ENTELECHY

By proving that entelechy is not identical with or a consequence of any chemical compound, or the constellation of such compounds, we by no means have solved the problem which deals with the relation between entelechy and substance as a *category*. May not entelechy though absolutely unlike everything that can be called substance in the inorganic world—whether it be conceived purely chemically or in the sense of a theory of matter—may not entelechy be called a " substance " in the most general philosophical sense of the word, that is, in the sense of a something irreducible, which remains the always unchangeable bearer of its changeable qualities ?

Then there would be two substances with regard to nature, and our theory would become very similar to some theories of the past, though with the remarkable difference that our view would not allow us to regard one of these two substances as " psychical ", as all other similar theories have done. There would be one spatially extended substance—" matter "—and one non-spatial intensive substance—" entelechy "—both substances forming part of *nature*.

Let us first note a few very characteristic features of what may be called the behaviour of entelechies ; the analysis may perhaps afford us materials to decide our problem.

The Concept of Divisibility not applicable to Entelechy

At the risk of shocking you with an apparent absurdity, I might say that entelechy has the power of preserving its specific intensive manifoldness in spite of being divided into two or more parts. The fact which we have called the genesis of complex-equipotential systems seems to favour this view at the first glance, and so do all the experiments relating to the development of isolated blastomeres of a germ into whole organisms of smaller proportions. Moreover, we directly founded our second proof of vitalism upon the evidence that, though a typical machine-like constellation of agents, different in its arrangement along the three axes of space, cannot be divided and remain whole at the same time, yet there exists in the living organism a something which *does* show these two incompatible characters.

The question now arises whether in a deeper sense we are entitled to speak of entelechy as remaining whole in spite of its " division " into parts.

It is very difficult to free the philosophical analysis of entelechy from all that is familiar to us from our acquaintance with extensive phenomena ; and yet we *must* free it from all that belongs to extensity. It was the great achievement of Kant to show that space is the inevitable form of our intuition of the Extensive. Now, as to entelechy, there is no intuition, and therefore space and all sorts of relations about space have practically nothing to do with entelechy. Entelechy itself is *con*ceived only ; it is *per*ceived only in its extensive results. Entelechy is not spatial, but only acts into space—I do not say

" in " space—and the word " into ", of course, is itself not at all of a " spatial " character here. In this respect, as will come out fully later on, there is quite a gulf between entelechy and such natural agents as forces and energies, though the latter are also concepts, not percepts. Now it is clear that " dividing " is always understood as something spatial, and therefore it follows from all we have said that this word in its strict meaning is not at all applicable to entelechy. When we speak of " dividing " we always think of a something which we can cut into pieces. But entelechy cannot be cut in this manner, for the simple reason that it has no spatial dimensions at all : the " having dimensions " would contradict altogether the meaning of the term.

Therefore we had better not speak of entelechy as an agent which " remains whole in spite of its division into parts ", but simply say that entelechy may manifest itself wholly even after the division of a certain organic body, on which, had it remained one whole, entelechy would have manifested itself as *one* whole also. Entelechy always *manifests* itself individually : but our analysis proves that so-called individuality of the real organic *body* is not without further discussion to be identified with the deeper meaning of entelechian individuality.

So much at present about this important problem.

The Concept of Localisation or Seat not applicable to Entelechy

An agent which is of a non-spatial nature cannot be said to have a definite seat or a definite localisation in space. Entelechy therefore cannot possess a " seat ". It cannot at all be imagined like a point consisting of a something and moving through space, now in this and now in that direction. Descartes, as is well known, regarded the soul as having its seat in a specific organ of the brain, the so-called pineal gland. We may follow him so far as to say that there may be specific points of the organism with respect to which entelechy is active while at other points it is inactive. But these would only be points of mutual relation, not points of rest.

" Entelechy " so far a Mere System of Negations

I fully see how difficult it is to say anything positive about entelechy without contradicting other statements regarding it. I say once more that there is nothing at all to be " imagined " in a picture-like manner about entelechy : the non-spatial can never be realised by our imagination in spatial images. It may be hard on us, but so it is. And at the same time we always must bear in mind that in dealing with entelechy we are not dealing with anything psychical : we are analysing an agent at work in nature. We know concerning this factor that it cannot be spatial in any sense, that it has no seat in space nor any dimensions, but merely acts " into " space ; in one word, that it " is " not in spatial nature but only acts with regard to spatial nature.

In fact, the characteristics of entelechy form only a complicated system of *negations* so far, and little more. Nor can it be otherwise, unless we are prepared to change our whole view of reality, and of natural reality in particular, as in fact we very soon shall.

And thus at present the question whether entelechy is a " substance " must remain as open as the previous question about the relation of entelechy to causality. Entelechy was a kind of " quasi " causality, and now may be said to be an enduring " quasi " substance. But still we feel that our reason craves more than this.

ε. INSOLUBLE PROBLEMS

At the end of this chapter you probably will expect the discussion of a few questions which interest you more than any others, and the answering of which perhaps you have hoped would be the final result of all our analysis. But such remarks as I am able to offer about the origin and end of individual life, and the origin of life in general, can claim merely a subjective value. Materialists profess to know a good deal about all these eternal problems, but I confess that I know nothing at all about any of them.

The Origin and the End of Individual Life

In the face of these fundamental questions let us remember, firstly, that our present task is neither a truly psychological nor a metaphysical one. We therefore have nothing to do with the problems of immortality as relating to the Ego ; we are only studying phenomena in respect to the Ego. In fact, even if a " principle of the conservation of entelechy " could be established, and if we were able to speak about what might be called a phenomenological metempsychosis, it would all relate to phenomena in the first place, and it is well worth noticing that without further discussion spiritualistic phenomena, if proved some day, would also be mere phenomena to the Ego and nothing else. At the end of this book we shall devote some time to certain considerations that might probably lead us beyond this theoretical Egoism.

With the starting of a new actual individual, entelechy begins a new manifestation, and with death it ends one ; that is all we can say. What that manifestation, *qua individual*, was before that beginning, and what it is after death, is absolutely unknown to us. We are not even able to say whether it was and will be anything " individual " at all in these two periods or not —the words " was " and " will be " to be understood in a non-metaphysical sense, that is to say, in the sense of a " possible immediate experience ". For the ideal or Platonic existence of entelechy as an individualising agent does not, of course, guarantee any sort of permanence of the individuals which, on account of an entelechian manifestation, form part of the given universe at a given time.

What science knows about death is simply this : a certain amount of matter that was formerly controlled by entelechy becomes freed from this control, and then obeys the laws of physico-chemical causality exclusively. Does entelechy actively withdraw from matter or not, and, if actively, then why ? Why has " regulation " become impossible ?

J. Loeb has told us that each organic individual carries with itself from the beginning a certain amount of a certain chemical substance, characteristic for each species, and that life ends when that amount is, so to speak, used up. This theory is supported by the fact that cold-blooded animals live longer in low than in high temperature, as would be expected if something chemical stands in question. But why is that mysterious substance unable to be newly " assimilated ", as all other substances in the organism are ? And we know, on the other hand, that infusoria may multiply by mere division innumerable times and are materially " immortal " in this way—at least as far as there is no " corpse ". And the chain of sexual cells, connecting the series of generations materially, is " immortal " too. Why is just the life of the individual bound to a material substance that is used up ? We do not understand the main point.

R. Pearl, on the other hand, has confirmed the important discovery of Carrel, that *isolated* tissue cells, say of the chick, live longer than the normal life duration of the species prescribes. *Within* the individual, so he says, the tissues are poisoning one another, and this mutual poisoning leads to death. But why are the sexual cells not poisoned ? Again we are only moving on the periphery of the problem.

But enough of unapproachable questions—at least in this chapter.

Personal material death is a fact—that is all we know.

The Origin of Life in General

The question about the so-called primary origin of life is as incapable of being discussed as is the problem of death, in spite of the great number of popular works written about it. We certainly cannot grant that life has originated by a fortuitous concourse of inorganic constituents—that is clear, without any further discussion, from our analysis of entelechy in its relation to matter in general. Constellations do not create entelechy, but entelechy governs constellation. But nothing can be said concerning the absolutely primordial relations between entelechy and elemental materiality.

Whilst speaking about entelechy in its relation to intensities of energy, we mentioned that our theory postulates the continuity of life, which is well illustrated by the fact of inheritance.

From this we may conclude that there are no gaps in entelechian manifestations: there is a continuity of a constellation of specific kinds of matter always maintained by entelechy, always overcome, so to say, by its suspension of inorganic becoming.

If we accept the theory of descent, we may say that the type of manifestations of entelechy has changed in the course of their continuous line. But we never come to any kind of beginning.

In any case it must appear very strange that life is only known to us in immediate relation with very complex chemical compounds of a few classes. Why does not entelechy act upon the elements of matter directly? Or is the present state of relation between entelechy and matter a consequence of the long time that life has continuously existed? Has entelechy, so to say, altered its behaviour with regard to matter? Or are we simply in ignorance of other types of its manifestations?

We know that the green plants and certain kinds of bacteria are able to make use of so-called inorganic compounds (H_2O, CO_2, nitrates, etc.) for their synthetic metabolism. But—they are not "inorganic" themselves. Where did they come from?

And so the series of questions and problems might be continued—but there are no answers.

PART II

BIOLOGY AND PSYCHOLOGY

WE now enter the area of philosophy proper, and begin with some remarks on the relation between our vitalistic biology and *psychology*, leaving it to the reader to decide whether he regards psychology as a part of philosophy proper or not.

The relation between so-called *consciousness* and matter is the first problem that comes upon the scene. I say " so-called " consciousness, for the term " the consciousness " may suggest that the matter in question is of the type of a thing or even of a box—(think of the very bad and misleading expression, a " content of consciousness ")—and this is by no means clear at the very beginning. We, therefore, had better say that we shall first study the *relation between conscious phenomena and matter*. Now, it is a well-known fact that conscious phenomena can only be studied by introspection, at least in an immediate way ; or, in other terms, that *I* know *my* conscious phenomena exclusively, at least, in an immediate way. Let us then try to find out something about the relations between *my* conscious phenomena and *my* material body.

1. A CRITICISM OF PSYCHO-PHYSICAL PARALLELISM

So-called *psycho-physical parallelism* is a well-known theory that may be said to go back to the metaphysics of Spinoza, but was first established as a real scientific hypothesis by Fechner. Psycho-*mechanical* parallelism would be a better name for the theory in question, for this theory looks upon the brain as a purely mechanical system and pretends that there exists a " parallelism " between my conscious phenomena and the mechanics of my brain, both of them being ultimately one and the same thing seen from two different points of view —*una eademque res, sed duobus modis expressa*, in the words of Spinoza.

It is not very difficult for us to refute the usual parallelistic theory in a definitive way.

And our analysis of human action *has* already been a complete refutation, for we have been able to show that, even on the material side, the acting man is not a mechanical machine, but that his brain is used by a non-mechanical agent which we have called *entelechy* or *psychoid*. By this argument, a necessary implication of the usual parallelistic theory has been shown to be wrong, namely, that there *is* a "mechanics" of the brain during acting. And, according to a well-known principle of general logic, the destruction of an implication or consequence of a theorem destroys the theorem itself. Thus, then, there is *no* "psycho-mechanical parallelism"; for there is *no* "mechanics" in question.

There is still another argument against the usual form of parallelism, proceeding along very different lines, *i.e.* by comparing the "degree of manifoldness" between the Mechanical and the Psychical, in the sense of "my conscious possessions". But this argument does not belong here; it has been fully explained in my book on *Mind and Body*,[1] and in my *Crisis in Psychology*.[2]

But, though it has been rather easy to prove that psycho-*mechanical* parallelism is wrong, we have by no means refuted psycho-*physical* parallelism, in the most general sense of the word. On the contrary, we are forced to advocate a particular form of psycho-physical parallelism ourselves; and we may speak of a parallelism between the sequence of my conscious phenomena and the dynamics of the psychoid (or entelechy) of my body.

Psychological text-books tell us that if psycho-physical parallelism is wrong, the theory of so-called psycho-physical interaction must be true. But matters are far from being so simple. There certainly is no "interaction" between the matter

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[1] London, 1927, p. 67 ff.

[2] Princeton, 1925, p. 138 ff.

of my body, and of my brain in particular, on the one side, and my conscious phenomena *qua* "conscious" phenomena, on the other. For my conscious phenomena do not "act" in any way; they simply exist with respect to the Ego, they are *had* or *possessed* by the Ego—to use a very neutral term.

However, a kind of "interaction" is, beyond any doubt, in question. But this interaction occurs *within* the realm of the *Physis*, *i.e.* of Nature; entelechy, as a natural agent, acting upon the matter of the body and *vice versa*. And this entelechial-mechanical *interaction* within the sphere of Nature goes hand-in-hand with a *parallelism* between the acting of unconscious entelechy on the one side and the conscious life of the Ego on the other.

But this is not yet all there is to be said.

Seen from the purely psychological side, entelechy, or at least that part of it which regulates action, *i.e.* our psychoid, is the same entity which is usually called *soul* or *mind*, being the (unconscious) ultimate foundation of the (conscious) Ego, with all his experiences. If now we make use of this truly psychological concept we see that there are as many as three "parallels": acting of my soul = acting of entelechy (psychoid) of my body = my conscious life.

Metaphysically, of course, my soul and my body's psychoid are the same entity, and thus we may end the discussion with the statement: interaction within "nature" between soul-entelechy and matter, parallelism between soul-entelechy's dynamics and the Ego's conscious life.

This is the exact formula of what happens.

2. The Living of Life

The parallelism between my entelechy, as far at least as it is psychoid, and my conscious life may properly be expressed by the words *I live my life*.[1] And it is these words which we must now analyse a little further.

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[1] In German: *Ich erlebe mein Leben*; there is no corresponding short English expression for *erleben*, even the word to *experience* being not quite the same.

I live my life—but I " live " in the conscious way only a very small part of it. Of the rest *I* know nothing and will nothing. The embryology of my body, the physiological processes in my body, the healing of wounds—all this occurs, thanks to entelechy, in the sphere of the Unconscious, which, however, for this reason, is by no means mechanical.

And even from the point of view of pure introspective psychology, which puts the *soul* in the place of entelechy or psychoid, there are great gaps with regard to immediate conscious experience. If, for instance, we " think over " a problem, say a mathematical one, the Ego *qua* conscious Ego *does nothing*, but simply waits for the doing of " somebody else ", *i.e.* of the unconscious mind or soul.

In this way the conscious " living of life " does not even relate to that side of entelechy which we have called psychoid in its completeness. There is, then, *no* " living of life " *at all*, as far as the morphogenetic and properly physiological side of entelechy comes into account; and with regard to the psychoid side of entelechy, only *a very small part* of entelechy's action is accompanied by the conscious living of the Ego in a " parallel " way.

Let me illustrate the second part of this statement by a simple example: What about my conscious *living of life*, if I " will " something? I want to drink water from a glass on the table. This is the only thing which *I* consciously " will ". And then that which happens is the following sequence of events: stimulation of a motor centre in the brain of my body, stimulation of a motor nerve, contraction of certain muscles of my arm and my fingers, etc., etc. All these processes are *not* " willed ", nay, they are not even known to me, unless I am a physiologist. And yet they occur, carried out by my body's psychoid.

Here we see that *conscious* experience is a mere index of certain states of my psychoid, or my soul, if matters are regarded from the psychologist's point of view. Conscious experiences, in fact, may be called *epiphenomena* parallelly related, not, of course, to the mechanics of my brain, but to the states of the entelechy of my body.

Why do these conscious epiphenomena exist at all if, *qua* conscious phenomena, they seem to be a mere additional luxury to the dynamics of the unconscious soul (or psychoid) which alone is really effective ? But this question is to interest us in the last chapter of this book.

3. On Certain Forms of Connection between Conscious Phenomena and Vital Processes

In this place we leave the matter as it stands and briefly discuss another interesting question : Which kinds of conscious experiences are known to be in *connection*—I do not say "causal" connection—with vital processes ?

We know already that the conscious experience of *willing* belongs here, and that this is connected with the stimulation of motor nerves and with muscular contraction. But there are more such kinds of connection.

Pawlow has made the important discovery that certain feelings, as, *e.g.*, the feeling of hunger, and certain sensations, as the smelling of good food, may have as their sequence—(again I avoid speaking of " causal " sequence)—secretion on the part of the salivary and other glands. This connection is subjected to the law of association, and dogs, *e.g.*, could be trained in such a way that secretion began upon the sound of a specific tune, if, in the past, this tune had always been heard when food was offered.

It is also a well-known fact that certain emotions make the heart beat, or are connected with transpiration, trembling, blushing, etc.

In the third place we have the physiological effects of suggestion and auto-suggestion, so well studied in our days by Coué, Baudouin, and their school. Bleeding may be stopped or provoked, as in so-called stigmatisation, and very many other physiological processes may be called forth by—(or rather " after ")—suggestive commands. And if this book had to deal with *Psychical Research*, there would be a still greater number of other cases of connection between conscious shapes and material processes in the organism.

But almost nothing is understood here, even in the field of normality, and we therefore turn to other problems.

4. The Problem of a Univocal Causal Connection between Conscious Phenomena and Cerebral States

We have refuted the theory of psycho-mechanical parallelism, *i.e.* the hypothesis that every conscious experience *is* a certain material state in the brain seen " from the other side ". But might it not be that every single conscious experience during the so-called " stream of consciousness " is univocally *related* to a certain material state in the brain, there being a specific causal relation between matter and entelechy (or psychoid) in every single case, a relation of which the conscious experience is an index ?

There certainly is such a univocal connection in the case of sensation, quite apart from the problem whether J. Mueller's law of " specific energy " of the single nerve fibres or the single localities in the brain be right or wrong (page 224 f.). With regard to all other sorts of conscious experiences, however, as, *e.g.*, feelings, willings, " thoughts ", etc., the question of univocal correlation must at least remain open. Bergson and Carr have advocated the view that no such univocal co-ordination exists; that, in other terms, the same specific state may exist many times in the material brain and yet the conscious experiences be different in each case. This would mean that there is a sort of causal connection *within* the psychoid (or, from the other point of view, the soul), besides the causal relations between psychoid on the one side and matter on the other. There would be what we might call an *intra-entelechial* (or intra-psychical) *series* of causal events, the singularities of which are *not* related to the material side of the body *qua* singularities.

I regard it as highly probable that this intra-entelechial series exists. For it seems to me that all objections against psycho-mechanical parallelism also hold good against the theory that every single conscious experience is connected in a causal way with a specific single material brain state. For the momentaneous state of the brain *qua* material brain is a state of matter and of nothing but matter, *i.e.* a specific constellation of electrons and protons, and it is impossible to imagine how mere diversities of *constellation* should be univocally related to the *qualitative* diversities in conscious life.

If our views were true, this would mean that entelechy (or "the mind") is an *ens* with its own inner causal dynamics, which only occasionally influences the material body with which it is connected, and is only occasionally influenced by it. But, of course, we are moving on very hypothetical grounds here.

5. The Psycho-Physical Person

Conscious life can only be experienced in an immediate way by the one who is in possession of it. Or, in strict *solipsistic* terms, *I* know about *my* conscious life exclusively.

My body, on the other hand, is but one among many bodies of the same or of a similar kind, an organic body. And yet *my* body is unique to me in some respects, for all sensations of pain, all so-called motor (kinesthetic) sensations, and a good many other things are only experienced by myself when *my* body is stimulated. Other bodies may only be "seen" or "touched".

My body in its uniqueness and *I*, in the strict solipsistic sense, form a duality which, though a duality, is inseparable, as far as experience goes. Let us call this inseparable duality: *my psycho-physical person*. But let it be well understood that this is only a short expression for a rather complicated set of relations, which we explained whilst speaking of parallelism: there is the matter of my body in its causal relation to my body's entelechy; part of this entelechy, the psychoid, is in "parallel" relation to my soul, as established in psychology proper, and part of this psychoid-soul is self-conscious in the form of *I*.

In a popular way I am allowed to speak of *many* psycho-physical persons, viz., the other men, and, in a wider sense, all organisms. It is true, in an immediate way these *other* persons are only known to me as *bodies* endowed with a certain *behaviour*. But on analogy I say that these bodies, behaving in a particular way, which leads to the concept of their entelechy and psychoid, are also related in a very complicated way with a *soul* and an *Ego*.

The problem of the " other Ego " has been very much discussed among German philosophers during the last twenty years. Personally, I should like to advocate the old theory of " analogy " with regard to this point. For I do not believe that the knowledge of the " other Ego " is given to us in an immediate aprioristic manner.[1]

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[1] For a full discussion, comp. *Crisis in Psychology*, page 105 ff.

PART III

BIOLOGY AND LOGIC

1. The "Essence" of an Organic Being

In any case, whether the theory of analogy be right or wrong, there are in practice *many* psycho-physical persons. What is the very *essence* of these persons ? Or, in other terms, what is the very nucleus of a living psycho-physical person ?

Let us discuss this question a little more fully.[1]

A dog " has " legs, eyes, etc., an oak " has " leaves. *Who* is the one that " has " in these cases ? The popular answer to this question will be that " the dog " or " the oak " has them. But who is " the dog " and " the oak " ? Is this nothing but the body of a dog or an oak minus legs or leaves ? Is it not, rather, a certain totality which is incomplete if legs or leaves are taken away ? But what do the words " totality " and " incomplete " mean here ?

And a good many other complications enter the scene. Let us put an earthworm in the place of our dog : if we cut off the head of the worm, it will regenerate. Who " has " the faculty of regeneration, and, even more, who " has " the faculty of propagation ? Quite certainly not the matter of the earthworm's body *qua* matter.

Thus we come back to our entelechy, this being the " very nucleus " of a living person we are in search of. *Entelechy* is this essence and entelechy " has " all the features we have mentioned. The body with all its different parts is nothing but a manifestation of entelechy. Or, rather, it is the effect of

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[1] A complete discussion of these problems is to be found in my little book *Der Begriff der organischen Form*, Berlin, 1919.

entelechy as far as entelechy has manifested itself into matter. For entelechy is more than the results of its manifestation; it also embraces all potencies for further manifestation, such as regeneration and propagation, for instance. And all sorts of adaptive manifestation are also implied in entelechy.

Entelechy, then, is a living person's essence. And this essence exists at a given moment in a double form: in part it has actually manifested itself, in part it has the potency for manifestation.

It, therefore, possesses the faculty of transforming potentialities into actualities. Entelechy as we know (page 279 f.), is affected by material conditions and always reacts to this affection in quite a particular way, transforming from potentiality into actuality that part of its *intensive manifoldness* (page 245) which must be transformed in order to establish or to re-establish *the individual whole* in its material existence.

Or, to express the same thing in different words: there are certain material systems in nature, the organisms, which are of such a kind that, after a change of their own constellation or after a change of the medium, something happens in them which restores wholeness. The ultimate source of that which happens we call *entelechy*. This entelechy is the expression of a certain permanent totality *qua* totality in the form of a typical (intensive) manifoldness; and it is at the same time an agent or factor in nature, as far as it may transform some of its sides from the potential into the actual or dynamic state, this transformation leading to an extensive manifoldness of a particular kind, *i.e.* certain specific events and results in the realm of a certain material system, called the organism or the psycho-physical person.

It seems to be a consequence of what we have said that entelechy is *substance* as well as *causality*,[1] and thus the two

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[1] We might also call entelechy a *constant* in the most general sense (page 267 f.), for it is responsible for the specificity of that which occurs in a certain system controlled by it, in the same way in which the final temperature of a piece of iron not only depends on the amount of heat which this piece receives from outside, but on its own "specific heat" also. But, of course, the *constant* of iron relates to quantity exclusively, whilst the essence of entelechy relates to order. Because of this difference, I do not lay much stress upon the concept of *constant* as applied to entelechy.

questions we have raised in several preceding chapters seem now to be answered: entelechy seems to be "substance" in so far as it is a "permanent totality", and "causality" in so far as it is an "agent or factor" in nature.

And yet our answer is not quite definitive.

Remember that the concept of *wholeness* or *totality* has been several times applied by us, and it is this concept which now requires further analysis.

2. The Concept of Wholeness or Individuality

a. THE CONCEPT ITSELF

We have spoken of a "further analysis" of the concept of wholeness, and must now confess, at the very beginning, that just an *analysis, i.e.* a proper definition of this concept, is impossible.

What *totality* or *individuality* or *wholeness* means is known to everybody—but by immediate intuition exclusively.

This is the case with a good many other concepts too. Try to "define" what *not,* what *relation,* what *so many* means, and you will see that you are only able to define these terms by applying the meaning that is to be defined; in other words, that you are only able to "define" by a circle.

So it is with our concept,[1] except in the realm of pure logic, which deals exclusively with concepts or meanings *qua* concepts or meanings. Here you may say that a concept is *whole,* because its essence is destroyed as soon as you take away any element. The concept A is no longer A in this case, but is replaced by a concept from among the great variety of the *Non-A's*. Suppose that A is a "rectangular triangle of red colour". Take away "red colour" and you have

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[1] The reader who is acquainted with the philosophy of Kant may be told that a so-called "deduction" of the category of wholeness or individuality from the "table of judgments" may easily be given, if the complete conjunctive judgment (S is P_1 and P_2 and P_3 and . . . Pn) is added to the judgments of relation. I have tried this deduction in an article in *Kantstudien*, vol. xvi. In effect, I believe that Kant's deduction is a kind of self-illusion. For how did he find the "table of judgments" except by immediate intuition? But it has been interesting to show that, if you accept the Kantian deduction altogether, a "deduction" of the new category is also possible.

" rectangular triangle ", which is not the former concept A, but a new concept B.

So much for *logical* wholeness or individuality.

Let us speak of *objective* wholeness or individuality as soon as we enter the sphere of " things " and " events ", *i.e.* of empirical reality. Things and events are not concepts, but are meant or designed *by* concepts, as if they existed independently—this at least, as long as metaphysics is avoided.

Now we know well that a table, a steam engine, a dog, or a plant are *whole*. But is any definition possible here ? May we say, as in pure logic, that *whole* is a thing, when you destroy its *essence* by taking away a *part*. Which part, then, or how many parts must be taken away, in order that a dog ceases to be *whole* ? You may say, a leg. Very well. But think of the hairs of a dog. If you shave him you might say perhaps that his essence is destroyed, the " being haired " belonging to a dog's essence. But what, if you cut off three hairs ? Or what if you cut off all except three ? *How* many, then, must you cut ?

And in the earthworm, we may not even say that cutting away the head destroys wholeness in the deepest sense, as the head exists still *potentiâ* and may be restored by regeneration.

Thus, we must be satisfied to say that we know by some sort of instinct what objective wholeness is. But this is by no means satisfactory in the deeper sense, and at least some *criteria* of wholeness in the objective meaning seem to be required. And there are such criteria.

β. CRITERIA OF OBJECTIVE WHOLENESS

We approach our subject if we say that a thing or event is *whole*, if it exists in innumerable cases or copies, all of them possessing the same typical combined form. Then organisms and manufactured products would be whole, at least if we do not consider the position of the single cells in each organism (page 276) or, in manufactured products, the position of each atom. But what we have said cannot be the last word with regard to our problem, for works of art are also *whole* though they exist in a single copy only.

In the second place, we may say: *whole* is that which is restored if its typical material constellation is disturbed. This would hold good for many organisms which are able to restore themselves, and also for products of manufacture which may be restored from outside, *i.e.* on the part of a human being. But there are many cases, in mammals, *e.g.*, where no regeneration is known—and yet they are whole.

The only criterion of wholeness, so it seems to me, which stands criticism is this: whole is that which owes its origin to non-mechanical, *i.e.* (page 270) to non-sumlike, natural agents. This is a negative criterion, of course, and implies, further on, that all non-mechanical agents in nature are tending towards wholeness at the same time.

But, in any case, practically, this is the only criterion we can make use of; and if we do, all organisms and all things depending on the activity of organisms are certainly *whole*.

3. The Union of the Concepts of Wholeness and Causality

Wholeness, however, is not the only concept we need, in order to understand the organism in a logical way. We need something more, as our last criterion will already have revealed to you. We need some sort of *combination* or *union* of the concepts of wholeness and causality.

And the discussion of this union will now lead us to a very important question, which may be called *the very centre of a logical justification of our vitalism*, namely, the question: *Are several elemental forms of causality logically possible*, or "must" causality be of the mechanical type, the word "mechanical" being taken in the most general sense (page 269 f.)? If the latter were the case, our whole vitalism would have to be subjected to a very severe revision; whilst, if causality should turn out to be a concept of a very wide range, of a range much wider than mechanical or summative causality, our theory of the autonomy of life would have received its *logical justification* in the fullest sense of the word. For it would have been proved to be the factual illustration of an aprioristic logical possibility. And at the same time our problem whether entelechy is a form of causality would be solved.

a. THE CONCEPT OF CAUSALITY

Causality may be said to be the application of the concept of *consequence* or *implication* to empirical events. It is not the same as consequence, but something more. But consequence is a part of it.

Consequence or implication relates to concepts or judgments : the one concept or judgment is, *because* the other is. Causality, as we have said, relates to events : the one event happens *because* some other events have happened and because certain conditions are realised. You see that both kinds of relations are expressed by the word " because " Causality is the *because* in the stream of *becoming*.

Causality is more than mere temporal sequence though it is realised within its realm. For causality is not the mere *post hoc*, but the *propter hoc* ; it implies the meaning of effectuating or of " force ", in the most general meaning of the word.

Causality is also more than mere functional dependence in the mathematical sense, as expressed by an equation, though it implies functional dependence. An equation may be read from the left to the right or from the right to the left. Causality, to put it briefly, goes only from the left to the right.

Some authors have tried to eliminate the concept of causality from science and to replace it by mere functional dependence. But such a philosophy is incomplete. It may be granted that it is very difficult, in many cases, to formulate causal relations in a strict way. But this is not a reason for abolishing the concept of causality, which is a very clear concept in itself.

That the concept of causality is applicable to nature, is not, as Kant believed, known *a priori*. We may only say that the concept of logical consequence is an aprioristic concept—(or an " innate " concept, to speak in psychological terms)—and that we have the innate endeavour to apply it to becoming in the particular form of causality. But that this endeavour is practically successful is by no means guaranteed *a priori*, but is a "happy fact", to apply a term used by Lotze. And that there are real causal *laws*, *i.e.* that causal connections are classes with many equal (or similar) cases, is another happy fact. If the concept of causality were a real aprioristic category, the problem of freedom, in the sense of indeterminism, would be meaningless. But it is not meaningless.

So much for causality in general.

β. THE POSSIBLE FORMS OF CAUSALITY

We now raise the important question: May natural causality have several different particular forms, or can it have but one, the mechanical, form? In order to decide this question we must first study some details with regard to the concept of causality.

First: We have said that the logical concept of consequence is one of its integrating parts. The primordial form of consequence is pure implication. One concept (dog or triangle) *implies* the other (animal or figure) with regard to its content. Now, there exists one most general principle with regard to all implication, and this may be formulated in the following way:

That which implies is always richer[1] *in manifoldness* (*i.e.* number of elements, including relations) *than that which is implied*. The concepts of "dog" or "triangle", *e.g.*, are richer in manifoldness than "animal" or "figure". Or, in other words: we need more elements (and relations) in order to define "dog" or "triangle" than we need in order to define "animal" or "figure".

This should be well kept in mind for all that is to follow.

Secondly: To speak of *causality* means to regard every event as an *effect* of "something" that is earlier in time. It does not mean more; it does not say *a priori* of *what* the event may be the effect.

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[1] So we say here, for the sake of simplicity. Quite strictly speaking, we had better say "never poorer". For there may be an equal degree of manifoldness on both sides.

Thirdly: As causality implies logical consequence, the general principle we have spoken of, relating to all consequences, must be valid for all causal relations. And this means that the effect with regard to its manifoldness must have its equivalent in the manifoldness of the cause; or, in other words, that the effect cannot be more manifold than the cause. If, therefore, there seems to be an increase in manifoldness during an event, this increase must be accounted for within the cause.

In short: *A system, in the course of becoming, is unable to increase its manifoldness by itself*—at least, if there is no " freedom ".

Fourthly: This topic does not relate to causality *qua* causality, and is yet indispensable for our discussion.

What are the ultimate data upon which rests all our knowledge about natural reality? So we ask. And the answer to this question is, that all those data are of the form: a *such* is *now here*. Or, if we use the language of a theory of matter and apply the general cover of "atom" to the material elements, that the ultimate data upon which all our knowledge of natural reality rests have the form:

Here is now an atom.

The totality of all data of the form *Here — now — atom* is what may be called the rough material for all empirical science.

And now we are prepared to discuss the *possible forms* of *causality*. Mere *possibilities* are discussed here. But these may be discussed aprioristically *on the assumption* that the concept of causality is a valid concept—(which, as we have said, is not known *a priori* in itself)—and on the foundation that data of the form *Now—here—atom* are the ultimate data of our knowledge about Nature.

The possible forms of causality:

(*a*) There is a material system of n elements (atoms). At the time t_2 this system is in a certain state B, characterised by specific spatial relations among the atoms. At the time t_3 the system is in another state C, there having been an *event* (becoming) in the temporal interval between t_2 and t_3. If now, though the states A and B are different, their degree of manifoldness is the same, and if, further, every *single* change in the system may be related back to a *single* change in the same system, that has happened in the time from t_1 to t_2, we are " causally " satisfied. But we are also satisfied, if there is an increase in manifoldness in the system, whilst it is transformed from state B to state C, but in such a way that every singleness in this transformation may be related to a single event that has come from without.

A simple example may illustrate what we have said: Imagine a number of balls on a billiard table, moving without friction. At the time t_2 they are in the state B, each of them being on a specific locality and endowed with a specific velocity. At the time t_3 there is the state C. Between t_2 and t_3 there has been an *event*, leading from B to C. But every singleness of this event may be related back to a former singleness of an event, which, in the time t_1 to t_2, had transformed the state A of our system into the state B. We are satisfied.

But we are also satisfied in the following case: The balls are moving on the frictionless billiard table parallel to the short sides, all moving with the same velocity between the long sides, moving endlessly to and fro, as the table is without friction. This system has a very low degree of manifoldness, or, in other words, we only need few concepts to describe it. Suddenly the manifoldness of the system is increased: one ball moves in this direction, another in that. But—people have pushed the balls in very different ways with their cues. We are satisfied again, for every singleness of the increase in manifoldness could be related to a single *cause* from without.

Let us speak of *singular causality* in all these cases.

(*b*) A system is at rest at the moment t since an indefinite time. Suddenly change begins. We *suppose* that we *know* that *no* cause in space has affected the system from without—(this is a " possibility " and we only speak of possibilities at present). What shall we do? Shall we give up the postulate of causality? You may do so if you like, for causality is a mere postulate and not a categorical axiom. But if you want to keep to the causal postulate, you must say: Some sort of *motion creating causality* has been at work, a sort of causality that has worked *into* space.

(*c*) At a given moment there are n elements (atoms) within the system. Suddenly there are $n + a$, and we *suppose* that we *know*—for this is *possible*—that no element has entered the system from outside its boundaries in the spatial sense.

What is to be done? Either giving up the postulate of causality, or introducing some sort of *matter creating causality*.

(*d*) A system of n elements (atoms) possesses the state A, characterised by a specific degree of manifoldness, at the time t_1. At the time t_2 it has acquired the state B. There has been no increase with regard to the number of atoms (as in *c*), nor has becoming been initiated whilst there had been rest before (as in *b*). But the *manifoldness of spatial relations* among the elements has been greatly increased and we *suppose* that we *know*—for this is *possible*—that nothing within the system or outside of it in space can account for this increase of the manifoldness of relations; in other words, that this increase is not preformed or predeterminated in any arrangement or structure of matter and spatial forces.

A particular form of this case would be realised, if state A has been of a rather simple form, the n elements being arranged, say, in the corners of squares, whilst state B represents an arrangement which is typically *whole*, say the form of a fish or a flower.

What shall we do? Again: either give up the postulate of causality, or introduce a new specific causal type, which *a potiori* we may call *individualising causality*.

These are the four *possible* forms of causality. No other forms are possible, and *any* natural event that *may* possibly happen *must* belong to one of these forms. Even if we should like to agree that there are "ghosts", "phantoms"—and whatever else—they would fall under one of our four headings. For no other forms would be accessible to our experience, which is bound to data of the form *Now—here—atom*. We have, in fact, discussed in a *complete* way all that can be experienced with regard to the temporal sequence of such data.

γ. THE REALISED FORMS OF CAUSALITY

So much, then, for causal *possibilities*. What about their *realisation*? Or, to express it differently: Which of the four possible forms of natural causality are empirically realised?

This is by no means clear from the beginning. For all considerations of the *a priori* type refer to formal possibilities only, and it is absolutely impossible—at least for man—to say anything about the existence or the particular quality of empirical things and events in an *a priori* way. We can only say *a priori*, either that certain forms of empirical reality would be logically desirable, so to speak, or, if for certain reasons some such "desirable" form is empirically realised, that there only exists a certain limited number of possibilities. The first is the case with respect to causality in general, the second with respect to its different forms.[1]

Now, as far as we know, only the first and the last of the four possible forms, *i.e. singular* and *individualising* causality, are realised. The realm of the first form is inorganic nature, the realm of the fourth form is the realm of organic life. The second and the third forms, *i.e.* the two forms of *creation*, are not empirically realised—as far as we know. If entelechy were able to create energy and thus to break the conservation principle (page 254), the second form would be realised also. But, as we know, there is no reason to accept this.

This has been the *logical justification* of the theory of the autonomy of life. For we have proved that entelechy acts according to one of the four causal schemes which are logically possible: it transforms an equal or summative distribution of possibilities into an actual individuality or totality (page 264). And this is just what has been shown to be logically possible under heading *d*.

Thus the concepts of *individuality* and *causality* have come

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[1] Certain modern German authors, of the school of so-called *phenomenology*, have been rather careless and rash with regard to the problem of *a priori*. They either believe that all sorts of empirical particulars of quality, as, *e.g.*, the "essence" of life, are known in an *a priori* way, or even that certain particulars of quality "must" necessarily exist in nature. But, in fact, we do *not* even know that there *must* exist that strange thing which we call *Nature* in general, quite apart from all particulars.

together, and so we may be allowed to come back once more to the general question, in which sense entelechy may be said to be *substance* and *causality*.

δ. TELEOLOGY, CAUSA FINALIS, AND EVOLUTION

But a few particular additions to what we have said may first be apposite.

Teleology or *purposefulness* may be called the psychological form of individualising causality. We know already that these terms ought to be applied on analogy only to biological phenomena in the proper sense (page 243), and, thus, it does not seem to be necessary to say much about them.

The old term of a *causa finalis* may be applied to individualising causality, if it is understood correctly. The *finis*, the end, of course, cannot work, but an agent having a tendency towards an end within itself, or, in psychological terms, an agent that has the " idea " of the end in its imagination, may act causally, and therefore you may, if you like, call entelechy a *causa finalis*.

More important is the introduction of the term *evolution* in relation to our analysis. By this name we shall design any process which occurs in successive paths or steps, each of them being regulated by individualising causality. Embryology therefore, and probably phylogeny also, are evolutions.

The counterpart to evolution is *cumulation*. This, then, is a sequence of events which may be understood by single causal acts, *i.e.* by singular causality. The geological process is cumulation, and the same is true most probably of human history.

All sciences which study cumulations are sciences of the second order, resting upon a science of the first or primordial order. Geology as a science rests upon physics and chemistry, history upon physiology, psychology, etc.

Biology is a primordial science, for it is occupied with evolutions.

ε. ENTELECHY AS A FORM OF SUBSTANCE AND CAUSALITY

If now, finally, we return to the problem, how entelechy is related to the concepts of substance and causality, we are allowed to say in a final way that it is *substance* in the sense of an intensive manifoldness of the form of wholeness and totality. But it may appear under the form of a potential and of an actual state. And as far as it is entelechy *actu* it is *causality* of the *individualising* form. Some sides of it, in each case, are manifesting themselves in this form.

Thus both concepts, substance and causality, may be applied to entelechy, if united with the concept of wholeness.

4. EMPIRICAL ILLUSTRATIONS OF WHOLENESS AND INDIVIDUALISING CAUSALITY

We have seen that *individuality* or wholeness, *individualising causality* and *evolution*, are legitimate concepts; that, with certain restrictions with regard to the concept of causality itself, they may be called " categories " the meaning of which is known *a priori*. We may call these concepts possible forms of natural things and events.

Now we know already that the individual organism illustrates, so to speak, the categorical form of individuality, and that individual morphogenesis illustrates individualising causality. But it may seem to be worth while to enumerate *all* groups of natural facts and events which may be said to illustrate empirically the two concepts in question. But this will be done only very briefly in this book, as part of those groups of events does not belong to our theme, the philosophy of the organism, and as the other part has already formed the subject of a detailed discussion in the previous parts of this work.

We may say that it is the wish or liking of *logic*, this word being taken in the wide sense of a *theory of order*, to conceive all empirical Reality as *one great ordered whole*, in which every singularity of being and becoming occupies this very definite place.[1] Then, what I have called a *monism* of *order* would be realised. But this sort of monism must remain a mere ideal. For the structure of Reality *is* dualistic, *i.e.* a *mixture* of wholeness and non-wholeness or " contingency ".

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[1] For a full discussion of this question, which belongs to general philosophy, see my *Wirklichkeitslehre* (2nd ed., 1922), page 149 ff., and *The Possibility of Metaphysics* (London, 1926), page 42 ff.

In the second place, we may ask whether in non-living nature, taken in its totality, there are not at least some indexes or signs of wholeness, in spite of all contingency that prevails here. But this problem does not belong to our theme,[1] and I, therefore, only say in this place that Henderson in his very important book *The Fitness of the Environment* has discovered some such indexes, all of them relating to a certain " fitness " of the inorganic world *for* the existence of life, or, in other terms, to a certain pre-established harmony among life and its medium.

Thirdly, there are the organic individuals, fully discussed in this book. They illustrate all our concepts most fully, though wholeness is also here mixed up with certain contingent features in the dualistic way (page 276).

Next we mention phylogeny, also spoken of in this work. Here we have most probably wholeness and evolution in a super-personal form. Our positive knowledge, however, is very slight.

And, finally, there is human community (civilisation, " culture ") and human history. In my opinion, no evolution is found here, but only psychological cumulation, though some indexes of wholeness as such may be found, of which the existence of moral feeling is the most important. This problem has been discussed elsewhere.[2]

Almost all our knowledge of wholeness and evolution is hypothetic, as real criteria (page 315 f.) are lacking. Only the personal organism, fortunately, forms an exception. *Personal biology, therefore, is the very prototype of the doctrine of objective wholeness, individualising causality and evolution.*

[1] *Wirklichkeitslehre*, page 154 f.

[2] *Wirklichkeitslehre*, pages 175 ff. and 339 ff.

PART IV

BIOLOGY AND METAPHYSICS

1. METAPHYSICS

ALL discussions in this work, so far, have quite intentionally been carried out on the basis of what is generally called *naïve realism, i.e.* on the assumption that Nature *exists*. Now it is well known that this assumption is far from being " critical " ; the naïve realist is a metaphysician *malgré soi*, and the great philosophers of modern times, from Descartes, Locke, Hume, Berkeley, Leibniz, to Kant, have made it their principal endeavour to show that the existence of a something *in itself* is by no means a simple and evident matter.

But our whole discussion of the central biological problem may easily be transferred from the naïve basis to a truly critical one. We may even go as far as to a critical *solipsistic theory of order*, saying that it is the task of philosophy, at least as far as it is logic in the widest sense of the word, to discover and to establish *order* within the realm of the something which is given to my consciousness. *Nature*, then, becomes a concept of order ; natural objects behave *as if* they existed independently, they are not regarded as absolutely existent. Nothing, in fact, would be altered with regard to the details of our analysis. And the problem of vitalism is a mere problem of order also, and *is by no means a metaphysical question from the outset.*

And yet, a true metaphysics, critically established, seems to me to be possible in the form of an hypothesis. This sort of metaphysics is by no means *naïve*. From naïve realism, through the solipsistic theory of order, towards critical metaphysics—that has been its road. I have fully discussed these questions in my systematic works, written in German,[1] and the main lines of my argument have been explained in my little book *The Possibility of Metaphysics*,[2] containing a course of lectures which I had the honour to deliver before the University of London in 1924.

Let us then, at the very end, regard our vitalism as forming part of a truly critical metaphysics, which claims that there *exists* something in an *absolute way*, and that this something is given to us in the form of *appearance*.

The great metaphysical question is, whether or not the realm of appearance may be transgressed with regard to particulars, or, in other words, whether or not at least certain specific sides or features of metaphysical Reality may be known as they are " in themselves ". I believe that some such knowledge is possible, and have explained, in the books quoted, how far it may go.

In this place I will only briefly mention some of the most important metaphysical problems in the realm of vitalism, and only one of these problems shall be discussed in full.

There is, first, the problem of *dualism*. We have defined dualism as the duality of wholeness and non-wholeness (or " contingency "), and have found that this dualism penetrated all spheres of empirical reality (page 324 f.). Now, empirical reality is absolute Reality in the form of appearance. But the most general forms of order, which are found in the realm of empirical reality and which imply wholeness and non-wholeness, may be attributed to absolute Reality ;[3] and we, therefore, are allowed to say that absolute Reality has also a dualistic structure. There is a permanent struggle between wholeness and non-wholeness in Reality, a struggle between *form* and *matter*, in the sense of Aristotle, and even in the individual organism this struggle is clearly realised. For, as we have said, only the general type of form is guaranteed in the living individual by entelechy, the size and position of the single cells in the various organs being contingent.

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[1] *Ordnungslehre*, 2nd ed., Jena, 1923; *Wirklichkeitslehre*, 2nd ed., Leipzig, 1922.

[2] London, 1926.

[3] *Possibility of Met.*, pages 26, 45.

In the second place, the problem of *freedom,* in the sense of indeterminism, may at least be mentioned.[1] Naïve realism and the critical theory of order, both of them, postulate univocal determination (page 249). But they cannot do more than " postulate " it. May this not be due to an " all too human " restriction ? May not, in phylogeny at least, the super-personal entelechy be an *ens* which is " in the making ", in the sense of Bergson's *élan vital,* phylogeny being *not* determined by a fixed given *essentia* of its metaphysical basis ? This is certainly imaginable. But there is no possibility given to us of deciding the question.

In the third place, let me say a few words on the hypothetic last goal of phylogeny. What is its ultimate end or its ultimate " purpose " ? Does it not seem as if the phylogenetic process were tending towards the formation of *conscious* beings of various forms ? Does it not seem as if super-entelechy were trying again and again to come out of its unconscious or subconscious state into a state of clear self-consciousness ? This is far from being a new idea. And it also is by no means new to assume that the ultimate task of consciousness is redemption, in particular if the conscious beings are regarded as being " free ".

Super-entelechy, bound into matter, *wants to know* what it has done in a *quasi* instinctive way, suffering from its own products. Finally it *does* know, and it now has the means of a conscious rectification of all its mistakes. Here metaphysics of the highest form enters the scene, and so does ethics.

But we leave the matter where it stands, referring to our purely philosophical books.

Let us, then, return to the strict philosophy of the organism, and let us study one more of the problems of this particular branch of philosophy in a detailed way, within the realm of a general metaphysics.

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[1] *Possibility of Met.*, page 37 ff.; *Crisis in Psychology*, Princeton, 1925, page 243 ff.

2. THE ONE AND THE MANY

We only *know* life in the form of many living individuals, and, therefore, if we refer to our vitalistic doctrine, we must say that we only know entelechy in its individual manifestations. This is a fact.

In a provisional way, now, we have spoken of several kinds of entelechy, manifesting themselves in one and the same individual. The psychoid, governing the behaviour, has been one of these kinds, and another kind has been morphogenetic entelechy. And the fact of self-differentiation (page 77), leading to very strange results occasionally (page 280), did even suggest the view that morphogenetic entelechy was split off, so to speak, into several subentelechies, regulating the morphogenesis of the separate elementary organs, *i.e.* of ectoderm, endoderm, etc.

But would it not be rather strange to say that several entelechies are at work on one and the same individual organism ? Would it not be better to speak of but one entelechy with regard to each individual, manifesting itself in different directions ? So it seems. The strange fact remains, however, that, under certain conditions, ectoderm and endoderm, or any other elementary organs, may undergo morphogenesis after material separation from one another and, therefore, without material connection. The subentelechies, therefore, that we have spoken of, must be conceived in any case as connected in a radically non-material way. There is one entelechy, but there are two (or more) points of partial manifestation, which may become materially separated from one another.

Here the problem of *one and many* enters most clearly into the scene ; even more so than if behaviouristic and morphogenetic entelechy are taken into consideration.

We now return to our embryological experiments from a higher point of view.

Biology proper is concerned with form and function exclusively. And here we have found that a material system, *i.e.* one egg, which, undisturbed, *would have* given *one* whole form and one totality of functions, *may* give *several* such forms and totalities; whilst a material, *i.e.* two eggs, which undisturbed *would have* given *two* whole forms and two functional totalities, *may* be forced to result in but *one*.

In short, then: *instead of one, many; instead of many, one.*

So much from the point of view of biology proper.

But now we know (page 304 f.) that, according to the true parallelistic theory—not, of course, according to the impossible psycho-*mechanical* parallelism—what is the psychoid from the scientist's point of view, is mind or soul on the platform of psychology; psychoid and soul, of course, being one and the same real *ens* for the metaphysician. And some sides of the mind, or rather, of the metaphysical *ens* appearing under the double aspect of soul and psychoid, are again parallelly connected with one *Ego*. In the form of the Ego, then, part of the metaphysical *ens*, which is the ultimate common basis of the soul and of that part of entelechy which we call psychoid, *knows itself*.

Let us briefly say, that the Ego is that part of (metaphysical) entelechy which is self-conscious.

If we connect these considerations with our results in the field of biology proper, which have their foundations in the results of our experiments, we are now permitted to say:

A material which, undisturbed, *would have* given *one* totality of form and function and *one soul and Ego, may* give several such totalities and *several souls and Egos*; whilst a material which, undisturbed, *would have* given two totalities of form and function *and two souls and Egos, may* be forced to give but one such totality *and one soul with one Ego*.

You would not like, perhaps, to speak of the "soul" of a sea-urchin. But you can easily imagine that experiments, identical to our own, were carried out on the *eggs of man*—which is impossible only for practical reasons. And all of us agree, so it seems to me, that man "has a soul".

What then with regard to the problem of *one and many* in the face of a vitalism that has been enlarged psychologically? What about the triplicity *entelechy—soul—Ego* forming *Many instead of One* and *One instead of Many*, as circumstances require?

What are the "circumstances" here, and how do they determine whether One or Many are to be formed, and that with regard to form, to soul, and to Ego?

We might say, perhaps, at the first glance, that there is no entelechy altogether at work as early as in the cleavage states, that the cleavage stages are pure matter, and that entelechy (including soul and Ego-ness) begins its manifestation only at the end of the cleavage. But such a view would break the continuity of life.

On the other hand: may the *entia* of the triplex-form *entelechy—soul—Ego* be "divided" or "fused"? This seems unimaginable (page 298).

We must therefore say, so it seems to me, that our biological results, psychologically enlarged, teach us what follows:

There is a certain metaphysical *ens*, which may exist in two states or *modi*, in the *one-modus* and the *many-modus*. It depends on material conditions in which form it manifests itself. But, in the case of the embryological experiment, this *ens* may be forced to change its modus of manifestation *after* it has already begun its work, retracting, so to speak, the one-modus and replacing it by the many-modus, or *vice versa*, as circumstances require.

The problem gets even more difficult if we consider the fact of regeneration, or any other form of restitution. The annelid Amphiglena, *e.g.*, or the flatworm Planaria, may be cut into any number of pieces you like, and this in the *adult* state; and after a few days you will have as many worms as you had pieces. Here the hypothesis that entelechy does not begin its work before a certain moment, whilst before that moment the organism was not yet a real "organism" but only an aggregate of matter, fails from the very beginning. For an *adult* organism has been subjected to the operation. Only one hypothetic way, therefore, is left us here: the same we have already taken definitively in the embryological case. Entelechy "retracts" the one-modus, including all its results, and sets in *de novo* with its many-modus—and this with respect to form, to soul, and to Ego.

But man, and not only man, you will say, cannot be "cut into pieces " and give " as many men as you have pieces ". Of course he cannot. But most probably only for particular very secondary reasons, that is to say, for quite particular features of his organisation—his circulation system, for instance. For, at bottom, most, probably all, cells of every organism are " equipotential " and also equally endowed with restitutive potencies, these potencies, unfortunately, being merely handicapped in many cases.

In any case we are *forced*, in the face of the experiments, to assume, so I believe, that there *must* be some sort of *One*-modus of entelechy, besides the many-modus which is empirically known. For the metaphysical *ens* in question cannot be " divided " or " fused ".

This has been the first time that we have really been *forced* to attribute some *super-personal* modus of existence to our triplicity *entelechy—soul—Ego*. And this idea will now prove to be of an enormous importance as we go on—and this along *different* lines.

At first, then, let us follow the road we have already taken, and let us go to its end. What about the metaphysical basis of the children of one mother? They come from her eggs. But all the eggs have been but *one* cell in an early stage of the mother's embryology. The problem of the *One and Many* presents itself in a form not quite identical with the form suggested by the embryological and regeneration experiments, but rather similar to that form. The " Anlage " of the ovary in the mother's body is an index of the One-modus of entelechy, whilst the single eggs are indexes of the Many-modus.

But the children of the mother have children again. There is some sort of material continuity of life in the course of generations. Not, as we know (page 143), in the strictest sense, but, at any rate, in so far as two generations are always connected by " the same " matter in the narrowest sense. In this way, all the following generations of a given species are " within " any individual chosen at random. This individual represents the One-modus that is to be replaced by the Many-modus in the course of time.

And, finally, if we accept the theory of descent, *all* organisms are ultimately related in some way. For other reasons, we have already spoken of one super-personal entelechy being the foundation of the phylogenetic process. We now come to the same conclusion from a rather different aspect. There is not only a certain truth in the theory of the old evolutionists, so strongly advocated by Leibniz, that all subsequent generations of mankind existed already in Eve's body, but this theory is true on a larger scale as soon as we accept the idea of descent instead of the dogma of the constancy of the species; and the only thing we have to do is to put our vitalistic conception of life in the place of the mechanistic views of the ancient thinkers.

We shall not say much about phylogeny, as our knowledge is so very poor in this field; only this topic must necessarily be emphasised, that, if one super-entelechy is at the bottom of that process, it must be conceived as endowed with an immanent evolutionary force, in such a way that the *many* which are the result of its successive manifestations change their type, as time proceeds. But whatever we may think about these very problematic matters in detail: the concept of a *One-modus, i.e.* a super-personal modus, of entelechy, has in any case now been established in two different ways. The analysis of phylogeny itself has led us to assume such a modus, *and* so do all considerations that have filled this chapter so far, beginning with the discussion of the embryological experiments, then proceeding to the analysis of what it means that one mother may have many children and that the subsequent generations are materially connected, and ending with the phylogenetic problem considered as the material connection of all life.

Before we turn to consider our problem of *One and Many* from quite a new point of view, let us say still a few words more about another phenomenon, in which the fact of a One-modus and a Many-modus also enters the scene, though in a very different form.

I am speaking of the so-called *dissociation of personality*, so well studied in France and America. This topic, of course, does not by itself belong to our subject—it is purely psychological. But it may serve as an illustration of the more general problem. The fact is this :

There is one body with one soul-entelechy. But two or more Egos are in correlation to this body ; and they may either influence one another whilst in activity (*subconsciousness*), or use the various organs of the body simultaneously in an independent way (*coconsciousness*). The state of dissociation sets in after a mental disturbance. This is to say that there had been one Ego before. And at the end of all, if healing of the mental abnormality is successful, there is but one Ego again. Thus the problem of *One and Many* relates to the Ego-part of the soul in this case, *i.e.* to that part of the soul which " knows itself ". The soul plays the rôle which the super-personal entity played in the biological cases ; and another difference is, that only one body is concerned in dissociation, whilst several bodies play their rôle in biology. But some sort of alternation between a One-modus and a Many-modus of one and the same type of essence is realised in both cases.

3. The Problem of Death

Let us now proceed to considerations of a very different kind, which may also be founded upon the discovery of the super-personal, and upon our distinction between the (super-personal) One-modus and the Many-modus of one and the same metaphysical *ens*. It is the problem of *death* that is in question. We have already referred to it in another chapter of this book, but only in an empirical and provisional way (page 301 f.).

The empirical effect of death is a certain change with respect to the matter of an organic body. This body has been a *living body* ; it now becomes a *corpse*. And the corpse obeys purely mechanic laws with regard to all its changes ; it is no longer an " organism ", there is no " behaviour " in it, but simply " change ".

Thus something has disappeared that had been present and active before. And vitalism has shown that this something is not a mere peculiarity of material structure. A particular *ens* has gone, which had before been working with the matter of the body in question. Whether there are any material *causae occasionales* of death or not (page 301 f.), its result is in any case the separation of that *ens* from the body's matter.

Where has the immaterial *ens* " gone " ?

If we now remember our considerations about the super-personal, and about the distinction between the One-modus and the Many-modus of one and the same metaphysical *ens*, three possibilities of the metaphysical significance of death present themselves for discussion : the *ens*, *qua* personal *ens*, may be conserved after death ; or it may enter the super-personal One-modus and completely lose its personal form ; or, finally, it may enter the One-modus in a certain unknowable way and yet remain personal.

The first possibility has to be cancelled from the very beginning ; for the concept of a super-personal One-modus of entelechy-soul is an absolutely necessary concept in the face of the biological experimental fact (page 332). Thus we have only to be in search of a decision with respect of the second and third possibilities. The third possibility would imply, in a critical form, what is usually called " immortality ", whilst the second would give no place to it—at least not in the usual, *i.e.* the personal, sense. The third alternative, then, means : personal permanence of the *ens* which during life has been a " person ", and yet union of all persons within a certain super-personal One.

The question, now, is whether there are any indicia in favour of a metaphysical permanence of " person " *qua identical* person, though within the realm of a super-person.

This is the problem studied most actively in our days within the sphere of *Psychical Research.* There is no definite answer from this side at present, so it seems to me. But I must confess that the theory of so-called personal survival becomes more probable from year to year, even if we intentionally put aside all stories of apparitions, phantoms, etc. It is within the realm of *mental* psychical phenomena that the strongest support comes to the hypothesis of so-called spiritualism. I do not say decision, but support. And this support consists in the fact that the faculties of a so-called medium in the state of trance very often show the characteristics of a quite specific *limitation* and *personification*. And this in such a way that they lead to performances which are most simply and least artificially explained on the assumption that there really *is* a particular formerly-living mental personality " behind " the medium. For all the utterances on the part of the medium very often are such that their contents have once belonged to the sphere of former knowledge of one particular personality, who is now dead, and that the medium knows about nothing that did not belong to that personality's former knowledge. Animistic explanation, though not absolutely impossible, is yet very artificial in such cases. It would have to suppose that the medium " reads " one part of what it knows in the mind of one living person, and the other part in the mind of another ; many of these persons being not even present during the time of experiment.

But there is one more point that tends in the direction of what we may call the permanency of identical personality, apart from Psychical Research. And this is the fact that the acquisition of experience must begin *de novo* in each individual. This is, at least, true in man and his systematic relatives. It appears as an enormous waste of time ; and it seems as if there were some sort of primordial and fundamental handicap with regard to the transmission in a hereditary way of experience already acquired, from one generation to the next. Such a handicap would exist, if we were allowed to assume that personalities possess an identical essence of their own, that they are more than mere indifferent parts of a super-person, though embraced by it in an unintelligible way.

I freely confess that other difficulties appear : permanent identity after death seems to imply permanent identity before " birth ", to express it briefly. And this would lead, either to the theory of *monads*, as established by Leibniz, or to the Indian idea of *metempsychosis*, and, in the latter case at least, there would be no handicap to a " remembrance of past life " —which, however, does not exist, as far as we know.

But let us stop here. For it is not the intention of this book to go beyond the boundaries of a philosophy of the *organism* and to enter the fields of general metaphysics.

The aim of this book has been to establish the doctrine of the *autonomy* of organic life in a careful and thorough manner, and to follow this doctrine into all its ramifications and consequences.

I hope that my readers will agree that this aim has been reached; in other words, that biological mechanism has been beaten along the whole of its line, and that the consequences of vitalism have been studied as far as has been possible.

Uexküll has said that the biological views of the natives of the Fiji Isles are nearer to the truth than modern mechanistic theories.

It seems to me that this is a very sound statement. And I also agree with another dictum of Uexküll's: Vitalism, he says, has given back to mankind the problem of immortality. This is certainly also true, as far as the problem in question *qua* problem is concerned. Vitalism itself, in fact, does not give any kind of solution here; but on a mechanistic foundation, even the discussion of immortality would be meaningless. Vitalism has cleared the way.[1] This, quite certainly, is not all that is to be done. But it is better than nothing.

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[1] Comp. my "Presidential Address" in *Proc. Soc. Psychical Res.*, Part 99, 1926.

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