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ON THE RELATION BETWEEN THE QUANTITY OF BRAIN AND THE SIZE OF THE BODY — IN VERTEBRATES —

BY

Prof. EUGÈNE DUBOIS

Physiology. — *"On the relation between the quantity of brain and the size of the body in Vertebrates"*. By Prof. EUGÈNE DUBOIS. (Communicated by Prof. H. ZWAARDEMAKER).

(Communicated in the meeting of November 29, 1913).

It is obvious that, in general, in different species of animals, the relative quantity of brain must be a measure for the degree of the organisation of the nervous system. There are however still other factors influencing the quantity of brain. In the first place the size of the body, but especially also the age and the individual deviations, further possible deviations caused by the living of the animal out of the state of nature.

Of these factors the three last mentioned ones can easily be excluded, the age, by choosing only full grown animals for comparison, the individual deviations, by taking averages, or (which in some cases may be preferred) by choosing individuals representing the norm. Then remains still the factor of the size of the body. Its influence cannot be appreciated by simply calculating the relative quantity of brain. For a long time it has been known already that

in this way the required measure for the organisation of the nervous system cannot be found, but on the contrary false relations are obtained. Then Man is indeed not only inferior to some small Monkeys but even to the Mouse. The latter would then be four times better provided with brain than the Brown Rat, and the Cat five times better than the Tiger or the Lion.

In general we find, not only in Mammals, but in all Vertebrates, that the smaller species of closely allied animals, relatively to the weight of their bodies, have a great quantity of brain.

If we exclude, however, as much as possible, the above mentioned factors which, besides the size of the body, influence the quantity of brain, if we thus compare animals taken in the state of nature, which are as near as possible to one another, systematically, in their manner of life and in the shape of their bodies, but differ as much as possible in the size of their bodies, then it must be possible, to discover at least, if it is not a simple proportion, some relation existing between the quantity or mass of brain and the size, the weight of the body.

About twenty years ago the necessary, trustworthy evidences, chosen and explained with critical discernment, were very rare. Thankfully it may be remembered here that it was Max Weber, who, by procuring them, was one of the first that prepared the way for the treatment of this problem, at least in so far as regards Mammals [1]).

At all events the size of the body remains a very important factor amongst those determining the quantity of brain, for the Lion e. g. possesses absolutely 7 times as much brain as the Cat, the Brown Rat 6 times as much as the Mouse. Evidently the weight of the brain is, after all, a (mathematical) function of the weight of the body. If the quantity of brain does not increase proportionally to the volume of the body, expressed by the weight, it might be that this is really the case with regard to the superficial dimensions, as being proportional with the receptive sensitive surfaces and with the sections of the muscles, thus measuring the passive and active relations of the animal to the outer world, for which in this way the quantity of brain can be a measure. Then, in animals equal in organisation and shape, but not in size, the quantities of brain must increase as the $\frac{2}{3}$ power or the power 0.66.. of the weights of the bodies.

In those comparable Vertebrates of different sizes the longitudinal dimension might likewise be the measure of the quantity of

[1]) Especially in his "Vorstudien über das Hirngewicht der Säugethiere". Festschrift für Carl Gegenbaur. Leipzig 1896.

brain, on account of the segmental structure, and the movement by the contraction of muscle-fibres, working on levers proportional to the length of the body in this tribe of animals.

Again, the extension or the specification of some definite receptive surface (of sense) may likewise determine the quantity of brain. As the former in its turn must be a (mathematical) function of the size of the bodies of animals that are equal in shape and organisation, it must, according to some (arithmetical) power-proportion of the weight of the body, be one of the factors determining the quantity of brain.

However insolvable, at first sight, the problem indicated by the title of this communication may seem to be — as no organ is more complicated of structure and in its physiology more obscure than the brain — in this way it must be possible to make it fit for solution. It must, at all events, be possible, likewise for groups of animals of different grades of organisation, to represent the *cephalisation* by figures, and thus to compare them.

Be r the required exponent of correlation (indicating the correlation of the brain quantity to the mass of the body), be e (encephalon) the weight of the brain, s (soma) the weight of the body of the smaller animal, E and S the weight of the brain and the weight of the body of the larger animal and k (kephalisation) the coefficient of cephalisation, equal for both, then we have the following equations:

$$E : e = k\,S^r : k s^r$$

$$E : e = S^r : s^r$$

$$\left(\frac{S}{s}\right)^r = \frac{E}{e}$$

$$r = \frac{\log E - \log e}{\log S - \log s}$$

$$k = \frac{E}{S^r} = \frac{e}{s^r}$$

When working these equations by evidences contributed by MAX WEBER and others I found in 1897 [1]) at a seven times repeated

[1]) The proportion of the weight of the brain to the size of the body in Mammals. Verhandelingen der Kon. Akademie van Wetenschappen te Amsterdam. Volume 5. No. 10. Amsterdam 1897.

Also in French and German text: Sur le rapport du poids de l'encéphale avec la grandeur du corps chez les Mammifères. Bulletins de la Société d'Anthropologie de Paris 1897. p. 337 — 376.

Ueber die Abhängigkeit des Hirngewichtes von der Körpergrösse bei den Säugethieren. Archiv für Anthropologie. Band 25. Heft 1 und 2. Braunschweig 1897, p. 1—28.

calculation for each time two Mammals of different orders: Primates, Ruminants, Carnivores, Rodents, always only values varying mutually between 0.54 and 0.58, with an average of 0.56 or about $\frac{5}{9} = 0.55\ldots$

Arranging according to k calculated in this way, we see indeed the great confusion prevailing in the arrangement of Mammals according to the relative weights of their brains, give place, in a generally satisfactory manner, to an arrangement that is pretty well in conformity with the natural system. A few deviations continue to exist, the Elephant e. g. takes his place between Man and the Anthropoid Apes, the Rodents deviate mutually very strongly. On the other hand the different behaviour of Macrochiropteres and Microchiropteres indicates rightly their different origin.

In 1905 the above-mentioned method of investigation was applied to Birds by Louis Lapicque and Pierre Girard [1]. By 5 comparisons (Hooded Crow—Jay, Carrion Crow—Jay, Wild Duck—Summer Teal, Silvery Gull—Sea Swallow, Buzzard—Kestrel) they obtained for r a value that was so near the one I found for Mammals, that their conclusion, that for Birds the same exponent of correlation may be accepted, was entirely justified. According to the value of the coefficient of cephalisation calculated by this method, Birds, though not entirely after the natural system, yet with regard to the nearest affined ones, may be classified in a natural way. Parrots, the Monkeys among Birds, stand highest in the list [2].

Afterwards a few other comparisons (Swan—Summer Teal, Eagle—Kestrel, Parrot—Parrakeet, which species showed greater differences in the sizes of their bodies), could be added by Lapicque [3] to the first 5 comparisons; in this way still better results were obtained.

The 5 most thrustworthy comparisons gave now an average $r = \mathbf{0.558}$.

This constant returning of "cette puissance étrange" 0.56, the meaning of which is absolutely incomprehensible according to Lapicque [4], likewise in Birds, where the anatomical composition of the brain is certainly very different from that of Mammals, must indeed be called exceedingly striking.

Under these circumstances it was of great interest to investigate

[1] Comptes rendus des séances de l'Académie des Sciences. Paris 1905, 1, Tome 140, p. 1057—1059.

[2] Bulletins du Muséum d'histoire naturelle. Paris 1909, p. 408—412.

[3] Revue du Mois. Paris. 10 Avril 1908.

[4] Revue du Mois. Avril 1908. p. 445. Further: Bulletins et Mémoires de la Société d' Anthropologie de Paris. Séance du 2 Mai 1907. 5me Série, Tome 8, fasc. 3. Paris 1907, p. 261.

the relation between quantity of brain and size of the body likewise for the lower classes of Vertebrates. This is connected here with greater difficulties, for whereas in Birds the relative weight of the brain is still of the same order of amount as in Mammals, it descends in the inferior classes, both absolutely and relatively, as low as to the order of magnitude of about $^1/_{10}$ of that of the two highest classes. The quantities of brain we have to deal with are thus absolutely little, and we can only make use of those rare cases of the usually very scarce evidences about these classes, in which the weights of the bodies show great differences. A few accurate evidences are found in WELCKER's "Gewichtswerthe der Körperorgane bei dem Menschen und den Thieren", published after the author's death by A. BRANDT [1]). Further L. LAPICQUE and H. LAUGIER [2]) gave in 1908 some trustworthy determinations of weight, and lately G. WATERLOT, who had made himself conversant with the technical method in the Laboratory of LAPICQUE, published a great number of weights of brains and bodies of Vertebrates, among which also Reptiles and Amphibia, determined in Dahomey [3]).

As early as 1855 and 1856 E. CRISP gave trustworthy evidences concerning a Reptile and a Fish [4]).

Among WATERLOT's Reptiles were a Monitor and a Gecko, belonging both to the same sub-order of the Lacertilia as likewise the Emerald-Lizard, of which LAUGIER and LAPICQUE communicated the weight.

All were full-grown animals, the Monitor (Varanus niloticus) was a subject of mean size; four individuals of the little Gecko (Hemi-dactylus Brooki) were weighed and consequently average weights can be calculated. The weight of the body of the Varanus is 1600 times that of the Gecko and almost 450 times that of the Emerald Lizard. Under these circumstances trustworthy results may be expected. A third good comparison of Reptiles affords a Viper (Vipera berus), of which CRISP weighed 7 individuals, with a Cobra (Naja melano-leuca) of Dahomey, weighing almost 28 times as much. A few other Reptiles have been inserted into the following table. The values of k calculated with $r = 0.56$ are likewise indicated in it, as well as the average diameter of the eye-ball of some species [5]).

[1]) Archiv für Anthropologie. Vol. 28 (Braunschweig 1902), p.p. 55—61.

[2]) Comptes rendus. Soc. de Biologie. Paris 1908, Vol. 64. p. 1108.

[3]) Bulletins du Muséum d'Histoire naturelle. Paris 1912, p. 491.

[4]) E. CRISP, Proceed. Zool. Soc. London. Part. 23. (1855), p. 191. Ibid. Part 24 (1856), p. 106.

[5]) N⁰. 1, 2 and 4 have been borrowed from WATERLOT (l.c.), 3 and 8 from LAPICQUE (l.c.) 5 from CRISP l.c. (1855), 6, 7 and 9 from WELCKER—BRANDT (l.c.). — An Alligator mississippiensis from HRDLICKA, cited by LAPICQUE (Bull. et Mém. Soc.

	S	E	k	Average diameter of the eye ball, in m.m.
1. Monitor (Varanus niloticus) (1)	7500. G.	2.440 G.	0.0165	12.5
2. Little Gecko (Hemidactylus Brooki) (4)	4.7	0.043	0.0181	4.1
3. Emerald Lizard (Lacerta viridis) (aver.)	16.8	0.093	0.0191	5.8
4. Cobra (Naja melanoleuca) (1)	1770.0	0.646	0.0098	7.0
5. Common Viper (Vipera berus) (7)	64.2	0.105	0.0102	
6. Common Lizard (Lacerta agilis) (2)	12.507	0.076	0.0185	
7. Slow Worm (Anguis fragilis)	16.252	0.039	0.0082	
8. " " " "	18.9	0.037	0.0071	2.8
9. Greek Tortoise (Testudo graeca)	993.58	0.360	0.0075	

Herewith the following values for r are obtained. By comparison of *1* with *2*: 0.5476, of *1* with *3*: 0.5355, *4* with *5*: 0.5478. The average for the examined Reptiles is **0.5436**.

All these values are again so near to 0.55 . ., or $^5/_9$, that there is no doubt but the same exponent of correlation may be accepted for the three highest classes of Vertebrates. Here already I point to the low value of k both of the Slow Worm (Anguis fragilis) and of the Snakes in contradistinction to the Lizards.

Regarding Amphibia I have not been able to obtain entirely satisfactory data for the calculation of r. The giants among these, as the American Bullfrog (Rana mugiens or Catesbyana) and the Indian Tiger-spotted Frog (Rana tigrina), reach only 5 times the size of the nearest related species to be compared with. For the Bullfrog I have calculated of DONALDSON's[1] 6 largest individuals the value of s 244.4 G. and of e 0.204 G. A comparison of the latter with our Waterfrog (Rana esculenta), according to LAPICQUE's averages for s and e, gives only an exponent of correlation of 0.3843. Compared with LAPICQUE's Rana fusca (aver.) r becomes on the contrary = **0.5501**. It seems that the Bullfrog, at least in the organisation of the nervous system,

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d'Anthrop l. c. p. 263), with $s = 11.34$ KGM affords, as not full-grown, probably too high a k (0.0268). For a "Crocodile" mentioned by Manouvrier ("Sur l'interprétation de la quantité dans l'encéphale". Mémoires de la Société d'Anthropologie. Paris 1885. 2me Série, Tome 5, 2me fasc. p. 167) of about 70 KGM body weight, we find $k = 0.0290$.

[1] Decennial Publications. University of Chicago. Vol. X. (1902), p. 7 and Journal of Comparative Neurology. Vol. 8 (1898), p. 330.

is more closely allied with the European Landfrog than with the Waterfrog. The similarity in the modus of living with the latter has no influence in this respect. The following calculations of k for some Amphibia prove indeed that other factors are predominant there.

Valuable evidence for the calculation of the exponent of correlation for this class might be obtained from the Japanese or the American Gigantic Salamander (Megalobatrachus maximus and Cryptobranchus Alleghaniensis). The former is certainly more than 100 times heavier than the Spotted Landsalamander, and surpasses the Crested or Great Newt more than 400 times in weight. But, as far as I know, this evidence does not exist.

If we admit for Amphibia the same exponent of correlation as for the three highest classes of Vertebrates, then we find the following values for k.

	S	E	k
1. Waterfrog (Rana esculenta) (aver.)	44.5 G.	0.106 G.	0.0127
2. Leopard Frog (Rana virescens) (5)	73.35	0.153	0.0138
3. Bullfrog (Rana Catesbyana) (6)	244.4	0.204	0.0094
4. Landfrog (Rana fusca) (aver.)	53.0	0.088	0.0095
5. Common Toad (Bufo vulgaris) (aver.)	44.5	0.073	0.0087
6. Shackletoad (Alytes obstetricans) (aver.)	7.7	0.041	0.0131
7. Treefrog (Hyla arborea) (aver.)	4.8	0.043	0.0179
8. Spotted Landsalamander (Salamandra maculosa) (1)	24.88	0.047	0.0078
9. Great Water-Newt (Triton cristatus) (2) [1]	7.46	0.019	0.0062

The comparatively high value of k in the two first mentioned species, likewise in Alytes obstetricans and especially in the Treefrog, has evidently some relation with a higher organisation of the nervous system, and not with the surroundings in which the animals live. Rana Catesbyana lives, as likewise R. esculenta and R. virescens, in water, ranks however near to R. fusca, the Landfrog. The deviation of k in this respect is in the latter analogous with

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[1] N°. 1, 4, 5, 6, 7 are borrowed from LAPICQUE and LAUGIER (l.c.); 2 and 3 from DONALDSON (Journal of Comparative Neurology. Vol. 10 (1900), p. 121 [the 5 largest Rana virescens (♀)], Journal of Comparative Neurology. Vol. 8. (1898), p. 330. Decennial Publications. Chicago. Vol. 10. (1902), p. 7 [the 6 largest Rana Catesbyana]; 8 and 9 from WELCKER-BRANDT (l.c., p. 57 and 58).

that of Salamanders and Newts, where the latter, which live in water, have however lower cephalisation than the Landsalamander. In general the value of k does not differ much from that of Reptiles.

If now we find in the lowest class of Vertebrates, the Fishes, for r the same value as for the three highest classes, then it is ·certain that also in the Amphibia, which rank between them, the same relation exists between weight of the body and weight of the brain.

Of the following evidence regarding Fishes the greater part has been borrowed from WELCKER-BRANDT [1]).

	S	E	k
1. Carp (Cyprinus carpio)	1817.3 G.	1.270 G.	0.0190
2. Crucian (Carassius vulgaris)	˙5.22	0.470	0.0186
3. Gudgeon (2) (Gobio fluviatilis)	42.196	0.159	0.0195
4. Perch (Perca fluviatilis)	67.27	0.162	0.0153
5. Stickleback (2) (Gasterosteus aculeatus)	1.447	0.022	0.0179
6. Pike (Esox lucius) [2])	12700	4.860	0.0245
7. Conger (Conger vulgaris) [3])	10000	1.050	0.0060
8. Eel (Anguilla Anguilla) [3])	650	0.170	0.0045

·When comparing each time two, the nearest affined species, the following values for r are found: *1* with *2* · 0:5633, *1* with *3*: 0.5522, *4* with *5*: 0.5201, *6* with *2*: 0.5949, *7* with *8*: 0.6661.

With the exception of the last, to which I shall revert afterwards, these values are also all near to 0.55 ... The average of the four is **0.5576**.

Eels (Muraenidae) excepted, the comparatively high values of k, in which most Fishes equal even the examined Reptiles, are striking. In the low value of k in the Eels we find a similar phenomenon, the probable cause of which I shall indicate afterwards, as

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[1]) L. c., p. 59—61. There 3 more perches. The statements for them deviate however so much from what may be admitted as normal for this species, that they cannot be used separately for trustworthy calculation of r. Compared with the 2 sticklebacks they give for r values ranging from 0.437 to 0.644. The average of 4 comparisons is 0.525.

[2]) E. CRISP in Proceed. Zool. Soc. London. Part. 24. (1856), p. 106.

[3]) L. LAPICQUE, Bull. et Mém. Soc. d'Anthrop., l.c. p. 263.

in the Snakes and the snake-shaped Slow Worm, but the deviation is here still greater on account of a second cause.

The results obtained in this way seem to prove with certainty the existence of a law that can be applied to all Vertebrates, indicating the relation between quantity of brain and size of body.

In species of Vertebrates that are equal in organisation (systematically), in their modus of living and in shape, the weights of the brains are proportional to the $^5/_9$ power of the weights of the bodies.

Before we try to discover the meaning of this law, it is important to determine the value of the exponent of correlation for the brainweight of large and small individuals in one and the same species. The differences of size of the body are, in most cases, comparatively much less here than those between the species mutually, and we are generally obliged to take averages of a great number of individuals, to make the errors attending each special observation balance as much as possible against one another. With the exception of such species as the Dog, having many races of very different sizes, the best evidences can consequently be found for Man.

The result I obtained in this respect for Man, in 1898, was completely contradictory to what I found for different species of Mammals.[1]) The exponent of correlation proved to be an entirely different one. For obvious reasons we cannot dispose, with regard to Man, for this calculation of sufficient evidence, relating to normal weights of the body belonging individually to the weights of the brain. In order to be able to compare these quantities, we may follow two indirect ways. In the first place it is possible to *calculate* the weight of the brain of living Man. According to the method of WELCKER, which has proved to be very trustworthy, I calculated the weights of the brains of four groups, each of 10 strong, healthy, and not fat young men, from the dimensions and shapes of their heads, which evidences OTTO AMMON had been kind enough to provide me with. It had been ascertained for those 40 men that they did not grow any more. They were all small farmers and day-labourers from Baden. In this way I found an exponent of correlation of about 0.25, the value **0.245** (of two of the six combinations possible) is probably more correct.

Taking the second way I calculated *r* from the *directly determined* weights of the brains of Englishmen (Londoners) with average weights of bodies of men of the same social class, according to the

[1]) Ueber die Abhängigkeit des Hirngewichtes von der Körpergrösse beim Menschen. Archiv für Anthropologie. 4⁰. Bd 25. Heft 4. Braunschweig 1898, p. 423–441.

unsurpassed data of JOHN MARSHALL [1]). Here the value of **0.219** was found for r.

I tried to explain that strongly deviating behaviour of individuals of Man, differing in size, in comparison with species of Mammals of different sizes, by the uncomparatively great supremacy of the brain over other organs and parts of the skull in Man. The inferior augmentation of the brain with the size of the body might be a consequence, in my opinion then, of an exceptionally strong progressing folding of the grey cortex, going hand in hand with that augmentation of the brain as a whole. At the present state of our knowledge, now that we know that in all Vertebrates in general, independently of its shape and structure, the augmentation of the brain is equal for all species that are of a similar organisation, the interpretation then given, that can only be applied to Man, must be entirely abandoned. I should certainly immediately have rejected it, if I had known that, a few months previously in 1898, LAPICQUE, when applying the relation I had found for Mammals, to dogs of different sizes, according to evidences borrowed from a series of RICHET, had obtained the same result, as I now found for Man. That result had, moreover, only been communicated by LAPICQUE in a report of the proceedings of the meeting of the Société de Biologie on the 15th of January 1898, in hardly a single page of printing [2]) together with the announcement of my memoir on Mammals.

His conclusion ran: "Tout ce que je veux établir aujourd'hui, c'est que la puissance de P (the weight of the body), suivant laquelle varie l'encéphale d'espèce à espèce étant 0.55, dans l'espèce chien cette puissance est 0.25, c'est à dire extrêmement différent". Simultaneously with my paper on Man of 1898, in the "Archiv für Anthropologie", LAPICQUE published with DHÉRÉ another article [3]), in which the authors communicate as briefly the result for the Dog, mentioned above, and, on account of an examination of the chemical composition of the brain, try to find an explanation of the exponent found for this species in the relative amount of white and grey

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[1]) On the relations between the weight of the brain and its parts, and the stature and mass of the body. Journal of Anatomy and Physiology. Vol 26. London 1892. p. 445. There the weights of the bodies of living men, according to JOHN BEDDOE (Memoirs. Anthrop. Soc. London. Vol. III. 1870, p. 533).

[2]) "Sur la relation du poids de l'encéphale au poids du corps" in "Comptes rendus hebdomadaires des séances de la Société de Biologie". Paris 1898. N⁰. 2 (21 janvier 1898), p. 63.

[3]) "Sur le rapport entre la grandeur du corps et le développement de l'encéphale". In "Archives de Physiologie normale et pathologique", N⁰. 4. Octobre 1898. Paris. p. 763—773.

substance varying with the size. They ask themselves the question, if the law found for the Dog may in general also be applied to other species, and give a negative answer to it. "*A priori*, on doit estimer que non, et nous avons soin de dire que notre étude porte sur un cas particulier." (p. 765). In conclusion they say: "Il y a donc, en passant des petits aux grands chiens, une différence sensible de la composition chimique, et, par suite, l'unité de poids ne repré-sente pas pour les uns et pour les autres des valeurs physiologiques identiques", (p. 773).

It is clear, that by LAPICQUE and by me, independently of each other and unprejudiced, an identical result has been obtained for two very different species of Mammals. If this circumstance increases considerably the importance of this result, then it appears at the same time that neither of us surmised he had found an interindi-vidual exponent of correlation equal for all species.

Calculating the value of r for the dog found by LAPICQUE, proportional to the number of observations used for each comparison, afterwards[1]) communicated by him, I find it to be $= 0.235$. When he repeated the investigation applied to Man, which had caused me to find the two above mentioned values of r 0.245 and 0.219, with other evidences, according to the second method, he found for Man 0.23 and for Woman 0.224. A comparison of the averages of 7 larger with 7 smaller individuals of an American Squirrel (Sciurus carolinensis), which 14 individuals with a smaller American species (Sciurus carolinensis) (6 individuals) had furnished an exponent of correlation of 0.56, gave an interindividual exponent of 0.20[2]). With two groups of 5 female Moles of MANOUVRIER I find 0.234[3]). The average of these seven observations is **0,228**.

A number of other comparisons, with less good evidences, however, constantly furnished values that do not differ much from the average found in this way. When I compare the above-mentioned weights of the six largest Bullfrogs of DONALDSON (l. c.) with the six next in size of the same species, I find an exponent of correlation of 0,2516.

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[1]) "Le poids encéphalique en fonction du poids corporel entre individus d'une même espèce". Bulletin et Mémoires de la Société d'Anthropologie de Paris. Séance du 6 juin 1907. 5me Série, Tome 8, fasc. 4. Paris 1908, p. 315.

[2]) LAPICQUE, "Le poids encéphalique en fonction du poids corporel entre individus d'une même espèce", l. c. p. 327.

[3]) There must be errors in MANOUVRIER's statements (Mémoires Soc. d'Anthrop. Paris 1885, p. 213 and p. 297) concerning two groups each of 7,♂ moles, as the heavy individuals should on an average only possess 1 m.g. more brain than the lighter ones: the average likewise points to these errors. Consequently these groups are useless for the calculation of the interindividual r.

Taking into consideration that the certainly still more correct l i n e s of DONALDSON[1] give to r a value of 0.2316, we may call this result very satisfactory. On grounds to be discussed afterwards we may admit that indeed *the exponent of correlation within the same species of all Vertebrates* is **0,22**...

In my previous communication of the result for Mammals I had borrowed, on behalf of a provisional comparison with Man, for the calculation of k available evidences from the 2nd edition (of **1893**) of VIERORDT's "Daten und Tabellen". Calculating with the general exponent of correlation 0,56 I found then a somewhat different value of k for Man and for Woman. If I had made use of more accurate evidences, the cephalisation would have been found identical for the two sexes, as has indeed been proved by LAPICQUE[2]) in **1907**, and at the same time it would have been proved that between Man and Woman of different size the same exponent of correlation obtains as between species that are equivalent with regard to the organisation of the nervous system, but differ in the size of the body.

I can now affirm this by two more series of evidences. Placing namely the four groups of English men of average size, borrowed from MARSHALL, used for my calculation of the exponent of correlation for Man, beside the four groups of average English women of his Table XVIII (l.c., p. 498) we find 63685 G. and 54432 G. for the average weight of the bodies and 1353.7 G. and 1233.2 G. for the average weight of the brain. The result of the calculation is $r = 0,594$.

For the average weights of the brain of English and Scottish men and women we obtain 1375 G. and 1235 G., according to seven different observers, cited in the new edition of VIERORDT's "Daten und Tabellen".[3]) The weights of the body for full-grown men and women of that nationality, according to ROBERTS, cited there, are 63010 G. and 52170 G. (deduction made for what ROBERTS indicates for the weight of the clothes). With this value r can be calculated at 0,568.

Calculating with the weights of the body according to ROBERTS and the weights of the brain according to MARSHALL we find 0,498. The average of these three results is **0.553**.

There are no sufficient evidences at hand for testing this sexual difference in species of animals. KOHLBRUGGE[4]) gives the weights of

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[1]) For these comparisons E and e were borrowed from the graphical representation in DONALDSON's publication of 1898 (l. c. p. 322).

[2]) "Le poids encephalique en fonction du poids corporel entre individus d'une même espèce". l. c. p. 344.

[3]) Dritte Aufl. Jena 1906, p. 23—24, 75—76.

[4]) Zeitschr. f. Anatomie und Morphologie. Bd. II (1900), p. 51—55.

the body of the Javanese Budeng (Semnopithecus maurus and pyrrhus) relating to 11 female and 7 male individuals and the weights of the brain of 4 female and 3 male individuals. It is a great pity that a few errors must have slipped into these precious statements of the weights of the bodies [1]). It is, however, possible to calculate 0.553 or 0.586 for the intersexual exponent of correlation, either when correcting the presumable errors or when omitting these erronical weights of the body.

What has been stated for Man, considered in connection with the rational meaning of the exponent of correlation 0.55 still to be discussed, gives us already a right to admit that for Vertebrates in general the following law exists: *The sexes differing in size of one species are in the quantity of brain proportional to each other as two different species with identical organisation of the nervous system.*

. The attention may here be called to the fact that this law is in accordance with the result of the latest investigations about the hereditary transmission of sex [2]), as with those of DUMBAR on the sero-biological behaviour of the sexes in plants and animals.

Further I want to point out that there is a connection between the relation of the two sexes found and the non-existence of the disproportion in the relative length and thickness of the bones, which is so striking a feature between the large and the small individuals of one species. [3]) Both sexes behave, in this respect too, as nearly related species of very different sizes.

[4]) [The uniformity of the correlation found between quantity of brain and size of body in all classes of Vertebrates, however striking, cannot, properly, surprise us, as we did eliminate a priori all other important influences on the quantity of the brain, save *the size of the body*. That uniformity affords proof that indeed we succeeded in eliminating those other influences and, moreover, that the size of the body influences the quantity of the brain in the same way in all classes.

One may, however, consider it strange that the well known increase of the relative amount of white substance (composed chiefly of medullated fibres) contrary to the grey substance (containing the

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[1]) It seems indeed that in three cases pounds are written erroneously for kilos.

[2]) C. CORRENS and A. GOLDSMIDT, Die Vererbung und Bestimmung des Geschlechtes. Berlin 1913.

[3]) Species with a relatively slight difference of size (as e.g. Hylobates syndactylus and H. leuciscus) show a disproportion in a reverted sense: between species of very different size this is scarcely perceptible.

[4]) The passage between brackets is added in the English translation.

bodies of nerve cells), an increase going on, systematically, with increasing quantity of the entire brain, does not appreciably corrupt those results.

It was this consideration that induced DHÉRÉ and LAPICQUE to investigate the chemical composition of the brain in large and small dogs.[1] From their results it is obvious that the real disproportion between the two constituents in large and small brains of nearly related animals, though existing, is insignificant when compared with what it seems to be on sections of those brains and from superficial mathematical reflection. We may infer that the seemingly very striking disproportion is, to a very large amount, corrected by other variations going hand in hand with augmentation of the quantity of brain, namely increasing thickness and folding of the cortex and less rounded form (i.e. relatively more extended surfaces) of the larger brain, these three processes (or two in the brains without folding) tending to increase the relative amount of grey substance]

The positive knowledge, obtained in this way, of the relation between quantity of brain and size of the body, in species and individuals, gives now a meaning to that "puissance étrange" 0.55.. and at the same time 0.22.. by which those relations are determined.

Referring to the arguments in my memoir of 1897 on the peculiar relation of the eye to the size of the body, and continuing the analysis of the exponent 0.56 or 0.55.., I believe that it will be easy to prove its rational character, as well as that of. the exponent 0.22.. In this way the correlations we found are raised to the rank of real biological laws.

In the memoir of 1897 I had already pointed out that the factor that expresses the deviation from the simple relation between weight of the brain and superficial dimension of the body is the cube-root of the linear dimension of the body.

$S^{0.55...}$ can be analysed as follows:

$$A. \quad S^{0.66-0.11} = S^{\frac{2}{3}-\frac{1}{9}} \qquad\qquad B. \quad S^{0.22+0.33} = S^{\frac{2}{9}+\frac{3}{9}}$$

$$= \frac{L^2}{L^{\frac{1}{3}}} \qquad\qquad\qquad\qquad = L^{\frac{2}{3}} \times L$$

The relations found above can then be described as follows:

I. In species of Vertebrates that are alike in the organisation

[1] "Sur le rapport entre la grandeur du corps et la développement de l'encéphole." l.c. (1898).

of their nervous system and their shape, but differ in size, and also in the two sexes of one and the same species, the quantity of brain increases:

A. as the quotient of the superficial dimension and the cube-root of the longitudinal dimension.

B. as the product of the longitudinal dimension and the square of its cube-root.

II. In individuals of one and the same species and of the same sex, differing in size, the quantity of brain increases as the square of the cube-root of the longitudinal dimension of the body.

Consequently we find between the exponents 0.22.. and 0.55.. a relation of a simple nature.

Moreover the factor $S^{0.22}$ or $L^{\frac{2}{3}}$ in B is the square of the denominator in A.

The fact that, in different species, a factor determining the quantity of brain is to be found in the superficial dimension of the body, which is the measure of the sensitive surfaces as well as of the muscular force, was discussed at large in my memoir of 1897. It is neither incomprehensible, that individuals of different size in one and the same species distinguish themselves from, for the rest closely resembling species differing in size, because only in the latter case an increase of the quantity of brain proportional to the longitudinal dimension takes place, as a consequence of segmental growth, increase of sensu-motorical unities in segmentically constituted species of animals.

From the investigations of I. Hardesty[1] it appears that in the Elephant, which is 180000 times heavier than the Mouse, and in Man, who is 3628 times heavier than the Mouse, the masses of certain nerve-cells of the spinal-cord are proportional as the imaginary longitudinal dimensions of the mentioned species.

If we admit that to every nerve-fibre a definite central cell-mass answers, then these masses must increase with the number of nerve-fibres, in segmentically constituted animals indeed as the longitudinal dimension.

But what is then the meaning of $L^{\frac{1}{3}}$?

The answer to this question was likewise prepared in my memoir of 1897. It is to be found in the very special relation between the size of the eye and the body in animals of different sizes. The longitudinal dimensions of the body and the eye of these animals

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[1] Journal of Comparative Neurology. Vol. 12 (1902), p. 125—182.

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are not proportional to each other, neither are they absolutely equal; in other terms, the smaller animal has, in proportion to its body, a large eye, yet it is absolutely surpassed by that of the larger animal. We find here evidently a similar relation as between the weight of the brain and that of the body, and can try to fix this relation in a similar way, by calculating an exponent of correlation.

Most fit for this comparative investigation are again species that differ as much as possible in size, and have at the same time absolutely large eyes. Instead of the simple diameter of the eye-ball (which in its shape and in the thickness of the sclerotica is variable) it is preferable to compare the linear sizes of the images on the retina. More than twenty years ago MATTHIESSEN[1]) made exact measurements of the sizes of the images on the retina, amongst others in Whales, which together with others were already formerly discussed by me. He does not indeed indicate the sizes of the animals them-selves, but if we admit for them the averages of the full grown species, then the error resulting from this insufficient information cannot be very great.

Let us thus compare the largest of the four examined species of Whalebone-Whales, Sibbald's Fin-Whale, with the smallest, the Humpback Whale, and calculate according to what exponent of correlation of the length of the body proportionality with the size of the image is obtained[2]).

Proportion of

	linear sizes of the images (in Millimeters)	lengths of the body (l) (in Meters)
Larger Fin-Whale (Balaenoptera Sibbaldi) and Humpback-Whale (Megaptera Boops)	$\dfrac{39.78}{30.23}$	$\dfrac{30}{15}$

We find then that on an average the lengths of the body must be involved to the power 0.3964 to become proportional to the lengths

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[1]) L. MATTHIESSEN. Die neueren Fortschritte unserer Kentnis von dem optischen Baue des Auges der Wirbelthiere. Festschrift für H. von HELMHOLTZ 1891, p. 62-63.

[2]) The Porpoise (mentioned by MATTHIESSEN as "Delphinus communis") and the Whalebone-Whales belong to phylogenetically different orders, Ondontocetes and Mysticetes, which differ greatly both in the relative size of the eye and in the cephalisation (this in reverted proportion). Therefore they cannot be compared here

of the images, i.e. *almost* $\sqrt[3]{l}$ or $\sqrt[9]{S} = S^{0.111}$, correctly $S^{0.132}$ or $\sqrt[7.6]{S}$.

In the interesting essay of AUGUST PÜTTER [1]) I find, in text and in figures, statements both of the retina-surface and of the size of the body of full-grown individuals of Hyperoodon rostratus, the Bottlenose-Whale, and of Phocaena communis, the Porpoise, both Odontocetes. The lengths of the bodies are proportional as 6 : 1, and the diameters of the retina as 2 : 1. From this follows, that those diameters increase as $\left(\dfrac{S}{s}\right)^{0.133..} = \sqrt[7.5]{\dfrac{S}{s}}$.

In my memoir of 1897 a Lion was also compared with a Cat for the calculation of the exponent of correlation. The exponent of correlation I found was 0.5466. The coefficient of cephalisation, calculated with 0.55.., gives therefore a different result for them. In order to obtain equality, the S of the Lion must only be a little diminished (according to the proportion that presumably existed between the two individuals examined by MATTHIESSEN). Then the proportion of lengths of the images in the eyes, measured for both species, $= \dfrac{18.95}{11.80}$, is exactly equal to $\sqrt[7.5]{\dfrac{S}{s}}$.

An equal relation is found between the Sea-eagle and the Hawk.

The general validity of this relation is especially obvious when comparing little animals with enormously large ones. The shapes of the bodies can then even be greatly different, if only there is no great deviation in the coefficient of cephalisation. Among the animals of which MATTHIESSEN has measured the lengths of the images, are also the Fox, the Cat and the Rabbit. The weights of the bodies of these animals and also of that of Sibbald's Fin-Whale, (of which several individuals have been examined) are approximately known. Between these the following relations are found:

	$\left(\dfrac{S}{s}\right)^{0.133}$ in Kilograms	Proportion of the lengths of the images (in Millim.)
Sibbald's Fin-Whale and Fox	$\left(\dfrac{100000}{6}\right)^{0.133} = 3.643$	$\dfrac{39.78}{9.42} = 4.223$
„ „ „ Cat	$\left(\dfrac{100000}{3}\right)^{0.133} = 3.995$	$\dfrac{39.78}{11.80} = 3.371$
„ „ „ Rabbit	$\left(\dfrac{100000}{1.5}\right)^{0.133} = 4.381$	$\dfrac{39.78}{9.19} = 4.329$
Average	— 4.006	— 3.974

[1]) Zoologische Jahrbücher. Abtheilung für Anatomie und Ontogenie der Thiere. Jena 1903. p. 240, 243, 273 and 280.

LAPICQUE has measured the diameters of the eyeballs of a number of Vertebrates and found for Mammals an exponent of correlation first of $\frac{1}{8}$, afterwards of $\frac{1}{7}$ [1]). For the examined Mammals the measurement of the diameter of the eye-ball was generally sufficient in order to ascertain the size of the retina. He concludes then, as was to be expected from what could be shown already in 1897, that in most cases the size of the eye runs parallel with the weight of the brain.

Those meritorious measurements of the eye-ball by LAPICQUE thus furnish a welcome affirmation of the results obtained here with regard to the images on the retina. We may admit that the linear dimensions of the images vary as $\sqrt[7.5]{S}$ or $S^{0.133\cdots}$.

If the result had been $\sqrt[9]{S}$ or $S^{0.111\cdots} = L^{\frac{1}{3}}$, then we should have here the same factor as in the coefficients for the brain, and we should immediately be convinced of its rational character. Now it can, again, not be by chance only that even in apparently absurd comparisons (as those of Sibbald's Fin-Whale with species of little land-animals) that same exponent $^1/_{7.5}$ constantly returns. What is the meaning of this fact?

The answer to this question too is not difficult, for $9 : 7.5 = 0.66\ldots : 0.55\ldots$ If now we consider that, in accordance with the augmentation of the brain with the size of the species of animal, the sensitive surfaces must increase in the same proportion to the superficial dimension of the body, then it becomes comprehensible that the receptive sense-elements in the retina do not remain entirely equally thick with the larger animal as with the smaller one, but become thicker and less closely placed [2]), *in the same proportion*. For this reason the *number* of the nerve-elements in the retina increases only linearly as $\sqrt[9]{S}$ or $L^{\frac{1}{3}}$, in the superficial dimension as $\sqrt[9]{S^2} = S^{\frac{2}{9}}$ or $S^{0.22\cdots} = L^{\frac{2}{3}}$.

In this way a connection has been established between the exponent of correlation for the eye and the exponent of correlation for

[1]) "La grandeur relative de l'oeil et l'appréciation du poids encéphalique". Comptes rendus de l'Académie des Sciences. Paris, Tome 147, (1908), 2, p. 209. "Relation du poids encéphalique à la surface rétinienne dans quelques ordres de Mammifères". Ibid. Tome 151, (1910), 2, p. 1393. On lower Vertebrates: L. LAPICQUE et H. LAUGIER in Comptes rendus de la Société de Biologie. Tome 64, (1908), p. 1108.

[2]) Compare the data in A. PÜTTER, Organologie des Auges. 2nd Ed. Leipzig 1912.

the brain with the mass of the body, within one species, as well as from species to species.

Still it remains, however, an open question why the lengths of the images, as measured by the number of sense-elements, increase exactly as $L^{\frac{1}{3}} = L^{0.33\ldots}$.

In order to find an answer to it, we must consider, that the eye distinguishes itself from the other senses by giving at a distance a representation of the exact place of the energy-source that acts as a stimulus. Consequently it orientates about the direction from which that stimulus comes. Object and image, that is the place of the stimulated sense-elements, answer to each other.

Under these circumstances the distance to the objects must exactly stand in the mentioned relation to the linear dimension of the body. Indeed the receptive nerve-elements of the retina placed in the linear dimension of the image, increase then numerically in the proportion of $L^{0.33\ldots}$ in the larger animal, *their mass* in the linear dimension as L, their mass for the surface of the image as L^2. But that mass determines the amount of the transition of energy that is connected with the stimulation of the sense-elements.

It appears now that the long since known intimate connection of the organ of vision, as exquisite sense of room finding its principal function in governing the movements, can be expressed in a definite measure [1]). As in the movements of animals, differing in the size of their bodies, the mass that is to be removed, increases in the proportion of L^3, the muscle-power however only as L^2, an L-fold sensu-motorical stimulation is required for it. And as all senses are more or less, as the optical sense is absolutely, organs of room, their receptive elements must, in the aggregate, increase in mass in that proportion of L, that is in linear dimension as $L^{\frac{1}{3}}$ in superficial dimension as $L^{\frac{2}{3}}$, or $S^{\frac{2}{9}}$. But the nerve-fibres, the peripherical extremities of which are connected with sense-elements in the retina and also in all other sensitive surfaces, and the corresponding cell masses in the brain must increase as $\sqrt[9]{S^2} = S^{\frac{2}{9}} = S^{0.22\ldots}$.

The denominator of the coefficient $\dfrac{L^2}{L^{\frac{1}{3}}}$ can thus be explained as a relative reduction of the brain of the larger animal proportional

[1]) In a striking way this connection is demonstrated by PÜTTER (l. c. p.p. 85 et seq. and p.p. 402 et seq).

to the relative reduction of the sizes of its images, a diminution of the distance from the objects of his sphere of feeling and acting and a diminution of the rapidity of movement in proportion to the lengths of the bodies.

The conclusions we have thus obtained give an explanation of a number of otherwise incomprehensible deviations in the value of the coefficient of cephalisation.

For Bats I calculated in 1897 a (mutual) exponent of correlation of 0.66... It appears that it can be applied both to Macro- and to Microchiropteres. A very large insectivorous Bat from Dahomey (Scotophilus gigas) supplies a welcome control and affirmation of my former results. In Bats the influence of the eye is almost entirely excluded. The senses of touch and hearing determine the quantity of brain and the factor $S^{0.11}$. or $L^{\frac{1}{3}}$ disappears. Calculated with their own exponent of correlation the coefficient of cephalisation still diminishes for the two phylogenetically different groups, of which the Microchiropteres are lowest.

Rodents deviate mutually considerably in the values of their cephalisation. This cannot be explained, as LAPICQUE surmises, by different size of the eye, though it may play in some cases an inferior part. It is the other senses especially, which, by taking the lead in the nervous life of the animal, determine here the quantity of brain. According to numerous evidences the cephalisation of the Brown Rat and the Black Rat and likewise that of the Housemouse is half that of Hares (and Rabbits) and only a third part of that of Squirrels. In the Hares the sense of hearing, in the Squirrels, the Desert Jerboa (Dipus) and the Garden Dormouse (Eliomys) especially the organ of touch, on account of its high specification (in the hand), has caused the increase of the brain.

The value of k falling very low in Shrews, is trebled with the affined East-Indian Tupaja, which lives like the Squirrel.

Canides have about twice as high a cephalisation as Mustelides, on account of the greater development of their senses of hearing and of smell. Among the last-mentioned family, Otters are hand-animals, and, for that reason, they surpass very considerably the other Mustelides in their cephalisation. They reach the rank of Canides.

The Elephant surpasses the other Hoofed Mammals three times in cephalisation. He ranks even much higher than the Anthropoid Apes. He owes this to his trunk, which has become a prehensile and touch hand, with high "specific energies", and possesses the same combination with a chemical organ (here of smell) as the feelers of Ants.

Some of the American Monkeys (Ateles), which are higher cephalised than the Monkeys of the Old World, *not excepted the Anthropoid Apes*, obtained a third prehensile and touch hand in their tail.

Man certainly likewise owes his high rank to his hand; his cephalisation is almost equal to nearly four times that of Anthropoid Apes, consequently he has risen still higher above the latter, than the Squirrel above the Rat, or the Elephant above the other Hoofed Mammals.

Even in the Amphibia we see the cephalisation of the Treefrog which uses its fore-feet as hands, increasing considerably.

Among Birds, Owls have a high cephalisation, not so much on account of their large night-eyes, which cause only an enlargement of the images on the retina (in comparison with the Day-Birds of Prey), without augmentation of central nerve-cell mass, but on account of the extremely developed sense of touch in the skin and their very quick ear. The touch-corpuscles at the base of the feathers are incredibly numerous. [1]

The Parrots owe the high value of their k to their handlike paw and pincerlike beak.

In all these cases greater influence of the factor $S^{0.33}$ by specification of the organ of touch occurs.

The comparatively high cephalisation of Sea-Mammals, usually represented exaggerately (as few full-grown animals have been examined), and that of the Hippotamus, however low in the general organisation of the nervous system, can now easily be explained.

According to the evidence now available, the coefficient of cephalisation of Seals can be computed at 0.6, that of Toothed Whales (Odontocetes) at 0.7 and that of Whalebone Whales (Mysticetes) at 0.4. Seals owe their high cephalisation certainly *partly* to the specifically high development of their sense of touch. But Odontocetes, whose cephalisation is equal to that of Anthropoid Apes, lack certainly a similar high development of the organ of touch. They distinguish themselves from the plankton-eating Whalebone Whales by seeking their subsistence at usually greater depth, even to where perfect darkness prevails. In connection with this fact their eye is smaller than that of Mysticetes, but they possess a still more developed sense of hearing than the latter; in the quiet water of the great deep this organ can function perfectly as a sense of room. In all these Water-Mammals, but mostly in the Odontocetes amongst them, the ear is the most important organ [2]. It is doubtless the crepuscular

[1]. E. Küster, Morphol. Jahrb. Bd. 34. (1905), p. 126.

[2] G. Boenninghaus. Das Ohr des Zahnwales. Zoologische Jahrbücher. Bd. 19 (1904). p. 338—339. — Compare O. Abel, Palaeobiologie. Stuttgart 1912, p. 458.

light prevailing in the water that makes other senses than the optical one predominate in these Mammals, as likewise in the Fishes, and probably in the Crocodiles (hearing very quick), in comparison with Amphibia and most Reptiles. In the Fishes also the olfactory organ and especially the sense-lines are predominant. This has caused augmentation of the quantity of brain, because the surfaces of the mentioned predominating organs of sense (in opposition to the eye, which forms definite images) increase simply proportional to the superficial dimension of the animal (consequently with the exponent of correlation 0.66...). So in these animals a very considerable increase of the quantity of brain does not signify a high degree of organisation. Calculated by means of the exponent of correlation 0.66...) k becomes for Whalebone-Whales 0.07, for Toothed Whales 0.20 and for Seals 0.18.

In the Snakes and the Slow Worm and likewise in the Eels, on the contrary, the great length of the body is the cause of the low value of k, though this does not therefore indicate an inferior degree of organisation. In proportion to the weight of the body the not specialised segmental sensu-motorical unities are too equivalent for a representation in the brain, proportional to that of other Reptiles and Fishes. The body becomes thereby, as it were, to a certain amount, a ballast for the brain. This is in a more literal sense the case in the Tortoises. In the shell-bearing Vertebrates and also in the elongated animals the influence of the factor $S^{0.33}$ in the analysis B has thus diminished. In the Eels a second cause of diminution of the quantity of brain exists *moreover*, in their life as animals of darkness, by the disappearance for the greater part of the eye-factor $S^{0.22}$ in the analysis B and at the same time of the eye-factor in the analysis A (as in the Bats). On account of the latter circumstance their r becomes $= 0.66$.

The influence of the not segmentally constituted eye *in itself* remains in all cases restricted, from the nature of the factor $S^{0.22}$ which depends on it, and is thus less capable of increase. Even the Horse, which possesses an absolutely larger (day-) eye than the Elephant, rises still little above the average level of k for Mammals. On the other hand can the other factor $S^{0.33}$, the segmental factor in analysis B, grow, as it were, endlessly with the development of "specific sense-energies" in the different segments. The tactile organs have therefore always the lead with the higher organisation of the nervous system.   25 November 1913.