AN

EXPERIMENTAL INQUIRY,

&c. &c. &c.

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EXPERIMENTAL INQUIRY

INTO THE

FUNCTIONS OF THE OPHTHALMIC GANGLION.

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PART FIRST.

Incomplete as our knowledge of the physiology of every part of the nervous system undoubtedly is, it will be readily admitted that modern investigations have done less to elucidate the functions of the ganglia than of the other nervous centres. The actions of the ganglionic system are indeed at present assumed rather than proved; inferences from what is probable rather than deductions from established facts. There is great difficulty in submitting any ganglion to satisfactory experimental procedure, and when this has been effected, the extensive connections of the ganglion with other nervous centres render the results obtained complex and difficult of analysis. The lenticular ganglion represents the ganglionic system in miniature. What can be proved with respect to it, may justly be taken as a safe index to the rest. From being comparatively accessible, and from its connections being limited and well-defined, this ganglion is the most eligible for the purposes of experiment. And from the effects produced on the eye being in great measure open to inspection, the results obtained are as little conjectural as the nature of such inquiries will admit of.

The results of previous experiments on the nerves of the orbit are sufficiently contradictory. Mr Mayo's experiments on pigeons appear to prove that the third nerve is the only motor nerve of the iris; his experiments on rabbits throw a doubt on that conclusion. Magendie found that division of the fifth nerve caused dilatation of the pupil in dogs and cats; contraction of the pupil in rabbits and Guinea pigs. Now, although objections have reasonably been raised against the accuracy of Magendie's mode of conducting his experiments, and especially on account of his omitting to describe the state of parts injured as it appeared after death, still such objections apply equally to both kinds of animals, and may therefore be left out of calculation for the present. The fifth nerve has been supposed to be the motor nerve for dilating the pupil; if so, whence the dilatation on destroying it in dogs and cats? If the nerve for causing contraction, either directly as a motor, or indirectly as an excitor to the third nerve, whence the contraction on its division in rabbits and Guinea pigs? Had contraction of the pupil invariably followed division of the fifth, we might reasonably have assumed that the fifth must be either an excitor or a motor nerve to the iris. On the other hand, had dilatation ensued in every animal, we might have doubted whether this was not owing to the great shock having produced blindness for the time, or otherwise, whether the fifth was not the nerve which governed the dilating movement. But such diametrically opposite results as we actually find can only proceed from some inherent differences in the conditions under which the experiment is performed, or in the relative connections of the parts injured. It has been stated that contraction is the natural state of the pupil in the rodentia, after death; and dilatation in cats and dogs. If true, this would not solve the difficulty; but I believe it to be erroneous. The pupil after death in every animal is of the medium size natural during life. The exceptions are numerous, and depend upon the state of the iris at the time of death, and upon the action of external agents after death. If the pupil is very large when death occurs, as in slow death from hanging, or prussic acid, it will retain this size for some time after death; as the body cools, the pupil lessens, but is seldom reduced to the medium size. But when death from prussic acid is instantaneous, the largely dilated pupils will contract in a few minutes after death to less than the medium size, and afterwards enlarge again. The varying degree of contraction of the *sphincter iridis* at the time of coagulation of the blood, (which *does* take place, at least in small vessels, after poisoning by prussic acid,) may perhaps account for this. If death occurs with the pupils contracted, these enlarge after a time, but do not generally attain the ordinary medium size. In practising operations on the eye of the human subject after death before the animal heat has vanished, a dilated pupil always contracts as the aqueous humour escapes. This, like the motion of a narcotized iris in extracting the lens for cataract, and like the contraction of the previously dilated pupil of a drowned kitten on exposing the animal to the heat of a furnace, in an experiment performed by Haller, is probably due to physical influence.

It has been stated that in the rodentia there is no ophthalmic ganglion, and hence inferred that the connection of the fifth nerve with that ganglion in the dog and cat, and the absence of any such connection in the rabbit and guinea-pig, might account for the different results of dividing it in these animals. The lenticular ganglion, however, does exist in the rodentia, although it is exceedingly small. Nor is there any adequate difference in its connections with the third and fifth nerves and the iris. I dissected many rabbits, squirrels, and guinea-pigs, without being able to satisfactorily distinguish a lenticular ganglion; until finding that nervous filaments always became lost underneath the optic nerve, and could not be pursued through the firm fat and small vessels on raising that nerve, I commenced differently by removing the floor of the orbit and dissecting down to the under aspect of the optic nerve. In this way may be found, beneath and closely connected to the optic nerve by its loose cellular sheath, a small enlargement on the junction of two nervous filaments from the third nerve. Proceeding from the front of this enlargement, a few filaments course along the under surface of the optic nerve on each side, as far as the eye-ball, which they enter. No filaments pass directly from the fifth nerve to this ganglion; but the fifth and third communicate freely with each other in the *foramen lacerum orbitale*, as they do also in the dog and cat. The nasal sends some ciliary nerves, which join the rest, but are not connected with the lenticular ganglion. In the rabbit there are also two distinct non-ganglionic ciliary filaments from the sixth nerve. Most of these ciliary nerves leave the optic nerve at its point of insertion, and passing with vessels in a groove in the sclerotica, pierce the eye-ball about a line and a half external to the insertion of the optic nerve. I have not succeeded in tracing any ciliary filaments from the sixth nerve in either guinea-pig or squirrel; but as they exist in rabbits, it is probable that they are to be found in other rodents.

In the dog and cat the lenticular ganglion is large, and is formed upon the inferior division of the third nerve exclusively. It receives no distinct root from the fifth nerve, but the fifth and third nerves communicate together by nervous filaments just before they enter the orbit; hence filaments from the fifth are probably bound up in the neurilemma of the third nerve. A naso-ciliary nerve applies itself to a fasciculus of the ciliary nerves, a line or two in front of the ganglion. That the motor nerve of the inferior oblique muscle has, in some animals, a functional connection with the ganglion, and does not merely pass by and in apposition to it, may be inferred from the constancy with which the ganglion is found in close relation to that nerve. In one kitten, the lenticular ganglion was a line distant from the main division of the nerve, instead of being, as usual in cats, a bulging on the nerve-trunk. In this instance, the nerve to the inferior oblique muscle was given off by the ganglion, and not by the nerve-trunk. In some animals there is not this close relationship. In the pig, for example, the lenticular ganglion is extremely small, ovoid, and lies on the outer aspect of the optic nerve, eight or nine lines from the eye-ball. Its only connection with the branch of the third nerve, which supplies the *obliquus inferior*, is by a nervous thread an inch and a-half in length.

In the sheep and ox the ganglion is moderate in size, and formed principally by the third, and slightly by the fifth nerve. The sixth nerve does not appear to furnish any ciliary branches.

Of birds, I have examined the fowl, goose, duck, hawk, owl, and parrot. The ophthalmic ganglion is most developed in the three last. In each of these the ganglion is placed on the third nerve; in each, the ciliary nerves from the fifth do not go to the ganglion itself, but join the fasciculus of ganglionic ciliary nerves just after these have left the ganglion. In all, the third and fifth nerves communicate within the cranium. Wagner remarks that no connection has ever been made out between the sympathetic nerve and the lenticular ganglion in birds, and he considers the fact important in explaining the voluntary power which he considers this class to possess over the action of the iris. If a connection with the sympathetic be sufficient to impede voluntary power, why should not the passage of the ciliary motor nerves through the lenticular ganglion, so distinct in birds, render them involuntary? I believe that birds have not any directly voluntary power over the iris, but merely, with cats, a great facility in accommodating the eye to different distances, the action of the iris being concomitant with, and probably an essential part of, such focal adjustment.

Of fishes, in the cod, there is a large mass of grey nervous matter belonging to the sympathetic, beneath the Gasserian ganglion. From this proceeds a filament which joins the third nerve just at the point of its division. Whilst invested with the surrounding loose jelly-like cellular tissue, this has somewhat of the appearance of a ganglion; but on dissection no ganglion is found. The eye-ball receives a few filaments from the third and fifth nerve, and, in larger proportion, twigs from the sympathetic, all loosely packed together. These penetrate the cartilaginous portion of the sclerotica behind the choroid body, in which many filaments appear to terminate. In the skate, haddock, whiting, perch, trout, and eel, except in the first as regards the choroid body, I found the arrangement very similar. Neither in these nor in such reptiles as I have examined (frogs and newts) is there any lenticular ganglion.

The connection between the lenticular ganglion and the sympathetic system is well demonstrated in the sheep, in which a large grey nerve may sometimes be traced distinctly from the ophthalmic to the cavernous ganglion. In the dog and cat also, grey filaments are given slightly to the third, and in abundance to the fifth nerve, as they pass by the side of the internal carotid artery. The oft-mentioned communication between the sympathetic and the sixth nerve is not so great as it appears. A band of white fibres passes from the sixth nerve, and some grey filaments to it; but of the latter the greater number, as Panizza asserts, merely twine round the sixth, and then enter the fifth nerve.

In man, Mr Dalrymple remarks, that the long root of the lenticular ganglion separates from the nasal nerve whilst within the cavernous sinus, "ramifying on the sides of the internal carotid artery, and within the bony canal that contains this blood-vessel, it unites with other sympathetic nerves, communicating directly with the superior cervical ganglion." I have little doubt that there is a distinct continuity of grey fibre between the superior cervical ganglion and the lenticular; but I have never found the long root exactly as thus described. I have always been able to trace it, most readily in the fœtus, as a distinct thread into the Gasserian ganglion, beyond which I could not follow it. The Gasserian ganglion in man, as in the cat, dog, sheep, and ox, receives grey filaments from the sympathetic beneath it. Some of these may enter the long root of the lenticular ganglion. I never could trace any filaments from this long root through the sensory into the subjacent motory portion of the fifth. I believe that the lenticular ganglion communicates with the cavernous plexus, chiefly if not solely through the medium of grey fibres which are inclosed in the sheath of the fifth nerve, and to a less extent in that of the third. Nervous filaments from the sympathetic have been described as being traceable into the lenticular ganglion by Fontana,* Bock, Hirzel, Cloquet, Lobstein, Ribes, Chaussier, and Hyrtl. Tiedemann and Arnold state, that a nervous filament passes directly from Meckel's to the lenticular ganglion. This I have never found either in man or animals. Hyrtl, who has examined this filament microscopically, considers it merely a fibrous chord.

The ultimate distribution of the ciliary nerves is perhaps not quite settled. That by far the greatest number may be distinctly traced into the ciliary circle, and their ramifications with care fol-

* Diss. Inaug. de Amaurosi Functionali. Auctore Ed. Stephens, M.D. 1827, (p. 16.)

lowed through this into the iris, is sufficiently established. But Chaussier and Ribes describe a minute nerve as proceeding from the ganglion to the *arteria centralis* where it enters the optic nerve; and Tiedemann traced this *nervus centralis* in the ox as far as the retina, where it accompanied the different branches of the central artery. He also thought that the lens and vitreous humour received some filaments. Hyrtl states that he has seen some filaments detach themselves from the ciliary nerves after these had traversed the sclerotica, and pass backwards ramifying on the choroid, but he could not assure himself whether or not these recurrent filaments reached the retina. Ribes believes that he has traced them into the retina.

The following are the general conclusions from the anatomy of the lenticular ganglion in different animals; that its size is always in proportion to the activity of the iris, which in turn always bears a direct relation to the strength and acuteness of vision, and to the nocturnal habits of the animal, and implies a proportionate development of the internal vascular apparatus of the eye; that it is always more intimately connected with the third nerve than with any other, and always with that division of the third nerve which supplies the inferior oblique muscle; that the size of the short root is in direct ratio to that of the lenticular ganglion, (the long sensory root observing no such relation;) that it is sometimes a mere swelling on the trunk of the inferior division of the third nerve itself, and then can scarcely be said to possess any short root; that it is always connected with the sympathetic, but that the nerves along which these communicating fibres pass, vary; that it is always connected with the Gasserian ganglion, receiving filaments from the sensory, never from the motory portion of the fifth nerve; these filaments being few in number and never terminating in the lenticular ganglion, which they enter either separately and distinct from the third nerve, as in man, or bound up within the same sheath as the third nerve, as in several animals; that there always exist other ciliary nerves from the fifth, which have no connection with the lenticular ganglion, although they ordinarily apply themselves to nerves which proceed from that ganglion. But in the rabbit, perhaps in all rodentia, there exist also ciliary twigs from the sixth nerve, which do not enter the lenticular ganglion.

Without this prefatory anatomical detail, certain points in the following experiments might appear unintelligible.

Experiment I.—A young dog was stunned by a blow on the head, and his skull opened as quickly as possible. Fine needles were inserted carefully into different nerves, and the wires of a small galvanic battery applied to the needles when inserted.

1. One needle placed in the optic chiasma; the other through

the cornea into the iris of the left eye. Both irides acted, contracting the pupils; both eyeballs were rapidly moved in different directions, and various muscles in the body contracted. Hence, the stimulation of the optic nerves acted not directly on the iris, but mediately through the motor nervous tract. This is further proved by the next observation.

2. The left optic nerve was divided, and both needles inserted into its distal portion. No effect.

3. Both needles were inserted, at a small distance from each other, into the ophthalmic division of the fifth nerve on the left side, the left optic nerve being already divided. The pupils remained immoveably dilated, but the eyeballs were moved quickly in different directions.

4. The same repeated after dividing the left fifth nerve at its origin. No movement whatever. Hence, stimulation of the fifth nerve can excite indirectly the action of the orbital muscular nerves, but has no direct motor influence over the orbital muscles; secondly, it has not directly either an excitor or a motor influence over the iris.

5. The left third nerve being separated from the brain, both needles were inserted into its distal portion. A brisk somewhat quivering motion of the left eyeball resulted; the cornea was occasionally turned with a semi-rotatory motion upwards and inwards under the inner canthus, and the pupil contracted. Hence the third nerve has a direct motor influence on some of the orbital muscles, and on the *sphincter iridis.*

6. The same repeated on the cerebral portion of the third nerve after dividing its trunk. No effect. The third nerve, therefore, does not cause contraction of the pupil by exciting other nerves.

7. The needles inserted into the right optic nerve, both third nerves being now divided. No effect. Hence the optic nerve influences the iris solely through the third nerve, since the other nerves on the right side were as yet intact.

8. The needles being applied to the right fourth nerve, the cornea of the right eye was rapidly revolved downwards and outwards, to attain which it swept round the lower lid, and was not drawn in a straight line to the axis it arrived at. Pupil unaffected.

9. On galvanising the sixth nerve in a similar way, the eyeball was retracted and directed outwards. Pupil unaffected. The two last observations point out the normal action of the superior oblique, abducens, and retractor muscles.

Experiment II.—The spinal chord of a large cat was suddenly divided between the first vertebra and the occiput.

10. Both pupils were immediately dilated to the utmost, and light had no effect on the eye.

11. Galvanism applied, as in the preceding experiment, to the optic nerves. No effect.

12. To the fifth nerve. At first there was a slight movement of the jaw. No effect on the iris or eye-ball.

13. To the third nerve ; to the iris itself; to the *recti oculi ;* alike without effect.

14. To the walls of the heart. No effect.

15. To the muscles of the trunk. Contraction ensued.

16. The cornea of the right eye was punctured with a cataract needle. On the following day the pupil of the right eye was less than the medium size ; that of the left (non-punctured) eye rather larger than the medium size, but considerably smaller than for some time after death. In this experiment the great and sudden injury to the medulla appears to have altered the conducting power of the nerves. The co-existence of the maximum dilatation of the pupils, with depressed or destroyed conducting power of the nerves in general, if that existed, is an argument against there being any special motor nerve for dilating the pupil.

Experiment III.—A young dog had a large dose of prussic acid poured through a blowpipe into his œsophagus. He turned over forcibly, protruded his tongue, and was dead.

17. Both pupils equally dilated to the utmost.

18. The skull was opened speedily ; but for four or five minutes it was impossible to distinguish the nerves at the base from the welling-up of blood. As soon as practicable, both needles were inserted into the right Gasserian ganglion. Slight quivering of the upper eyelid, movement of the jaw, no movement of the iris or eyeball.

19. Needles inserted into the optic chiasma. No effect.

20. Into third nerve. No effect. The absence of movement in this experiment might arise from the second and third nerves having had their conducting power impaired either by the exposure, or by pressure in sponging up the blood, or by stretching in raising the brain so as to reach the Gasserian ganglion. For an instant the third nerve did slightly respond to excitation of the fifth, by causing raising of the eyelid, but not to the usual extent, since there was no action of the muscles of the eyeball. The motor portion of the fifth having been less exposed in the experiment acted well when the needles were passed into it.

21. The roof of the orbit was then removed, and one needle stuck through the optic nerve near to the eyeball, and the other needle through the soft parts close to the outer side of the optic nerve. The eyeball quivered, and the pupil alternately contracted and dilated. The pupil of the other eye was unaffected during the changes in this, hence the effects were doubtless owing to the second needle being in contact either with the lenticular ganglion,

or the ciliary nerves, or with some branches of the third, and so directly stimulating the motor nerves of the iris; and this is the more probable since the intercranial portion of the third nerve must by this time have lost its conducting power. The oscillatory motion of the iris is what we should expect from an intermitting stimulation of its motor nerve, such as would arise from the mere application to the exterior of the nerve of a needle connected with a feeble galvanic battery.

22. After this, I could not perceive that any motion resulted from having one needle through the optic nerve and another in the iris; nor from one in the lenticular ganglion and the other in the iris. But the parts had become cold from exposure, and galvanism to the orbital muscles had no effect. When both needles were passed through the facial nerve, the muscles of the cheek twitched, but only to a slight degree. The poison appears to have lessened the irritability of the muscular system in general, as there was by no means the same amount of muscular contraction from galvanising the different nerves as in the previous experiment, (No. I.), although the two dogs had been about equal in size, age, and vigour; and the galvanic apparatus was the same.

23. The blood coagulated on the table.

Experiment IV.—A kitten was held under water, and its eyes kept open. It struggled violently.

24. The pupils were more contracted than before submersion. Haller states that the pupils of a cat under water are dilated. Doubtless they are so, when congestion of the brain has produced insensibility of the retina, but until asphyxia is complete, the general spasmodic action (struggling) of the muscles appears to be participated in by the *sphincter iridis.*

25. The cranium was opened and the *dura mater* cut through. Both pupils immediately became fully dilated.

26. Pricking through the Gasserian ganglion caused motion of the jaw, but had no effect on the eye.

27. Pricking and pinching the ophthalmic branch of the fifth nerve had no effect on the iris or orbital muscles.

28. Division of the fifth nerve had no effect. As the pupils were already of their maximum size, and as division of the fifth nerve usually in cats produces that state, no effect on the pupils was to be expected. But as the *portio minor* of the fifth was able to act, as proved by the movement of the jaw, the *portio major* probably was also. Hence, the non-contraction of pupil, and non-movement of any of the orbital muscles, prove that the fifth nerve has not *in itself* any motor power for causing contraction of the pupil or of the orbital muscles. That it may not be an excitor nerve to both the iris and the muscles of the eyeball is not proved by this experiment, since we have seen (§ 17) that its sti-

mulation will sometimes excite movement of the eyelid, which did not occur here. The same want of conducting power in the excito-motory chain which prevented the one action might also have prevented others.

29. The roof of the orbit was then rapidly removed, and the ciliary ganglion and its nerves exposed. Pricking the third nerve, or the ganglion itself, or pinching the fasciculus of ciliary nerves which proceeded from it, caused the previously large and round pupil to become smaller and elliptical; but on ceasing to apply the stimulus the pupil instantly expanded again. I think that the contraction of pupil was most marked when the ciliary nerves were irritated. The experiment was repeated on the nerves of the other eye with similar results. As the fifth nerve had previously been divided within the skull (§ 28), this experiment proves that the pupil will both contract and dilate, notwithstanding the fifth nerve is cut through. The proof, however, that the fifth nerve has no control over the action of the iris is not complete, since there might have been sufficient nervous energy left in the nerve-tubes to produce the actions manifested.

30. The other eyeball was removed from the orbit. Its pupil was at first dilated, but in two hours it had become very small. On the following day, it was rather enlarged again. In the eye which was left in its orbit, the pupil gradually diminished to nearly the medium size, and in that state remained until decomposition commenced. The greater contraction of pupil in the removed eye was probably owing in part to mere shrinking of the tunics from drying; favouring the *rigor mortis* contraction of the *sphincter iridis.* This would occur sooner in the exposed and rapidly cooled eyeball, and therefore whilst the fluids of the eye were in a state better fitted to allow of great contraction of the sphincter, than in the more tardily drying unremoved eye. The inequality in size of the two pupils illustrates the fact that the iris has a tendency to retain the condition in which it is left when all vitality ceases, this tendency being due to the empty or full state of the vessels of the iris, controlled by the elasticity of its tissue, at the time of coagulation of the blood.

Experiment V.—A pigeon.

31. When both eyes were equally exposed to a strong light, both pupils acted consentaneously. But if the right eye was shaded, its pupil dilated singly, the left pupil remaining small.

32. When the sun's light was concentrated by a powerful lens, and thrown into the pupil, the *membrana nictitans* swept rapidly across the eye, the eyelids attempted to close, and the pupil of that eye simultaneously contracted.

33. Suddenly touching any part of the head caused similar movement of the nictitating membrane and iris. An emotional

movement from fear. This consent between the muscle which moves the third eyelid and the iris is analogous to that between the iris and *obliquus inferior* in man.

34. The brain being exposed, and its anterior portion carefully raised, pricking the fifth nerve caused violent shaking of the head, but had no effect on the eye. Hence, as Mr Mayo long since proved with respect to the pigeon, the fifth is not a direct motor nerve for contracting the pupil, neither is it a direct excitor nerve for that action, since all the other nerves being uninjured, the pupil would have lessened if it were. But as the pupils were already enlarged, though not to their maximum size, this observation does not prove that the fifth nerve has no influence over dilatation of the pupil.

35. Pricking the third nerve caused sudden protrusion of the *membrana nictitans*, and contraction of the pupil. Direct motion.

36. Pricking the optic nerve had a similar effect. Indirect excited motion.

37. On passing a needle down close to the outer side of the optic nerve within the orbit, the pupil contracted, (§ 21.)

38. On destroying the *medulla oblongata*, the pupils became suddenly still more dilated, and subsequent irritation of any nerve failed to affect the iris or *membrana nictitans*. Another instance (§ 16) in which great injury suddenly inflicted on the *medulla oblongata* appears to have destroyed the conducting power of the cerebral nerves.

Experiment VI.—A canary bird.

39. The Gasserian ganglion of a canary bird was exposed and cut through. The previously dilated pupils underwent no change from the division of the ganglion. The shock of suddenly opening the skull causes the pupils to dilate, probably by producing temporary blindness, like that attending vertigo. As irritation of the fifth nerve under these circumstances does not alter this dilatation, we may infer that when the retina is insensible, the fifth nerve cannot directly or indirectly produce contraction of the pupil. It is merely an assumption, however, that the retina is insensible in this case.

Experiment VII.—A rabbit.

40. I concentrated the rays of a candle, and threw them into the pupil. Found contraction of the pupil very slight indeed; as also in another rabbit, and in a guinea pig, where the rays of the sun were employed. In the rodentia, the iris is extremely sluggish.

41. The skull was opened. The pupils slightly contracted. (§ 39.)

42. The upper portion of the cerebral hemispheres was removed.

Both pupils became widely dilated. The concentrated rays of the sun had no effect; the retinæ were probably insensible from the shock of the injury suddenly inflicted on the brain.

42. The third nerves were exposed and irritated; the pupils contracted.

43. The Gasserian ganglion was cut through to the bone; the lower jaw was violently moved for the instant; the pupils remained immovably contracted.

44. Optic nerves irritated; no effect on the already contracted pupils.

45. *Medulla oblongata* broken up; various muscles were spasmodically contracted, but the pupils remained small and unaltered.

46. In four hours after death, the pupils had increased to almost the medium size. In this experiment division of the fifth nerve (§ 43) was not proved to have caused contraction of the pupil, because that state had already been produced by irritation of the third nerve, and had not yet subsided; and, as the third nerve had not been divided, even if dilatation had come on before the injury to the fifth, though unobserved by me, and contraction again ensued on cutting through the fifth nerve, it would have been uncertain whether the fifth acted as an excitor or as a direct motor nerve to the iris.

Experiment VIII.—A young rabbit. The blade of a small knife was passed into the right hemisphere of the brain in such a way as to pierce probably the *corpus striatum* and *thalamus opticus*, but not to injure the nerves.

47. Both pupils contracted to a small but not to the minimum size; they dilated again, and alternately contracted and dilated, the contraction lasting longer than the dilatation.

48. The fifth nerve on the right side was then divided. The animal struggled violently; the right eyeball was greatly protruded, and its pupil gradually contracted to the size of a pin point. Left pupil of the medium size. On opening the cranium the optic and third nerves were found uninjured on both sides.

49. Irritation and then division of both third nerves caused pin-point contraction of the left pupil, but did not affect the contracted condition of the right one. Hence the third nerve in the rabbit, as in the cat and dog, (§ 42), has an influence over the *sphincter iridis*.

50. Division of the optic nerves had no effect on either pupil. Both third nerves being previously divided, the optic nerves could cause no movement of the iris through them; but as the fifth nerve on the left side was still uninjured, if the fifth have the power of directly causing dilatation of the pupil, this should have resulted in the left eye.

51. Division of the Gasserian ganglion on the left side caused

movement of the jaw and spasmodic *co-ordinate* movements of the paws, but had no effect on the contracted pupil. This and the preceding observation (§ 50) prove that in the rabbit the fifth nerve cannot be a direct motor nerve for dilating the pupil.

52. The right fifth nerve was found to have been imperfectly divided just in front of its ganglion. Its complete division did not alter the pupil. As this incomplete section of the fifth nerve affected the pupil just as greatly as complete section usually does, and as the former must keep up a state of irritation in the injured nerve, it is probable that the effect on the iris of complete division of the fifth is due to irritation of that nerve, and not to the loss of any motor power.

53. The encephalon was turned back, but not detached. The heart beat feebly, and there were occasionally slight convulsive movements of the body. On exposing the pericardium the auricles were seen to contract twice, and sometimes thrice for one contraction of the ventricles. The slow action of the heart permitted its motions to be readily observed. Diastole appeared to be at first active and sudden, afterwards passive and regular; the belly of the ventricle slowly swelling out as its cavity became full. During systole a series of changes occurred: first, the apex of the ventricle was tucked in; secondly, the lower part of the ventricle contracted, and its upper part bulged forwards; thirdly, this distended upper part was suddenly dimpled in, and at the same moment the apex elongated and tilted forwards. The entire systole presenting a sort of spiral movement, commencing quietly at the apex, spreading towards the base of the ventricle, and terminating abruptly by the dimpling in of the wall of the ventricle, and simultaneous elongation of the apex. The same kind of spiral twist made by the ventricles in contracting, I have likewise observed in the mouse and the dog. Is the dimple in the wall of the ventricle when most distended owing to the *carneæ columnæ* contracting so as to render the ventricular surface of the valves to which they are attached an inclined plane towards the orifice of egress, at the same time that the other ventricular muscular fibres contract to expel the blood?

54. Half-an-hour had now elapsed since the brain was first exposed; the action of the ventricles had become very tardy. A probe was pushed down the vertebral canal in front of the oblong and spinal chord, and left there. For three minutes there was no effect, then increased action of the heart, very rapid but feeble. In forty minutes from the first exposure of the brain the ventricles ceased to act. On pressing them so as to expel part of their contents, they twice recommenced contracting, and beat three or four times. In 46 minutes the auricles ceased to act.

55. The eyes were noticed from time to time when the ence-

phalon was turned back. They were, of course, separated from all their cerebral nervous connections. In five minutes after this both pupils had slightly enlarged; in thirty they were enlarged to almost the medium size.

Experiment IX.—A young rabbit was pithed between the first vertebra and the occiput.

56. Both pupils instantly contracted to the size of a pin-point. There was only momentary struggling, and the heart instantly ceased to beat.

57. The head being opened, the optic, third, and fifth nerves were successively pricked and then divided alike, without any effect on the contracted pupils. There was a slight grinding of the jaw on dividing the fifth nerve. As we have seen that irritation of the second, third, and fifth nerves produces in the rabbit contraction of the pupils, and as that state already existed here, this observation merely proves that none of these nerves on being irritated induce dilatation.

58. On opening the chest the right ventricle of the heart was blue and greatly distended ; the left ventricle contracted. Scratching the muscular texture of the heart had no effect ; neither did any action follow the pushing of a probe down the spinal canal, (§§ 16, 38, 54.) The lungs were dark-crimson, did not collapse, and contained tubercles, some of which were suppurating. In the rabbit (Exp. 8), the lungs were of a pinkish-yellow colour, and collapsed immediately on exposure to the air.

59. Two minutes from the time of pithing the pupils were slightly enlarged; presently they attained almost the maximum of dilatation, which in three days afterwards was still the same.

Experiment X.—A full-grown rabbit was stunned by a blow on the right side of the occiput, so directed that the line of concussion was along the right side of the head.

60. Both pupils had previously been of the medium size. The right pupil instantly contracted to its minimum; the left gradually enlarged to its maximum. The right eye was protruded;—precisely what is often observed in man as the effect of injury to the head. I afterwards found that the blow had driven fractured portions of bone into the right cerebral hemisphere, where also there was of course extravasation of blood.

61. The cranium was opened and the brain carefully lifted up. The optic, third, and fifth nerves were irritated and then divided on each side, in different order of sequence, but without any effect on the pupils. The brain was then taken away. The immediate effect of the injury had been irritation of the motor nerves of the right eye ; and gradual palsy of the retina, with dilated pupil in the left eye, from hæmorrhage probably. Here, as after other severe shocks, (§§ 16, 38, 58), none of the nerves would respond to mechanical irritation.

62. In three minutes the dilated left pupil began very slowly and gradually to contract. In twelve minutes the contracted right pupil began very slowly to dilate. In two hours the pupils were almost but not quite of equal size ; in twenty-four, the left pupil was still rather the largest. In each orbit a considerable coagulum of effused blood surrounded the optic nerve, extending amongst the orbital muscles and spread over the back part of the sclerotica.

Experiment XI.—A rabbit was tied, and its eyes watched for some minutes.

63. Under the influence of fear, the heart beating rapidly, and the breathing hurried, the pupil of the eye I was watching became very small, but not of its minimum dimensions ; the pupil of the other eye, in a darker situation, being large at the time. On turning this towards the light and examining it, its pupil contracted sluggishly, and that of the other eye (now in the shade) became dilated. There is not, consequently, in the rabbit the same degree of consent between the irides, which we see in man.

64. After admeasurement on a dissected rabbit, I pushed the knife blade into the left side of the head, so as to divide, as I supposed, the fifth nerve, just in front of the Gasserian ganglion. The animal shrieked and tossed its head about ; and the left pupil for the first few seconds was unaltered ; it then steadily and gradually contracted to the size of a pin-point, which it had attained in about a minute from the time of the puncture. There were now slight convulsions for a short time, and then the rabbit lay still and quiet. The left pupil was of its minimum size, and the surface of the eye insensible, and as a bright light did not cause winking or distress, probably the retina also was insensible. The right eye had its pupil of the medium size, active, and both conjunctiva and retina sensible.

65. In half an hour,—rabbit is still and hangs down its head, but walks when its legs are touched ; heart beats feebly and rapidly ; vermicular motion of the intestines can be seen through the integuments. The previously-contracted left pupil is now of almost the medium size ; the right dilated. The rabbit died quietly in about two hours and a half, after having tossed its head convulsively once or twice.

66. On the following day it was carefully examined. The narrow blade had passed across the floor of the left side of the base of the skull, slightly nicking the under surface of the left cerebral hemisphere, and passing beneath the *tractus opticus* without touching it, but not quite as far as the mesial line. All the nerves which passed through the left sphenoidal fissure were divided ; also the left internal carotid artery and the cavernous sinus.

The bone beneath was nicked. No other parts had been directly injured by the knife. Between the *dura mater* and the convexity of the left cerebral hemisphere was a layer of coagulated blood, forming a complete red coating. A large clot lay at the base of the brain pushing upwards both optic nerves, extending beneath their commissure, and pushing upwards also the third nerves. The entire spinal chord was coated with congealed blood, which extended as far as the *cauda equina* and filled up the interstices of the nerves there. The central vessel (vein ?) of the chord was gorged, forming a dark blue line through the entire length. The posterior fissure was filled by a layer of coagulum. This experiment was performed in imitation of Magendie's, in order to ascertain with what accuracy the results ascribed could justly be referred to section of the fifth nerve. For anything shown to the contrary, by experiments like this taken singly, we might attribute the contraction of the pupil with equal reason to section of the third, fourth, or sixth nerve, or to hæmorrhage affecting the brain and spinal chord, or to spasmodic action of the orbital muscles, as to mere division of the fifth nerve.

Experiment XII.—A rabbit a month old.

67. On removing the upper part of the cranium the pupils slightly contracted, the effect of the physical reaction of pain probably. In cats, dogs, and pigeons (§§ 26, 57, 100,) irritation of the fifth or any other sensational nerve fails to cause immediate contraction of the pupils; in the rabbit it does cause this. Hence pain excites contraction of the pupils in the rabbit, but not in the other animals above-mentioned.

68. The anterior portions of the cerebral hemispheres were removed. No effect.

69. The cerebrum was turned back, putting the optic nerves on the stretch. Both pupils instantly became largely dilated; probably from the tension of the visual nerves producing blindness.

70. The left optic nerve was divided close to the optic foramen. The pupil of the left eye instantly contracted to the medium size; that of the right eye remained dilated. The contraction of the left pupil was probably due to the cerebral cut end of the optic nerve irritating the left third nerve in the excito-motory manner.

71. The left third nerve was half-divided; minimum contraction of left pupil but for an instant only (*direct* irritation of the iridal motor nerve.) The nerve was next completely cut through. No effect.

72. Left fifth nerve was cut through close to the pons. No effect. Division of the fifth over the temporal bone produces pin-point contraction: division of the fifth close to its origin does not increase the amount of contraction left after division of the

third nerve, although this was not the minimum. Hence the pin-point contraction does not result from any direct motor power conveyed by the fifth.

73. Right optic and fourth nerves divided. No effect.

74. Right third nerve cut through before entering the sheath of the cavernous sinus. The right pupil instantly contracted, but not to its smallest size.

75. The right sixth nerve was divided *between its origin and the Gasserian ganglion before reaching the level of the latter.* The right pupil instantly assumed its smallest—pin-point—dimensions. Of all the nerves of the right eye the fifth and sixth alone had here been left intact. Division of the sixth nerve caused pin-point contraction of the pupil. The fifth nerve having no direct motor over the iris in the rabbit, any more than in other animals, (§ 72,) the sixth nerve must have caused this extreme contraction of the pupil by virtue of its motor power discharged under the irritation of the division of the nerve, or under irritation of the fifth as an excitor nerve. Why then did not division of the left fifth nerve equally cause minimum contraction of the left pupil (§ 72), since although the third nerve on that side had been divided the sixth had not? I can only account for this by supposing that the capability of producing motion in the excito-motory manner by irritating a sensational nerve may be lost earlier than that of inducing motion by directly stimulating a motor nerve. This view is supported by the non-effect at this period of the experiment of irritating the right optic nerve (§ 73), although the third nerve was uninjured.

76. The right fifth nerve was now irritated over the temporal bone from the point of exit backwards to the Gasserian ganglion, and then divided at different points, with the intention of touching any subjacent filaments from the sympathetic. No effect on the contracted right pupil. In two hours from the time of death, the pupils were equal, and almost but not quite of the medium size. In three days, unaltered in dimensions.

Experiment XIII.—The spinal chord of a young rabbit was divided close to the occiput.

77. Both pupils immediately contracted to less than the medium size.

78. In three minutes the pupils had enlarged to the medium size. In ten they were almost of the maximum size. In two hours the same; in three days after death the same. In the cat, dog, and pigeon (§ 38), on dividing the spinal chord close to the occiput, the pupils *instantly* dilate, probably from the blindness induced. In the rabbit they first contract and afterwards *gradually* dilate. Whence the difference? The rabbit must be as much blinded as the cat or dog. It is probably owing to

pain stimulating the sixth nerve in the excito-motory way, and partly also to direct stimulation of the motor power of the sixth nerve; since there is convulsive movement of the body generally in all animals on dividing the medulla; and there seems no reason why the sixth nerve should be exempt from such influence. In the cat, dog, and man, the third nerve, or at least that portion distributed to the iris, is completely controlled by the state of the visual apparatus. During violent epileptic paroxysms, we may have either dilated fixed pupils, or contracted or oscillating pupils: whereas if the third nerve were entirely regulated by the spinal centre, we could never have the pupils otherwise than contracted during general convulsions, provided the third nerves were not paralysed. It is not difficult to see a final cause for this arrangement. It would obviously be inconvenient were the pupils to be affected in size, and therefore the vision in correctness, by every acute sensation, in predacious animals whose habits expose them to painful injuries; and also in man.

Experiment XIV.—Exposed the *par vagum* and superior cervical ganglion, and upper cervical nerves of the left side in a rabbit.

79. Pupils of the medium size when the nerves were not irritated. Pinching the cervical nerves caused pain, general convulsive movements, and slight and gradual contraction of the pupils.

80. Pricking and pinching the first cervical ganglion of the sympathetic had no effect on the pupils, nor did it cause any general muscular movements. This ganglion was then *half* cut through, and the wound sewed up.

81. Incisions about the eyelids, and pinching the exposed infra-orbital branch of the fifth nerve caused struggling, and gradual and slight contraction of the pupils. Proving, with the preceding observations, that in the rabbit irritation of sensitive nerves sufficient to excite motion of voluntary muscles has also some effect in contracting the pupil, probably through the sixth nerve.

82. All the textures behind the right eyeball were cut through. The pupil contracted to its minimum. The eye was then removed. Removal of the eyeball in the cat causes at the time dilatation of the pupil (§ 30.); in the rabbit, contraction. In the first, blindness causes expansion in the absence of any power of the sixth nerve to contract the pupil. In the second, the injury to the sixth nerve causes contraction, notwithstanding the blindness. In both, the size of pupil undergoes alteration after the loss of all vitality. (§§ 84, 86.)

83. On being set at liberty, the rabbit walked about but without any revolving movement. This proves that the walking in circles sometimes witnessed in experiments on the encephalon is not owing to blindness of one side, as some have supposed.

84. The pupil of the removed eye remained of its minimum size for ten minutes, and then slightly enlarged. In four hours it was of the medium size. In thirty-six the eyeball was shrivelled and flaccid; pupil unaltered.

85. The pupil of the left (unremoved) eye in four hours after exposure of the nerves was of the medium size; cornea clear. In thirty-six hours cornea still clear; pupil rather larger than the medium, but active. No puriform secretion on conjunctiva, though its inferior segment had been uncovered. The moderate dilatation of the pupil might be owing to congestion and want of power in the brain as the animal became weaker, rather than to any direct influence of the injured cervical ganglion upon the eye.

86. In thirty-seven hours the rabbit died. Pupil at first of its minimum size; by the following day it had enlarged to almost the medium size; after this it did not change.

Experiment XV.—A full grown guinea-pig. The knife-blade was pushed into the left side of the head.

87. General convulsions. Left pupil contracted; right of medium size.

88. The spinal chord was divided close to the occiput. Left pupil unaltered; right was contracted for an instant and then was largely dilated (§ 78).

89. In ten hours after death both pupils were nearly of equal size.

90. On examination it was found that the instrument had not entered the cranium at all, but had passed into the orbit just in front of the *foramen opticum*. *All* the nerves and vessels of the back part of the eye were torn through. This was tantamount to removal of the eyeball, and illustrates a previous observation on the rabbit (§ 82.)

Experiment XVI.—A young guinea-pig. The instrument was passed into the right side of the head.

91. Right pupil dilated; left slightly contracted. The animal died in a quarter of an hour.

92. On dissection, there was extravasation extending over both cerebral hemispheres. The knife had cut through the right *corpus striatum*, *thalamus*, and *tractus opticus*, but had not injured the third, fourth, fifth, or sixth nerves on that side. On the left side, it had half divided the fifth anterior to its ganglion, had not cut any other nerve, but had nicked the under surface of the left cerebral hemisphere. From the guinea-pig possessing a very conical cornea, and a very dark-coloured iris, it is difficult to see distinctly the actual size of the pupil; hence guinea-pigs are unsuited for these experiments. Enough, however, has been shown to prove that they agree with rabbits in the phenomena presented.

Experiment XVII.—A kitten. The instrument was passed in to the cranium on the right side.

93. Both pupils instantly and equally contracted to their minimum size, but on letting the kitten raise its head, it looked about it, and both pupils enlarged simultaneously. The fifth nerve had not been divided, sensibility being perfect on both sides.

94. Divided the fifth nerve on left side. Left pupil immediately dilated to its maximum size. Right pupil of medium size, and obedient to the light.

95. Vision of right eye perfect. Left eye winks simultaneously with the right, when a threatening gesture is made so as to be seen by the right eye; but not otherwise, though the conjunctiva of the left be irritated. Hence the left *portio dura* was uninjured.

96. On being placed on the floor, the kitten walked briskly round and round, the left eye being towards the centre of the circle. It lived for two days, lying still and motionless the greater part of the time, but occasionally walking rapidly round in circles until at length it would fall down from giddiness. It was destroyed with prussic acid.

97. From the time of the injury (§ 94) the left pupil had remained largely expanded; the right had been active but usually very small: it now became equally dilated with its fellow, as the effect of the prussic acid.

98. Examined the following day. The puncture on the right side had merely penetrated the lower portion of the right cerebral hemisphere as far as the *corpora quadrigemina*, but had not injured the nerves. The puncture on the left side had divided completely the third and fourth nerves; partially cut through each of the three divisions of the fifth; not divided the sixth; cut through the left *crus cerebri*, *tractus opticus*, and the lower portion of the left cerebral hemisphere. There was red softening of the cerebral matter around, and a small clot filled up the cut. On the left side, slight extravasation of blood, but diffused inflammation of the membranes. Spinal chord normal. No extravasation in either orbit; the lids of the left eye were glued together, and there was purulent matter between them and the cornea: the cornea was clear; both pupils equal; less than immediately after death, but exceeding the medium size.

The simultaneous contraction of both pupils in the first place, (§ 93), was due to irritation of the *corpora quadrigemina*, to which the instrument had penetrated. The dilatation of the left pupil on dividing the left fifth nerve was probably due to concomitant division of the optic tract and third nerve; and proves, since the sixth nerve was intact, that in the cat there is not any such excito-motory action on the iris between the fifth and the sixth nerves as we find in the rabbit; unless, indeed, we assume that in the cat the sixth nerve dilates the pupil, which is disproved in the dog, (§ 9); and as the anatomy of the orbital nerves is very similar in the dog and cat, it is presumable that the physiology of them is so likewise. Could we manage to divide the third nerve in the cat, without at all injuring the optic visual tract in any part of its course, the primary effect on the pupil would probably be contraction, from the irritation of dividing the motor nerve of the *sphincter iridis;* dilatation occurring secondarily as soon as the irritation had subsided, or rather as soon as the nerve separated from its centre ceased to have the power of conveying irritation. But it is impossible to devise any mode of testing this, since, however carefully we attempt to expose the third nerve, the displacement of brain and consequent stretching of the optic nerves, independently of the shock, will invariably produce blindness and dilated pupils first; and when no longer controlled by the retina, the iris has always a tendency to retain for a time the state in which it is at the time blindness occurs.

Experiment XVIII.—Removed as much as possible of the outer part of the right orbit of a large kitten.

99. Right eye in a state of great tension from spasm of the uncut orbital muscles. Left eye also very prominent from attempts to struggle. Both pupils equally round and large. Hence although there is tension of the eye-balls in the rabbit, on dividing the fifth nerve, yet the contracted pupil which results cannot be ascribed to that tension. In all animals in which the third nerve is the sole motor nerve of the *sphincter iridis*, squeezing of the eyeball causes expansion of pupil, probably from producing temporary congestion of the retina.

100. When the animal was suffering great pain from the injury done to branches of the fifth nerve, the right pupil remained unaltered. Hence, unlike the rabbit, (§ 67), in the cat the action of the *contractor pupillæ* is not immediately excited by the fifth nerve.

101. It was impossible to see the lenticular ganglion on account of the bleeding, but the optic nerve could be seen distinctly. On pricking it with a tenaculum, there was a slight oscillatory movement of the iris of the right eye; left eye unnoticed.

102. The cornea of the right eye was then punctured with a couching needle. As the aqueous humour slowly escaped, the iris gradually and almost imperceptibly contracted, so that in two minutes the pupil was elliptical and small, but not of its smallest size.

103. The tissue of the iris was irritated with the point of the needle; no blood flowed, nor did the iris act.

104. Prussic acid was then given. The kitten struggled vio-

lently for half a minute and died. Both eyes were watched. The left pupil immediately attained its maximum size, so that nothing more than the narrowest rim of iris could be discerned. In the right (punctured) eye, the anterior chamber instantly became partly filled with blood, probably from the scratch previously made in the iris; but as far as could be ascertained, the size of the pupil remained the same. The sudden effusion of blood from the scratch in the iris, which did not bleed at the time it was inflicted, was owing to the vascular congestion of the eye during the violent struggles produced by the poison.

105. The left orbit was then opened. Mechanical irritation of the optic and third nerves caused no effect.

106. Both eyeballs were removed. The blood in the right eye had coagulated and obscured the iris. In the left eye, twenty hours after death, the pupil was elliptical and of one-third its maximum size. In forty-eight hours, when the tunics had become dry and shrivelled, the pupil was unaltered.

Experiment XIX.—Divided, as I supposed, the left optic nerve within the orbit in a rabbit.

107. The left eye became more prominent and the pupil contracted at first, but in a few minutes it dilated and afterwards so remained. Right eye unaltered.

108. On the day following there was a slight secretion of mucus and subsequently of purulent matter. The cornea next became opaque. In six weeks the cornea had become nearly as clear as ever; but the crystalline lens was pushed forwards partly through the pupil, and was opaque. The rabbit lived for five months, and was quite blind of the left eye.

109. On dissection the left optic nerve within the orbit was found closely surrounded by firm lymph, but had not been divided. External, inferior, and closely applied to the optic nerve was a red coagulum in a cyst of fine cellular membrane the size of a hazelnut. The globe of the eye had evidently sustained pressure from this coagulum, and was atrophied to less than half the size of the other eyeball; yet its shape was normal, though it was scarcely larger than was sufficient to inclose the lens. The changes of size in the pupil were referable at first to irritation, and subsequently to palsy either of the optic or ciliary nerves, or both. The experiment was undertaken with the view of ascertaining the influence of the ciliary nerves on the nutrition of the eye. On consideration it proves but little, since the atrophy might be due to loss of vascular power from division of the blood-vessels, to pressure from the clot of extravasated blood, or to want of functional exercise from injury done to the optic nerve. It was probably owing to all these conditions conjoined.

Experiment XX.—Some prussic acid was introduced into the nostril of a young rabbit.

110. The rabbit drew in one catching inspiration, and was dead.

111. Both pupils were at first extremely dilated, but gradually they contracted to less than their medium size, and finally enlarged again in a quarter of an hour to the medium size, which was not afterwards changed.

112. Three minutes after death, the integuments were stripped off the peritoneum without lacerating it. The viscera appeared quite motionless.

113. The skin was stripped off one hind leg. On irritating the substance of the muscles they duly contracted; but irritating the nerves had no effect.

114. The blood was fluid in both arteries and veins.

Experiment XXI.—A full-grown kitten.

115. The knife was passed into the right side of the head with the intention of dividing the fifth nerve a la Magendie. The right eye protruded and its pupil was dilated.

116. The instrument was then introduced into the left side of the head. The left pupil gradually contracted until very small, then dilated again, and then responded to light.

117. Spinal chord divided close to the occiput, gradual dilatation of both pupils until they attained the maximum size. In twenty-four hours both pupils were equal, of more than the medium size, but much smaller than immediately after death.

118. The cornea of the right eye was punctured. The following day this eyeball was more collapsed than the other, but its pupil had undergone no change.

119. On examination the third and fifth nerves were found to have been nicked, but not completely cut through, alike on both sides. Neither optic nerve had been injured, but the right *crus cerebri*, though not the *tractus opticus*, was divided. The alternate contraction and dilatation of the left pupil, (§ 116,) was due to incomplete section of the third and fifth nerves; the fixed dilatation of the right pupil (§ 115) must have been owing to the additional injury on that side, viz. division of the *crus cerebri*. Unfortunately I did not ascertain whether the right eye was blinded by the experiment, but as the optic tract was found not to have been injured, vision might be unimpaired. In that case, the divided portion of *crus cerebri* included nerve fibres which connect the optic nerve with the origin of the third nerve; fibres, the existence of which the occurrence of total blindness with active pupils had before rendered physiologically presumable.

120. The spinal chord had been almost completely divided. Some extravasation around it, and on the surface of the pons.

Experiment XXII.—The moment that a pig which had been stuck appeared to become insensible from loss of blood, a needle was passed through the cornea of one of its eyes.

121. Scratching the tissue of the iris itself, and subsequently scratching the retina, alike failed to affect the size of the pupil.

The following are some of the general inferences which may be deduced from these experiments:—

1. The third nerve is the only direct motor nerve for contraction of the pupil in dogs and cats.

2. The action of the third nerve, as far as concerns the iris, is mainly under the control of the visual nervous tract.

3. As both the third nerve and some portion of the visual tract must inevitably be injured in performing the experiment of dividing the fifth nerve after Magendie's plan, the experiments of that gentleman cannot be considered as evidence that the fifth nerve is either directly or indirectly the nerve which presides over dilatation of the pupil in dogs and cats; nor over contraction of the pupil in rabbits and guinea-pigs.

4. In animals in which division of the fifth nerve causes contraction of the pupil, it does so by excito-motory action through the sixth nerve, which in these animals supplies the iris in conjunction with the third. The sixth nerve, however, not entering into the formation of the ophthalmic ganglion, which in these animals is extremely small.

5. In these rodentia, pain of any kind, whether produced by irritation of the fifth, or of any other sensational nerve, will cause more or less contraction of the pupil at the instant, attributable probably to excito-motory action of the iridal fibres of the sixth nerve.

6. Irritation of the fifth nerve, or of any other sensational nerve in the cat, and dog, and pigeon, so long as it does not affect the brain to the extent of producing vertigo, *nor the visual sense in any other way*, has no immediate influence over the size of the pupil. Hence, although the fifth is an excitor nerve to the *sphincter iridis* in the rabbit, it is neither directly an excitor nor a motor nerve to it in the dog and cat.

7. As the third nerve can always, under favourable circumstances, be made to influence the movement of the iris, *immediately* on the application of irritation, and as the iridal portion of the third nerve in all animals, in which the iris is active, passes through the ophthalmic ganglion, it follows that *the ophthalmic ganglion offers no check to the transmission of motor influence along the motor nerve fibres which pass through its substance.*

8. As irritation of the fifth nerve does not in any animal affect the action of the iris *after* division of the cerebral connections of all the other ocular nerves, and as some portion of the fifth nerve always enters into the ophthalmic ganglion, it follows, *that the filaments of the fifth nerve have not the power of affecting those of the third nerve during their course together through the substance*

of the ophthalmic ganglion; or, in other words, *that the lenticular ganglion is not a centre of excito-motory action to the iris.*

The applicability of these inferences to human physiology must be deduced from other facts than those developed by artificial experiments. They will prove, if correct at all, to be not unimportant towards elucidating the mechanism of the actions of the ganglia in general, and also of the encephalon and spinal chord. The following conclusions, which I hope hereafter to prove, as being in part direct inferences, in part reasonable conjectures, are for the present subjoined as mere postulates. Should they ever be established, they will induce us to question whether the action of the spinal chord is literally reflex; though they will support the great point in Dr Marshall Hall's discoveries, viz. the independent and most extensive action of the spinal chord; they will tend to modify recent views on the so-styled reflex function of the brain, and on the duality of mind. In the mean time, although it would be unreasonable to expect that any importance could be attached to these observations in their present form, yet to prevent them from being classed as mere hasty fancies, I may state in self-defence that the anatomical investigations on which they are founded have been made as extensively as my opportunities permitted, and have occupied me more or less for seven years. The details I trust to be enabled to lay before the profession.

1. The connection indicated by Messrs Todd and Bowman as existing between the caudate vesicles and some of the nerve-tubes is, I believe, universal. Every nerve-tube which can be traced to its actual origin in a nervous centre at all, is seen first to lose its white coating; next, to become smaller in calibre and varicose; and finally to terminate in an irregular-shaped grey cell.

2. There are, however, innumerable spherical cells which have no such connection with the nerve-tubes.

3. The varicose condition of the finer translucent tubes in a nervous centre I believe to be normal, and not the result of *post mortem* changes, or of manipulation. These three observations apply alike to encephalon, spinal chord, spinal ganglia, and sympathetic ganglia. The constituent parts in all are essentially similar, though greatly modified as to minuteness and delicacy of texture, and arrangement of nerve-tubes.

4. There exists an anatomical arrangement in the nerves which enables them to contain the greatest extent of tubular surface in the smallest compass.

5. When different sensations occasion similar outward manifestations, the muscular movements are affected through the same nerve-tubes; there being one tract of nerve-fibres common to several cerebral organs of sensation, which connects these with the motor tract, and not a distinct connecting tract from each cerebral organ of sensation.

6. In like manner, there is a common centre of union in which

the peripheral fibres of the brain meet, where it may be presumed that different intellectual actions influence the same set of motor nerve-tubes.

7. These common centres are double, one proper to each cerebral hemisphere, yet so intimately connected together, that the two can act in unison as a single organ, or alternately as distinct organs; *e. g.* in jumping, the centres of volition act together on the motor tract, but in walking and running the right arm advances with the left leg, and *vice versa;* i. e. in ordinary progression, the anterior extremity is associated in the movements of flexion and extension with the opposite posterior extremity. This association results from alternate action of the two volitional centres.

8. All such centres of union consist of grey cells into which certain nerve-tubes open, and from which certain others (physiologically) proceed; this being one purpose subserved by every grey mass, insuring the greatest amount as well as the greatest harmony of action, at the smallest expense of nervous tissue, and of occupied space.

9. The different nervous centres can act to a certain extent vicariously; the action of one exciting, modifying, or preventing that of another, according to circumstances.

10. Through commissural (inter-central) nerve-tubes, the *vis nervosa* can travel in any direction. But through distributed nerve-tubes, whether organic, spinal, sensational, or volitional, the vis is transmitted centrifugally only, from its source (the grey cells), to its destination (the peripheral filaments.)

11. All nerve-tubes proceeding from the encephalon in part cross over to the opposite side; in part pass without crossing to their destination. I am not at present satisfied whether or not the olfactory nerve is an exception to this; but the optic chiasma, and the decussation of the anterior pillars of the *medulla oblongata* are merely the more obvious types of a similar disposition of the roots of other nerves, and of the nerve-tracts of general sensation.

12. Hence every (?) encephalic nerve has both direct and crossed roots. One purpose thus fulfilled, being the separate and distinct field appropriated to psychical (crossed tubes,) and physical (direct tubes,) centric action.

13. The cerebellum is not the co-ordinator of muscular movements, but the medium through which the cerebrum checks, controls, and suspends the action of the physical nervous centres. It is probably also a store-house of *vis nervosa,* under the control of the cerebrum, for all other nervous centres directly communicating with it.

14. When the operation of one nervous centre is frequently connected with that of another, but not essential to it, *e. g.* sensation and respiration; the first is situated superiorly to the last, through the grey matter of which it sends nerve-tubes. In its

normal moderate action, a nervous centre anatomically placed inferiorly does not necessarily call forth the action of one placed superiorly; *e. g.* the spinal chord when acting does not necessarily excite the physical centre of sensation, nor this last the psychical or the volitional centre.

15. But conversely, excitement of a nervous centre placed superiorly, if it affects the cell-origins of those nerve-tubes which pass through a lower centre, does, of necessity, call forth the conjoint action of this last, *e. g.* the volitional motor nerve-tubes pass for a certain distance before their exit from the spinal chord, through the sphere of the spinal grey matter, in this way associating with their own action, in all cases, that of spinal nerves.

16. There exist volitional and sensational (encephalic) fibres in the spinal chord, which are not merely commissural between the chord and the encephalon, but pass on, without interruption of continuity or apparent variation of texture, into distributed cerebro-spinal nerves.

17. The volitional nerve-fibres pass into the grey matter of the spinal chord, and then leave it again. The sensational fibres do not.

18. The cerebello-spinal fibres, (*i. e.* the posterior pillars and posterior strands of the lateral pillars of the spinal chord,) are merely commissural; not between different segments of the chord, but between cerebellum, centres of *medulla oblongata*, and the chord.

19. The major portion of the roots of a cerebro-spinal nerve, whether anterior or posterior, is made up of tubes which terminate in the spinal grey matter, as many passing downwards (sacrad) as upwards (craniad.) Stilling's views of posterior roots traversing the grey matter and emerging as anterior roots, I could never make out in my examinations with high microscopic powers.

20. The spinal ganglia transmit through their grey matter sensational and excitor nerve-tubes only. Sympathetic ganglia transmit encephalic sensational, but not volitional nerve-tubes, and spinal nerve-tubes, both excitory and motory. Both kinds of ganglia equally supply the capillaries with nervous power.

21. The purely ganglionic fibres can act alone without necessarily implicating the spinal fibres; as the purely spinal fibres can act without implicating the encephalon. But the purely spinal, as well as the purely cerebral fibres, which pass through the ganglia, when themselves in action always call into operation the grey cells of these ganglia. Hence either the brain or the spinal chord can excite ganglionic action.

22. As purely spinal action is not necessarily attended with any cerebral action (sensation, intellect, or will); so also, purely ganglionic action is not necessarily attended with any spinal action (involuntary muscular motion,) nor with any cerebral action.

23. The ganglia are centres of nervous action for the capilla-

ries, and for influencing and modifying the activity of the cell-metamorphosis which constitutes nutrition. They are never centres of sensation nor of muscular motion. Whether the muscular coat of arteries is under the influence of the purely ganglionic fibres is doubtful. There are reasons for considering that it is influenced only by spinal nerve-tubes which have passed through ganglia.

24. The spinal chord is the centre of all non-psychical muscular acts, with the exception of those which result from the merely physical operation of the sensational centres. It is never the centre of sensation, nor of changes in the action of the capillary blood-vessels. Hence, the operation of the physically acting part of the nervous system may be reduced to the principle of association. The spinal chord associates the muscles with the tegumentary surfaces—internal and external, and with all other parts in which spinal nerves terminate. The ganglia associate the capillary vessels and the processes to which these minister, with all parts supplied by the spinal and sensational nerves which pass through the ganglia, more especially with the surfaces with which the given organ is most closely functionally related.

25. Every sensation is in one sense double. It is obscure, diffused, and general, in so far as it depends on the common physical centre, (through the medium of the straight fibres,) and distinct, accurate, and special, in so far as it depends on the psychical centre, (through the crossed fibres.) By virtue of the former mode of action, all sensations have points of resemblance; by virtue of the latter, all have distinct and characteristic points of difference.

26. Except through nerve tubes continuous from one of these encephalic origins to the sentient surface, how many other centres soever these sensational fibres may pass through in their course, there can be no external sensation. If so, the sympathetic ganglia, apart from the cerebral fibres which they transmit uninterrupted in their continuity, cannot act vicariously as media of sensation under any circumstances.

27. In performing experiments on living animals, we have no means of artificially exciting to action the grey cells of any nervous centre. We can do no more than stimulate the white nerve tubes to discharge their already contained force. The appearance to the contrary has been due to excitement of the white fibres transmitted by the grey centres experimented on. We may, of course, excite inflammation of grey nervous matter, and thus indirectly and at a distant period induce phenomena attributable to the abnormal action of the nervous centre.

PART SECOND.

Influence of the sixth nerve on the iris.—That predaceous animals, by their habits constantly exposed to injury, should have correctness of vision insured by its non-connexion with alterations of common sensation, is nothing more than we should expect. Were the iris in the dog or cat under the direct control of the fifth nerve, a lacerated lip or bitten cheek would materially disorder sight. Why there should be a different arrangement in the rabbit and guinea-pig it is less easy to comprehend. These animals are fugacious, have their ears opening from behind, and can direct either eye by itself outwards and backwards, whilst the other is directed forwards, so as literally to look two ways at once. Is it not in order to associate the iris with the external rectus muscle, that the sixth nerve is distributed to both,—enabling the pupil of the everted eye to act consentaneously with the outer rectus whilst the pupil of the straight eye, in which the *rectus externus*, and consequently the sixth nerve, are at rest, is controlled at the time by its retina through the third nerve, in the ordinary manner? The fact that the pupils do not necessarily act together in these animals (§ 63), supports this view. It might appear easy to ascertain the truth by watching the eyes of a living rabbit; but from the dark colour and sluggish action of the iris, I have not been able to satisfy myself that abduction of the eye in the rabbit is invariably accompanied by contraction of the pupil.

Is there a motor nerve for causing dilatation of the pupil?—That the fifth nerve supplies no motor filaments for the dilatation of the pupil is proved by the experiments detailed. It has been conjectured that filaments proceed from the first cervico-spinal nerve, which, after passing through the superior cervical ganglion, become united with the sixth cerebral nerve, and ultimately reach the iris, over the dilating movement of which they preside. In support of this view, the principal facts adduced are, the contraction of the pupil, which results from removal of the superior cervical ganglion; the dilatation asserted to take place when that ganglion is irritated; and the following experiment of Guarini, "who having extirpated the superior cervical ganglion of an animal, and thus produced contraction of the pupil, administered a poisonous dose of strychnine (the effect of which generally is to dilate the pupil.) The pupil of the side operated on dilated but little, for the filaments of the third nerve now unopposed, maintained its contraction, whilst the pupil on the opposite side was enormously dilated, probably because of the radiated muscle (?) being put strongly into action by the stimulating effects of the strychnine on the spinal cord and so on the nerve (*i. e.* the cervical filaments inclosed with the sixth nerve) supplying this muscle."* Did the pupil dilate in obedience to a certain nerve, section of this nerve might cause momentary dilatation, just as we have seen that section of its contracting nerve causes momentary contraction; but on the subsidence of this effect of the immediate injury, we should expect *all* power of active dilatation, at least so far as the divided nerve was concerned, to be abolished. We should expect not that the pupil would dilate "but little," but that it would not dilate at all. Dr John Reid's experiments† are opposed to the assertion that irritation of the superior cervical ganglion causes dilatation of the pupil. In one experiment, on removing the lower half of the superior cervical ganglion in a dog, the pupil immediately contracted (Exp. III.) In a kitten, "when the sympathetic was compressed with a moderate force, the right pupil began to contract gradually, and became much smaller than that of the left eye; and it again resumed its former size on removing the pressure (Exp. IV.). If the compression in the latter experiment be considered to have paralyzed the assumed nerve of dilatation as it passed through the ganglion, the partial removal of the ganglion in the former must certainly have proved a mode of irritating any filaments connected with the unremoved portion of the ganglion. Yet, the effect on the pupil

* Ranking's Abstract, vol. ii. p. 316.

† Edinburgh Med. and Surg. Journal, No. 14.

was the same. Guarini's experiment with strychnine is also invalidated by Dr J. Reid's observation, that on poisoning a dog with Prussic acid, both pupils became equally dilated, notwithstanding one had been previously contracted in consequence of the removal of a portion of the vagus and sympathetic. The influence of the sympathetic over the eye is not restricted to the iris. In the dog, experimental interference with the superior cervical ganglion, whether by section, compression, or complete removal, produces the same phenomena. Contraction of the pupil, retraction and inversion of the eyeball, partial closure of the eyelids, protrusion of the cartilaginous membrane, and increased vascularity of the conjunctiva, with more or less intolerance of light, result. (Dr J. Reid.) Of these effects, the retraction of the eyeball and the protrusion of the third eyelid, are due to excitement of the sixth nerve; the approximation of the eyelids, either to the same from retraction of the eyeball removing the usual support of the eye from the lids, or otherwise to excitement of the facial nerve causing contraction of the *orbicularis palpebrarum*; the inversion of the eye, to excitement of the third nerve acting upon the *rectus internus.* To ascribe the contraction of the pupil, therefore, to abolition of the function of the supposed dilating nerve, is to assume that the same injury of the superior cervical ganglion, which indirectly *excites* the function of several muscular nerves, *destroys* the power of one, viz. the nerve for dilating the pupil. In that case the power of dilating the pupil would be permanently lost, which is not the fact. If, on the other hand, we suppose it to be stimulated in common with the rest, the nerve assumed to be sent to the iris through the superior cervical ganglion must be one for contracting the pupil, the addition of which to the third nerve seems unnecessary. A poisonous dose of prussic acid dilates the pupils in all animals in which I have tried it. It can scarcely be supposed to stimulate the dilating, and at the same time to paralyze the contracting nerve. Destruction of the spinal chord produces maximum dilatation of the pupils (§ 38), which lasts for a considerable time. Assuming the existence of a spinal nerve for dilating the pupil, the destruction of the chord would cause the now unnopposed contracting nerve to lessen the pupil. And were dilatation of the pupil under the direct control of the chord through the medium of a spinal nerve, either enlargement of pupils should attend every instance of undue excitement of the spinal centre, which experience contradicts; or else the contracting force must greatly exceed the dilating, which is irreconcilable with the action of belladonna. We should also expect, as "the spinal chord never sleeps," that the state of the pupil during sleep, if referrible to nervous influence at all, would be that over which the spinal chord presided;—dilatation, according to the view in question; contraction, according to fact. In experiments I have never witnessed instantaneous enlargement of pupil which could not reasonably be accounted for by the suspension of the contracting influence of the third nerve; or which could be explained, without manifest error, on the supposition of direct irritation of any imagined nerve for dilatation. Pathology supports this opinion. The fixed expanded pupil in palsy restricted to the third nerve, without any deficiency of power in the fourth, sixth, seventh, eighth, or ninth cerebral nerves, or in any of the spinal nerves, proves that the *sphincter iridis* derives no motor power from any nerve except the third: whilst the activity of the pupil in hemiplegia, provided the third nerve remains unaffected, equally proves that dilatation of the pupil is not owing to, and dependent upon, any motor influence supplied by the spinal chord. Neither does anatomy afford any evidence of the existence of a special nerve for dilating the pupil. Observing the large supply and equable distribution of ciliary nerves to all parts of the iris, either the dilating nerve-filaments must be packed up with the rest, proceeding from the ophthalmic ganglion, which the uniform occurrence of contraction of the pupil on irritating these fasciculi forbids; or, otherwise, there should exist as obvious a supply of iridal nerves from some other source, as distinct in their course, and equable in their distribution as the ciliary nerves. These we do not find. From anatomical, as well as from physiological and pathological considerations, therefore, we have at present no reason to admit that there exists any special nerve, either encephalic or spinal, for dilating the pupil. I have elsewhere endeavoured to prove that there are not really any radiated muscular fibres in the iris, and consequently that dilatation of the pupil is not a muscular act.*

Influence of the fifth nerve on the iris.—We have found that the fifth nerve is neither a motor, nor (as Valentin and others assume) an excitor nerve to the iris. Yet pathology is rich in cases inexplicable, unless we ascribe to the fifth nerve the power of affecting in some way the internal structures of the eye. Amaurosis from injury to the supraorbital nerve, or from the lodgment of a foreign body in the nostril; temporary blindness in severe facial neuralgia, in each case with corresponding alteration in the size of the pupil, illustrate this, and direct our attention to a fact which must be borne in mind in attempting to explain this subject,—viz. that whenever the size of the pupil is affected through the medium of the fifth nerve, there is invariably some modification of vision in that eye at the same time. The following cases are selected with reference to this question:—

Case 1. A dressmaker, aged 28, had a large, opaque, white

* Edinburgh Med. and Surg. Journal, 1844, p. 110.

cataract in the left eye, the result of a blow during childhood. Vision of the right eye perfect. Whilst both eyes were open the pupils were equal in size, and acted consentaneously. When the right eye was completely covered the woman could distinguish between a bright light and darkness with the cataractous eye, but could not discern the outline of any object. As she could see as well as feel brilliant light, it was evident that the retina was sound. On covering the right eye and directing a cone of concentrated solar rays through the pupil of the cataractous eye, the gaping pupil became slightly smaller, the iris acting in a sluggish manner, very different from its mode of action when the other eye also was exposed to light. Here the optic, fifth and third nerves, were all perfectly sound; yet, as the cataract prevented all but very faint rays of light from reaching the retina, the optic nerve could be only slightly stimulated, and hence the resulting movement of the iris was slight. Sometime after the cataract had been removed, the iris of the left eye responded to light as quickly and fully as that of the right eye. But might not the excitor nerves in this case be retinal filaments of the fifth nerve, which, during the existence of the cataract, could be only feebly excited by the rays of light? Such a conjecture is negatived by the next case.

Case 2. A shoemaker, aged 43. Perfect amaurosis of the left eye of three years' duration. Vision of the right eye perfect. Both eyes being open, the pupils were equal in size, and both irides acted alike,—proving that both third nerves were sound. When the right eye was perfectly closed the left pupil became largely dilated. Under these circumstances the concentrated rays of the sun were directed through the expanded pupil of the blind, left eye. There resulted no action of the iris, but in a short time a sense of uneasiness and warmth of the eyeball, an effort to wink, and slight lacrymation. The common sensibility of the parts was unimpaired, since the man could feel my finger when gently applied to the conjunctiva. Hence the fifth nerve was sound both on the exterior, and in the interior of the eye. The lacrymation proves stimulation of the lacrymal nerves; the effort to wink, stimulation of the facial nerve, both probably excited by the sensational portion of the fifth nerve. The immobility of the iris, although its motor nerve had been proved sound and capable, proves that stimulation of the fifth nerve sufficient to react on other motor nerves, excites no action in those of the iris.

These cases appear to prove that the optic is the only excitor nerve, and the third the only motor nerve, through which contraction of the sphincter pupillæ is produced: that the fifth nerve may be stimulated so as to induce closure of the eyelid in the excito-motory manner, and yet fail to induce action in the iris. To complete the pathological evidence, we should ascertain whether there can be perfect excito-motory action of the iris, although the fifth nerve has lost its power. There are cases of anæsthesia of the fifth nerve recorded, in which the iris is stated to have acted normally. I long searched attentively for such a case, when hospital practice furnished an extensive field for the purpose; but amongst many cases of anæsthesia of the fifth I never met with one in which the iris acted quite normally. The action appeared to be normal in some instances, so long as both eyes were open, but not after covering the eye on the sound side. In every case the visual power on the side affected was always more or less impaired; and the degree of impairment was the measure of diminished activity in the iris.

Case 3. A milliner, aged 40, a delicate and intelligent woman, for four years had been subject to occasional attacks of severe facial neuralgia. The paroxysms commenced suddenly with acute darting pains of the left cheek and forehead, lacrymation, dimness of sight and rapid winking, on the left side. In a few minutes the left eye lost all power of vision, so that on covering the other the woman could discern nothing. *Whilst the right eye was thus covered, the pupil of the left was largely dilated.* During the paroxysm the left side of the face was more flushed and hotter than the other, and until the anguish caused a flood of tears, the weeping was almost restricted to the left eye. The ordinary duration of a paroxysm was half an hour. On its subsidence, the power of sight gradually returned to the left eye. In the intervals between the paroxysms there was no deficiency of visual or of common sensibility, or of activity in the iris; hence the optic, fifth and third nerves were essentially sound. The motionless and dilated pupil of the left eye, at a time when the left fifth nerve was greatly stimulated, provided consent with the sound eye was prevented, proves that excitement of the fifth nerve does not necessarily cause contraction of the pupil. The agreement in size of the pupils when both eyes were open equally proves that excitement of the fifth nerve, if it lead to dilatation of the pupil, does not cause this by antagonising and overpowering the third nerve. On what, then, did the modified activity of the iris depend in this instance? The blindness proved that the visual apparatus was deranged; the dilated pupil was merely the outward sign of this derangement. Having seen that when visual sensibility is lost, the fifth nerve cannot affect the pupil,—that when visual sensibility exists the fifth nerve can affect the pupil,—and knowing that visual sensibility governs the normal action of the iris, we must infer that whenever the size of the pupil is influenced by the fifth nerve, it is so only through some intermediate affection of visual power. The question then arises, is the influence of the fifth nerve at all times essential to the maintenance of vision, or has the fifth nerve merely the power of influencing in some way the sentient parts of the apparatus of vision, so as to modify or prevent their normal action? Besides the *a priori* improbability of one nerve depending, for the ordinary performance of its function, on the assistance derived from another, a single authentic case of complete insensibility of the fifth nerve, and yet with perfect vision of the eye on the same side, would completely negative the first question.

How can the fifth nerve affect the sense of sight? We may presume in several ways. (1.) When stimulated, the fifth nerve might communicate its excitement to the centric part of the optic tract, and thus heighten the acuteness of vision. (2.) By exciting the grey cells of the Gasserian ganglion, it might cause ganglionic influence to pass along grey fibres to the lenticular ganglion and thence to the vascular coat of the retina. (3.) The fifth nerve might itself excite the grey cells of the lenticular ganglion, and thus react on the retina through the ganglionic nerves.

In the first mode, the fifth nerve could cause contraction of the pupil only; whereas under extreme pain, it sometimes induces dilatation. Is this dilatation owing to incapacity of the perceptive part of the nervous apparatus of vision, from such an amount of cerebral disorder having been induced as to render the sensorium unable to perceive visual impressions, although duly conveyed to the brain? In that case, as the fifth nerve is not more intimately connected at its centric termination with the optic than with the other nerves of special sense, we should expect deafness as well as blindness; loss of taste, if not of smell. These are not met with. Nor, if its impairment depended on cerebral disturbance, should we expect the sense of sight to be so rapidly restored on the subsidence of the irritation of the fifth nerve as it really is. We must consequently rather assume one or both of the two last modes laid down as those by which the fifth nerve reacts on the iris. Both equally require us to admit that cerebro-spinal nerve-tubes have the power to affect the ganglionic grey vesicles through which they pass; and the third mode requires us also to admit centrifugal action of sensational nerve-tubes; since the only fibres of the fifth which enter into the lenticular ganglion are traceable from it backwards into the Gasserian ganglion, and therefore could communicate no influence to the former, but what they had already conducted from the latter, *i. e.* excentrically. How can we otherwise account for any branch of the fifth nerve passing into—and through the lenticular ganglion at all? It is not required for the purpose of endowing the eyeball with sensibility, since the fifth nerve furnishes for that purpose a larger supply which is quite unconnected with the ophthalmic ganglion. It is not to confer motor power on the ganglion, since the third nerve supplies of itself, irrespective of the ganglion, all the motor nervous power which we can demonstrate in the eye. It cannot be merely to serve as a conductor of organic nerve-filaments from the sympathetic, for these might just as conveniently have been packed up with the third nerve, as some usually are. It is not needed to connect the retina with the facial nerve, in order that a dazzling light may excite closure of the eyelids, since the naso-ciliary nerves, which do not enter the ganglion, might have affected that. What improbability is there in conceiving that one purpose subserved by the peculiar relative position of the vascular coat of the retina, placed as it is in front of the retiform nervous expansion of the optic nerve, and amongst the minute papillæ which doubtless constitute the real sentient field of vision, is that of modifying the effects of stimulation according to ever-varying conditions of degree and quality of light and heat? It can scarcely be doubted but that mere excited circulation through this vascular coat, within limits, would heighten; tardy circulation diminish; and a congestive state greatly impair, the sensibility of the retina. As a mere hypothesis, therefore, it is allowable to conjecture that the small supply of fifth nerve which enters into the lenticular ganglion, passes through to the retina exclusively; that when in the ganglion, it can affect, during its own conduction of nervous force, the action of the ganglionic vesicles, and consequently call forth the influence, be that what it may, of the ganglionic nerves. Begging the question, for the moment, that one effect of the ganglionic influence is the afflux of blood to the part, we can understand how the stimulation of the retina by intense light may cause not only instantaneous contraction of the pupil through the third nerve, but also an altered state of circulation through the retina, through the medium of the fifth nerve, lenticular ganglion and ganglionic nerves, producing painful confusion of sight, or, in other words, dazzling and aching in the eye. The unusual supply of blood furnishing at the same time the means of recruiting the over-excited retina. We can understand how one amount of stimulation of the fifth nerve may have such a slight effect on the vascular coat as may merely stimulate the retina, and thus cause contracted pupil (*e. g.* ulcer of cornea, strumous ophthalmia): how a greater amount of stimulation suddenly applied, or the same amount greatly prolonged, may cause so much disorder of the retinal capillaries, as to produce temporary blindness and dilated pupil (*e. g.* severe *tic*). The fifth nerve being in the one case indirectly an excitor of contraction; in the other, of dilatation of the pupil.

If the nerve-tubes which pass through the ophthalmic ganglion have the power of exciting the ganglionic grey cells and their organic nerves, the third nerve must act in this way every time that it causes contraction of the pupil. Why then does it not likewise produce a similar effect to the fifth on the vascularity of the retina? Such an association would have interfered with correctness of sight; since when vision was required to be very minute and exact, as in examining a small and near object, the greatly contracted pupil would have had as its concomitant a gorged state of the blood-vessels of the retina. Still it is most probable that the third nerve, as well as the fifth, does affect the state of capillary circulation within the eyeball, and influences, through the medium of the lenticular ganglion, a still greater extent of vascular apparatus than that of the retina, viz. the capillary plexuses of the ciliary processes and of the iris, subservient as these probably are to focal adjustment, which is always attended with alteration of pupil. That the filaments of the fifth nerve, and those of the third, should excite different parts of the lenticular ganglion,—if they do so,—is quite conformable to what the physiology of all portions of the nervous system tends to confirm, that speciality of action depends solely on the centric connection and ultimate distribution of the nerve-tubes. Anatomy furnishes only the negative support of supplying no facts irreconcilable with this view. Nor can it fairly be objected that it ought to do more; since the only positive evidence would consist in our being able to follow an identical nerve-filament from the encephalon through the ophthalmic ganglion, noting its relations there, tracing it on into the eye, and ascertaining the exact point and mode of its final termination. Those most accustomed to difficult dissections will be the first to acknowledge the impossibility of doing this. Unless it be in order to associate them together in their action, there seems no reason why the sensational, motory, and organic nerves of the interior of the eye should be so intimately connected together in the form of the lenticular ganglion before proceeding to their destination. The excito-motory action of the iris takes place independently of the ganglion, has its nervous centre elsewhere, and therefore could have been effected without it. The fifth nerve does convey most of the common impressions, and therefore could have conveyed all without entering the ophthalmic ganglion. The sympathetic could have furnished directly the organic fibres. If we imagine an animal so placed that the medium in which it lives forbids any sudden or great variation of light from over-stimulating the retina, and therefore the focal adjustment of the eye, and the special sensibility of the retina, could not with advantage be placed under the influence of the nerve of common sensation,—in such an animal, there would be nothing gained by the ocular twigs of the fifth nerve passing in close relation to the ganglionic cells and nerves. If, again, the iris were nothing but a mere immovable, non-muscular septum, the pupil never varying in its size, there would be no reason for associating the ocular twigs of the third nerve with the ganglionic. And as neither the sensational nor the motor nerve required connection with the organic, the interior of the eye might derive its ganglionic supply directly from the sympathetic. This combination of conditions, imagined as theoretically probable, is precisely what we meet with in the fish.*

In birds and most mammals there is a movable iris; and wherever this exists there is always an ophthalmic ganglion. The constancy of this co-existence points out a functional relationship; and were the iris merely a muscle in structure and action, it would favour the supposition that the ganglion is for the purpose of presiding over its muscular action. But the *sphincter iridis* can never act without at the same time affecting the extensive vascular apparatus so intimately connected with it. Finding then, that when there is vascular structure without muscle, the ganglionic nerves are not connected with the motor ones; where there is vascular structure so connected with muscle that the two always act consentaneously, the ganglionic nerves are intimately connected with the motor ones; the conclusion is obvious, that such anatomical connection is for the purpose of permitting of functional association. Of what nature is this functional association of the three (physiologically) different nervous elements of the lenticular ganglion? As we have found that the fifth nerve does not act directly upon the third, nor the third nerve upon the fifth, through the medium of the ganglion, only two kinds of combination of function remain.

(1.) The action of the nerve-tubes transmitted, both sensational and motor, stimulates and calls forth the action of the ganglionic nerve-vesicles, amongst which they pass, and thus excites the organic nerves which proceed from these vesicles.

(2.) The ganglionic nerve-vesicles being themselves in action in the first instance, excite secondarily the action of the transmitted nerve-tubes.

Were both suppositions correct, we should never have contraction of the pupil without sensation, nor without action of the ophthalmic ganglion. Were the second true, we should never have action of the ganglion, assuming that the ganglion furnishes no check to the transmission of sensation, without contraction of the pupil and sensation as its attendants. We are not conscious of the changes of the iris in exercising sight, and therefore we can have no

* The function of the third nerve as regards the interior of the eye of the fish, judging from its distribution, and from the non-existence of any muscular tissue within the eye, is that of presiding over the fulness of the vessels of the choroid body, on which it is presumable the adjustment of vision for different distances depends. If so, the third nerve in the fish, as in higher animals, acts responsively to the optic nerve. As there is no lenticular ganglion, this would support the conclusion that the ganglion is not a centre of excito-motory action. It would also be an argument, as far as it went, that a nerve usually muscular can act on other structures if so distributed.

common sensation implicated. The first supposition consequently appears to be the true one. Provided that no error exist in the facts, and no unreasonableness in the considerations, which have been stated, as we cannot suppose the arrangement of the ophthalmic ganglion to be peculiar and distinct from that of other ganglia, we may educe two general laws ;—

(1.) That when encephalic, spinal, or cerebro-spinal nerves pass through the substance of a ganglion, it is in order to associate the influence of the organic nerves of that ganglion with their own.

(2.) But that, on the other hand, during ordinary excitement, the ganglionic nerve-vesicles have not the power of exciting to action, the white nerve-tubes, which lie amongst them, in their passage through the ganglion.

In the preceding remarks, several questionable points in the physiology of the nervous genglia in general, have been referred to, which it is desirable now briefly to examine.

Do the ganglia impede sensation? The sympathetic ganglia have been supposed to check the sensations which, it is presumed, would otherwise be conveyed from the viscera. In perfect health, the only feeling experienced from the viscera is the obscure sense of general comfort,—that surest sign that the vital organs are acting in harmony. But let the action become disordered, as in spasm of any part of the alimentary canal, and there is extremely acute sensation. This sufficiently proves that the ganglia do not always impede sensation. Nor, in the absence of proof, is it necessary to assume that they ever do so. A ligament communicates no marked sensation during the ordinary movement of a joint, but let it be stretched suddenly, and severe pain results. Here we have no ganglion implicated but the spinal one ; and, that spinal ganglia do not interrupt sensational action, is certain from their position on the posterior spinal nerve-roots. In both ligament and viscera the sensational nerves are so arranged at their distributed extremities as not to receive any stimulus except under unusual and irregular conditions ; but when from disordered action of the part they are stimulated, they communicate their excitement without any interruption from the ganglia. We cannot suppose that the Gasserian and the spinal ganglia impede sensation ; and there is no anatomical peculiarity about the ganglia of the sympathetic nerves to sanction our adding this to their endowments. The hypothesis that every ganglion lessens the sensibility of the sensational nerves which it transmits must therefore be considered as devoid of proof, against analogy, and unnecessary as well as insufficient for the explanation of the phenomena on which it was founded.

The diametrically opposite opinion, *that the ganglia are essential to sensation*, has greater plausibility from the circumstance that every sensational nerve is a gangliated nerve also. It is disproved by the fact that the posterior roots of the spinal nerves are sensitive before they enter the ganglia.

Do the ganglia prevent the transmission of the influence of the will? The motor nerves of voluntary muscles never pass through ganglia; those of involuntary muscles invariably do so. Hence the ganglia have been thought to obstruct the transmission of volitional power, and until Dr Marshall Hall had established the independency of the spinal chord, this theory was not unreasonable. Now, however, that the entire class of involuntary external excito motory acts are admitted to be performed by spinal muscular nerves which are not gangliated, the assumption is not required for the explanation of involuntary motion. Every involuntary muscle is either directly or indirectly connected with the spinal chord, and such connection is sufficient to account for all involuntary excited muscular action. The third nerve causes the *sphincter iridis* to contract, as we have seen, without sustaining any obstruction from its iridal filaments passing through the ophthalmic ganglion. By experiment we find that, through the medium of the spinal chord, we can excite, diminish, or destroy the contractility of involuntary muscles instantaneously, and as the chord can influence these muscles only through the medium of nerves which pass through sympathetic ganglia, it is evident that these ganglia offer no impediment to the transmission of spinal *vis nervosa.* As we have every reason to believe that the mechanism of nervous action is identical, whether the impulse to the action originate in the brain or not, it is a fair inference from analogy that the sympathetic ganglia offer no obstacle to the transmission of cerebral force. The viscera, though removed from the direct influence of the will, are greatly affected by mental emotion, which may in some measure be controlled by the will. We may conceive that the visceral nerves are connected in the encephalon with the centre of emotion, but not directly with that of volition. That certain nerve tubes have this arrangement anatomical proof will hereafter be furnished. That some of these nerve tubes have the destination above assigned, is, and probably must remain, purely a conjecture.

Do the ganglia supply motor nervous energy to the involuntary muscles?

Experiment XXIII. A small dose of prussic acid was given to a rabbit. The animal shrieked, was convulsed for thirty seconds, and then died.

122. During the convulsive action of the muscles, the pupils were first contracted, then dilated; in two minutes after death they began to contract again, and afterwards remained of less than the medium size.

123. The integuments were stripped off the abdomen without tearing the transparent parietal layer of peritoneum. Stomach distended with food. Intestines motionless.

124. On opening the chest and noticing the heart, the auricles were found to be contracting rythmically; the ventricles distended and motionless. Both auricles contracted together, then occurred a pause for two-thirds, then a slight but uniform contraction for one-third of the period. As nearly as could be ascertained, this regard to time was observed until the action of the auricles ceased entirely; the cessation being preceded not by the intervals becoming longer, but by every contraction becoming more and more feeble. On touching either of the ventricles with the scalpel point, both instantly responded by a tucking upwards of the apex of the heart; the muscular action not appearing to spread gradually from the spot irritated, but to affect instantly a distant part, viz. the apex. This contractility of the ventricles ceased in about five minutes; but after this, on pressing out part of the blood with the finger, the ventricles would for a moment afterwards respond to irritation. Hence their contractility was impaired by over-distension as well as by exhaustion.

125. Whilst the irritability of the heart yet remained the peritoneum was opened, the stomach lifted up, and the semilunar ganglia touched with the scalpel. Active vermicular motion of the small intestines immediately ensued, and continued for a short time after I had ceased to irritate the ganglia, but after quiescence it instantly recurred on renewing the irritation of either the ganglia or of the principal nerves issuing from them. When the action of the heart had entirely ceased, the intestines no longer responded to irritation of their ganglia, but as the heart could scarcely have ministered to the circulation previously, this may have been a mere coincidence, arising from the parts having been for some time exposed, stretched out, and cooled, and the nerves having perhaps become exhausted by the irritation simultaneously with the heart's loss of irritability. After the bowel had ceased to respond to irritation of the nerves, slight muscular contraction could be induced by scratching its coats.

126. Scratching the grey ganglionic mass about the origin of the renal artery had no apparent effect at any period of the experiment.

Experiment XXIV.—A full grown rabbit. Exposed the peritoneum so as to see the viscera through it. The animal gave no sign of pain.

127. The stomach and intestines were motionless. On making a small opening in the peritoneum some of the small intestines protruded, and the instant they were exposed to the air vermicular motion commenced.

128. A drachm of prussic acid was dropped amongst the intestines. This appeared to stimulate the muscular coat of the bowels to which it was applied; the peristaltic action being increased.

129. In twenty seconds the rabbit shrieked and was convulsed; the stomach and all the intestines were suddenly and forcibly protruded through the small aperture in the peritoneum; the action of the heart became weak and fluttering, and ceased in a minute and half.

130. The pupils at first contracted to their utmost, then dilated, until when the heart cased to beat they were at their maximum of dilatation. Not observed subsequently.

131. The peritoneum was slit up. Stomach and duodenum were distended with food. These distended parts were motionless. The remainder of the small intestines moved gently. On exposing the semilunar ganglia, and scratching the greyer portion, peristaltic action was instantly increased; but was still more suddenly and vigorously increased by irritation of the whiter portion, or of the nerves proceeding from the ganglia.

132. Some influence over the motion of the intestines was likewise manifested, but not to so marked an extent on irritating the renal plexus.

133. The blood-vessels of the viscera appeared to be full; and the arteries did not empty themselves after death. The heart also was full in every cavity.*

In these and similar experiments we have no proof that the ganglia themselves generate the motor nervous force which, under irritation, they impart to the muscular coat of the alimentary canal, since there is no ganglion that does not contain and transmit spinal nerve-tubes; and the contraction excited in the muscle is always considerable in proportion to the quantity of white matter, *i. e.* the number of spinal and encephalic nerve-tubes in the ganglion. If the ganglion is very grey and translucent it is difficult to excite any muscular contraction by irritating the ganglion; but if white and dense, (*e. g.* the cœliac) then contraction readily ensues, but never more readily nor more extensively than when the irritation is applied spinad or peripherad to the ganglion. We have therefore no proof that any ganglion either itself generates nervous force for muscles, or that it in any way affects the force

* By way of caution to others, I may state that I suffered considerably from carelessness in the use of prussic acid in conducting this experiment. Whilst intently observing the points above noted, my face was held very close to, and over, the parts, and was of course exposed to the warm exhalation conveying the vapour of prussic acid from the viscera. Eight or ten minutes had elapsed before I experienced any thing unusual, when suddenly dimness of sight, vertigo, and a peculiar feeling of expansion, and lightness of the chest, and want of breath occurred. On leaving the room, which of course I did instantly, I found I had scarcely any muscular power. Stimulants, cold water, and fresh air were freely used, but the uncomfortable effects lasted for several hours.

conveyed by the spinal nerve-tubes which pass through it. Whilst the contrary is proved with respect to the lenticular ganglion. To consider the ganglia centres of nervous energy for muscles appears superfluous when the spinal chord exists as a distinct centre for that express purpose. And if the ganglia were intended in any case to supersede the chord, why should we have spinal nerves passing through every ganglion ? A principal reason perhaps for assigning the functions of the chord to each ganglion, is the fact of many active but simply organised animals possessing ganglia as their only nervous centres. Here undoubtedly a ganglion acts as an excito-motory centre, and probably serves the purpose of sympathetic and spinal centre at the same time. But in asterias each of the five ganglia has an equal right to be considered the sensorium ; and were a loose analogy to guide us, we should therefore revert to Winslow's opinion, and consider every ganglion in higher animals a "lesser brain !" The very fact of separation as we ascend the scale is an argument against perfect similarity of function. Dr Carpenter has shown us how to deduce important inferences from the study of the nervous system of invertebrata.* To his conclusions the following may perhaps be added as having reference to the present question.

1. When different parts of an animal have similar functions to perform, but at the same time it is necessary that each part shall be capable of acting by itself, independently of the rest, each part thus functionally independent possesses a nervous centre of its own, *e. g.* Talytrus ; Scolopendra ; larva state of insects.

2. But when several parts not merely act in a similar way, but always act simultaneously, one nervous centre is common to all the parts thus functionally combined, *e. g.* the amalgamation of ganglia in various mollusca, (Limax ; Pecten ;) and in the imago state of insects.

3. When the habits of the animal are such that vision, common sensation, and muscular action need never be manifested singly or separately, one nervous centre is subservient and common to all these functions, *e. g.* Echinus ; Asterias.

4. But as we rise in the scale, and the circumstances of the animal require the ability to perform each of its more important and varied functions independently of the others, each different set of organs thus functionally individualized has its distinct nervous centre, *e. g.* Sepia ; Patella ; and the higher forms of all entomoid articulata.

5. Where the nervous centres preside over movements which usually and normally are performed in concert, there is a direct commissural connection between them, allowing excitement in one to be readily communicated to the rest, *e. g.* Articulata in general.

* Inaugural Dissertation, Prize Thesis, 1839.

6. But where such co-ordination does not exist, and would defeat the end, we find no such commissural connection, *e. g.* the non-connection of the pharyngeal with the pedal and palleal ganglia in several mollusca; also, that of the ganglia on the so-called recurrent nerve with the ganglia of locomotion in various insects.

7. The ganglia are not developed either in number or size in proportion to the sensibility of a part; but they are so, in proportion to the amount of independent muscular actions which that part was to perform, *e.g.* compare different Myriapoda, Crustacea, and the several stages of insect life.

8. Where sensorial control is exercised, nerve-tubes pass to the organs already supplied with nerves by their own nervous centres. These sensorial nerve-tubes form a tract distinct in its entire course from the nerve-centres over which it passes, *e. g.* Myriapoda, Crustacea, Cephalopoda, the higher insects in their perfect state.

9. From this sensorial tract some fibres pass into (through ?) each ganglion, thus associating the force of the ganglion with that of the sensorium in every volitional movement. Other fibres pass from the sensorial tract without being in any way connected with the ganglia. Are these true sensational fibres ? *e. g.* the same as the preceding.*

* In various Articulata there are three tracts discernible in each longitudinal chain of ganglia. The highest and smallest fibrous column proceeds from the supra-œsophageal ganglion over, and closely attached to the subjacent gangliated tract for its entire course, but does not enter into the ganglia. Assuming that the supra-œsophageal ganglion is the sensorium, this might be considered the sensorial tract. The two remaining tracts are amalgamated inseparably, and both enter into the formation of the ganglia, but the higher portion appears to contain fibres continuous with the supra-œsophageal ganglion ; the lower portion merely fibres which pass from ganglion to ganglion, and which never reach the supra-œsophageal. Of the two lower tracts, therefore, the higher portion may be distinguished as the gangliated sensorial tract, the lower as the ganglionic tract. Each compound nerve has three roots, corresponding to, and derived from these three tracts ; a large root containing fibres from the two lowest tracts, proceeding directly from the ganglion ; and a smaller root from the highest tract, which has no connection with the ganglion at all, but joins the rest of the nerve separately. This triply-compound nerve is distributed to sensitive parts, and to muscles which act both voluntarily and involuntarily.

Physiologists are agreed that the involuntary action, so far as it implicates the nervous system at all, is due to the ganglionic fibres alone ; but with respect to the function of the two remaining tracts, viz. the gangliated sensorial, and the non-gangliated sensorial, there is difference of opinion. Dr Grant, who first directed attention to it in this country, Mr Newport, and Dr Marshall Hall, appear to view the highest fibrous column as motor only ; and the next or gangliated tract, either as moto-sensitive (Grant), or as sensitive only (Newport.) Dr Carpenter deems it more probable that the non gangliated fibrous tract is both sensory and motory ; whilst Todd and Bowman, not satisfied that we have yet ascertained the exact anatomy on this question, seem to consider all the fibres as commissural only. The last view leaves the existence of the peculiar arrangement of these several tracts quite unintelligible. As no instance has been made out in which fibres pass directly from one of these tracts to their destination without being previously mixed up with fibres from the others, we have no means of ascertaining by the distribution of the nerves the functions of their source ; and as

10. Where sensorial influence, if greatly exercised, would interfere with the normal action of the ganglion inconveniently, such distribution of sensorial nerve-tubes is very small, *e. g.* the slight connection of the ganglia which supply the respiratory organs with the supra-œsophagal ganglion in insects.

11. The sensorial centre is that with which the nerves of the special senses are most directly connected. In proportion to its inferiority in size, are, judging from the habits of the animal, the volitional acts mere responses to sensations; the magnitude of a nervous centre being an exact criterion of its power; *e. g.* compare the imago with the larva state of insects; Julus with Scolopendra; the scorpion with the spider.

12. The concentration of the nerves appropriated to several dissimilar functions in one ganglion is a mark of inferiority in the scale of animals, indicating a small amount of independency in the several functions. On the other hand, the concentration in

the tracts are too minute to permit of experimental procedure, any attempt at explanation must be merely hypothetical. This being the case it is less presumptuous to dissent from the opinions of the above-named physiologists. It seems to myself most probable that the *non-gangliated* sensorial tract is sensiferous only, and that it has no connection with the ganglion in order to permit a sensational impression to affect the sensorium without of necessity calling forth ganglionic action; that the *gangliated* sensorial tract is the volitional motor column, and that its fibres *do* pass through each ganglion in order to excite its co-operation, since voluntary muscular movement is for the most part effected by the same muscles (as also in higher animals) as that which is produced in the excito-motory manner; and that both sensorial tracts arise in a centre separate and distinct from the chain of ganglia, in order that each ganglion may have the power of acting by itself, independently of sensorial influence (*i. e.* physically). Where sensorial influence is so little required, that it does not interfere with, and is possibly never manifested without the exercise of the other nervous functions, there has yet been discovered no such separation of nervous tracts (*e. g.* Echinodermata). In the arms of the octopus, Dr Sharpey discovered a double nervous column, one tract gangliated, the other not. The echinus fastens itself by means of tubular suckers, just as the octopus does, but it is sluggish, its hard exterior little sensitive, and all its powers comparatively feeble. Hence it has small demand for sensorial action. Whereas the octopus is active, energetic, and has probably very delicate sensibility in the surface of its pliant tentacula. Coexistant with superiority of sensibility and of sensorial power, therefore, we find the distinct *non-gangliated* chord. It is no real objection that in vertebrata the sensational nerve-tubes invariably do pass through ganglia, whilst the volitional motor nerve-tubes as constantly do not. If we consider the ganglia of invertebrata as so many isolated segments of spinal chord, I believe the analogy will prove exact. Nor is there any argument against this to be founded on apparent difference of relative position of the several columns in the two great divisions of the animal kingdom. The chord in vertebrata commences and continues dorsal; in invertebrata it commences dorsal (in the supra-œsophageal ganglion), but afterwards becomes ventral. In bending down to the ventral surface, that aspect of the ganglionic chain which was at first nearest to the surface—dorsad, is now nearest to the viscera and v. v. Hence the highest of the columns in the ventral chain is the analogue of the posterior strand of the spinal chord. This, according to Sir C. Bell's views, would countenance the function I have assigned to it—that of sensation. But in vertebrata the most posterior strands of the spinal chord are probably not sensational at all; still, as the sensational strands of the chord are situated posteriorly in reference to the volitional and true spinal nerve-tubes, the analogy as regards relative position is exact also.

one centre of nerves appropriated to perfectly similar functions and the conjoint existence of such a centre for each important class of organs indicates superiority, admitting of greater extent and association of similar actions, and of greater independency of dissimilar ones; *e. g.* compare the lower with the higher species in each class of invertebrata.

If these remarks be admitted, it results that the separation of the nervous matter into distinct centres is for the purpose of individualizing the action of each centre, but not of investing it with any distinct and peculiar kind of power; that its amalgamation into fewer centres is to ensure greater association, and to diminish independency in the action of the parts supplied; that in all the higher invertebrata the exercise of sensation and volition is restricted to one nervous centre, which is connected with the rest in exact proportion to the degree in which the sensorial functions are implicated; that the variety in the results of nervous action is due solely to the centric connection and peripheral distribution of the nerves, and not to any intrinsic difference in the nature of the change which takes place in the nerve-vesicles. This is obviously begging the question of the similarity of physical action between the supra-œsophageal (sensorial) and the other ganglia, but we could hardly explain otherwise the combination of all the nervous functions in one centre which we meet with in several of the lower animals.

As the ganglia of invertebrata are developed in number and in size in exact accordance with the muscular powers of the parts supplied, we should have here an argument in support of the visceral ganglia in higher animals being nervous centres of muscular action. Most physiologists, however, coincide with Beclard, Muller, and Carpenter, in concluding that there is no analogue to a distinct sympathetic nervous system in the invertebrata. Traces of that anatomical separation of centre, which is the only point of resemblance, are met with in the lowest vertebrate animals, in which muscular movement is still the result more of physical than of sensorial action. Hence the variation in number and magnitude of the encephalic lobes in fishes, according to the degree of intelligence possessed. Where intelligence is lowest and the true cerebrum deficient, there is no sympathetic system whatever distinct from the rest, (Cyclostomi). Where the median lobes are large, the cerebrum very small, there first appears a rudimentary visceral nervous system, but still the *par vagum* supplies many organs in place of the sympathetic, (most osseous fishes and serpents); in proportion as the median lobes are less, the cerebrum larger, we find the *par vagum* less, and the sympathetic more developed, (sharks and other cartilaginous fishes). Continuing the investigation through reptiles, birds, mammals, up to man, we find the rule universal, that the sympathetic nervous system is developed in direct ratio, not with the nutritive powers, not with extent of sensation, not with muscular energy, but with the amount of intelligence of the animal: and consequently in inverse ratio to the magnitude of the *medulla oblongata* and *corpora quadrigemina*; in direct ratio to that of the cerebral hemispheres and cerebellum. It was not, therefore, without some appearance of probability that the older writers referred certain psychical operations to the action of the visceral ganglia. The inference previously stated, however, that anatomical separation is to ensure functional individuality, leads us to the diametrically opposite conclusion; and we consider the separation of the sympathetic ganglia from the other nervous centres as the means of removing their action from interference on the part of the mind. An interference prejudicial in proportion to the degree in which the unequal irregular influence of mental action could operate, and an interference, therefore, provided against in exact proportion to the amount of intelligence. As comparative anatomy furnishes no argument in favour of the ganglia in vertebrata being centres of muscular action, as another centre exists which is proved to preside over excito-motory action, and as the lenticular ganglion is proved not to preside over the muscular action of the *sphincter iridis*, in the absence of direct proof to the contrary, we may conclude that the spinal and prævertebral ganglia do not supply nervous influence to muscles.

Real Functions of the Ganglia.—Since the time of Bichat, the idea has been prevalent that, in some way not clearly defined, the ganglia governed the functions of organic life. By many, the sympathetic nerve has been considered the factor-general of all the vital operations; an hypothesis of which it is the sole merit that it renders the action of all subordinate agents abundantly simple. Modern researches have proved that every proximate constituent of a living body contains, complete within itself, the means of performing its specific action, so long as the requisite conditions are observed. The most important of these conditions is the due supply of organizable material. To regulate the supply according to varying demands, and to ensure order in the discharge of complicated functions which are at once mutually related and yet entirely different, there must be some means of harmonizing various organic actions, and regulating the supply of blood according to the requirements of the different organs. No other system except the nervous presents the characters fitted for effecting this superintendence. Many conjectures have been formed as to the mode in which the nervous system regulates vascular action. Dr Alison has pointed out that no modification of the heart's action, or of the contractility of the arteries, singly or conjoined, can account for all the phenomena of the capillary circulation in inflammation. The subject, indeed, has been greatly mystified by an attempt to reduce it to a mechanical explanation, though as little susceptible of it as the process of which this is the abnormal form —nutrition. Of the cause of the afflux of blood in an inflamed part, three hypotheses are offered. 1. Increased vital affinity between the particles of the blood themselves, and between them and the surrounding tissues, producing secondarily dilatation of the vessels. (Alison.) 2. Suspension of the nervous influence by which the small blood-vessels are normally maintained in a state of tonic contraction; consequent relaxation with dilatation of the vessels and retardation of the flow of blood through them. (Henle; Billing.) In addition to this condition, and likewise consequent on the suspension of nervous influence on which it is dependent, the normal repulsion of the red corpuscles of the blood is lessened, and their closer aggregation, and consequent stagnation of blood, permitted. (Wharton Jones.) 3. Active dilatation of the blood-vessels, (John Hunter); from increase in the nervous energy supplied, (Macartney); that supply furnished by the organic nerves, (Copland.)

Without attempting to discuss so extensive and important a question as that of the pathological character of inflammation, we must find the best clue to the normal influence of the nervous system on the blood-vessels; in the exaggerated manifestation of that influence in disease. A nervous system is not essential to either normal or abnormal nutritive secretion, for we see both in vegetables. Abstractly considered, therefore, the local changes of inflammation might possibly occur without any implication of the nervous system at all. But in higher animals, at least, we never have these local changes without concomitant affection of other parts, however slight the extent or degree. To this association of action innervation must be deemed essential. But the nervous system does more than this. It is admitted that in some way the nervous system can influence the action of the capillaries, but the mode by which this influence operates is not ascertained. Those who explain the first stage of congestion in an inflamed part as the result of a suspension of the nervous energy having led to a passive enlargement of the blood-vessels, are obliged to assume that the capillaries possess contractile walls; that their contractility in health is maintained by a constant supply of nervous energy; that prior and leading to congestion there is palsy of the vascular nerves. From which it would follow, that when the blood-vessels are contracted and contain the least blood the vascular nerves are in a state of over-action, but when the small vessels are filled and distended, their nerves are temporarily palsied. Whilst digesting a meal the mucous membrane of the stomach is most vascular; its organic nerves must then be least active! Scratch the pale skin on the back of the hand, there is first a white line from the compression, then sensation, increased redness, and perhaps bleeding. The increased redness proves distension of the capillaries, the pain proves irritation of the sensational nerves; but what proof have we that such excitement of the sensational nerve momentarily palsies the vascular nerve? Henle ascribes it to a principle of antagonism between the two, which is merely another mode of stating the fact. Were there any such principle so easily called forth, nutrition would be subject to constant interference from sensation. Nor could it happen without our assuming, either that the same nerve tubes, which in the ganglion prevented action, in the spinal chord excited action, or else, that the sensational nerve tubes as they passed through a ganglion, themselves carried away the ganglionic energy, which, from the nature of the connection, is improbable, and which, as regards the lenticular ganglion, I believe, is proved not to occur. Dr Billing accounts for blushing by supposing that the emotion causes abstraction of nervous energy from the blood-vessels of the face, and thus permits their passive dilatation. But in terror we have a more intense emotion with a bloodless face. Here, according to the same hypothesis, there must be over-action of the vascular nerves of the face. Is it not more reasonable and more in accordance with their influence on other parts, to assume that depressing feelings diminish, and exciting emotions increase innervation for the time? Shame, the only moral case of blushing, is certainly not a depressing emotion; witness the action of the heart. Not, only, therefore, is this supposed suspension of vascular nervous energy not proved, but it is less probable than the "active dilatation" of J. Hunter. If a frog's foot be stretched and examined by the bright sunlight under the microscope, it will be noticed that there is no uniformity of rate between the flow of blood corpuscles in the capillaries and that in the arteries. After coursing on more slowly than before, then oscillating, the red globules in a given capillary tube will occasionally course back again towards the artery, and continue to do so with great rapidity for a minute or longer, then stopping, oscillating, and again resuming their course down the tube towards the vein. On the occurrence of any obstruction the globules, before becoming impacted together in the tubes contiguous, appear to be driven with force against the obstruction; they then recoil for some distance, and rush against the obstruction several times before they lose motion. During these varied directions and kinds of movement on the part of the blood globules, the capillaries appear to undergo no alteration in their dimensions. Consequently, the cause does not consist in their contraction or dilatation of the containing tubes. As the globules occasionally move against the direction of the *vis a tergo* just as freely as in the opposite direction, the action of the heart cannot be the influential agent. To ascertain whether we could affect these movements in the capillaries through the medium of the nerves, after examining the web of a frog's foot for some time, I exposed the lower part of the spinal chord and irritated the spinal ganglia on the side I was examining. The capillaries of the web were distended, obstructions from the aggregation of blood globules existed in several spots, and circulation was languid. At first I imagined the irritation of the ganglia might have caused something of this, but on exposing the web of another frog's foot in the same way to the light and heat of the sun for the same length of time, the state produced so nearly resembled that above described, that the observation as regarded ganglionic influence was evidently null. I have not succeeded better in other attempts to elicit ganglionic action on blood-vessels; but believing that we cannot in experiments induce the action of the gray cells of nervous centres, such a result is negative only, and of no weight until we have shown that some other effect can be produced in this way. This has not at present been done. Experimental physiology has so far acquainted us only with what the ganglia will not do; but that, if free from fallacy, is certainly an important step gained.

Are the attractions going on in the capillaries due to the vascular nerves? It is more in accordance with the facts of the vegetable and inanimate kingdoms to consider the affinities exercised in the capillary vessels as special attributes of the molecules which manifest them, and not as mere investments of these molecules by the nerves; just as muscular contraction and cell secretion are essentially the properties of their respective tissues. But just as these last are in a great measure controlled and affected by the nervous system, may be the capillary actions also. There are several modes conceivable in which this controlling power might operate. Energy of function depends on activity of molecular change in the organ engaged; this in turn depends on a due supply of pure blood, and in the few instances in which an organ has been seen in the active discharge of its function, it has been seen to receive at the time an unusual supply of blood.* Mere alteration of calibre in the capillary tubes, therefore, would affect the discharge of function in an organ; contraction of the capillaries lessening the amount of molecular change in proportion to the diminution in the quantity of blood received; dilatation of the capillaries increasing function in proportion to the increase of purified blood admitted. There is no instance in the economy of any part being endued with power expressly for the quiet and normal performance of its function only, and divested of that

* Dr Combe; Andral; Beaumont.

power whenever an augmented discharge of function was required. Yet this must be the case, if we admit that the capillaries are kept in a state of normal contraction by the force of the vascular nerves, and that their equally normal distension during functional activity is due to temporary removal of that force. Blushing, erection, neuralgic flush, counter-irritation, and the concomitant enlargement of vessels and local growth during gestation, during the budding of the deer's antlers, and in the generative organs during the procreative period in animals subject to periodical sexual excitement, are all better explained by supposing that excitement of the vascular nerves and increased afflux of blood go together, than the contrary. Could excitement of the vascular nerves cause the active dilatation of the walls of the capillaries? Notwithstanding the active elongation of the superior oblique muscle of the eyeball, and the active expansion of muscular canals as the result of spinal excitement, have been defended, they are not proved, not required, and against analogy. The iris and perhaps the heart are not exceptions, since, if these do enlarge actively, it is certainly not through any over-action of the same fibres which cause at other times their contraction in size. It is not proved that the capillaries are muscular tubes. I have never seen them manifestly contract on the application of a stimulus that could not act chemically on the surrounding tissue, and the contraction—always slight—which many have described as the immediate result of stimulation, may have commenced in the small arteries and subsequently appeared in the capillaries from diminished contents only. The contractility of the smallest bronchial tubes, and the non-contractility of the air-vesicles, is perhaps a type of a similar arrangement of the smaller arteries and the capillaries.* If this be so, dilatation and contraction of the capillary vessels must equally depend on the quantity and the pressure of the fluid they contain, which must, in turn, vary with the force of the heart's action, the tone of the large vessels, the quantity of blood in the system, and the amount of attraction going on between the blood and the walls—whatever their nature—of the capillaries themselves. Finding, therefore, that contraction of capillary vessels during functional activity is opposed to the fact of hyperæmia existing at that time; passive enlargement and active dilatation, alike opposed to analogy and insufficient for the explanation of all the phenomena produced, we infer that it is not by causing altered calibre of the capillaries in

* Capillaries are mere tubular excavations in tissues without any distinct membranous walls, (Mr Addison;) they possess distinct membranous walls, presenting remains of nucleated cells here and there in their substance, (Henle;) not merely distinct walls, but a double muscular coat, consisting of transverse and longitudinal fibres, (Dr Hughes Bennett.)

the first instance, that the vascular nerves indirectly influence the changes therein occurring.

For anything we know to the contrary, the nervous influence may cause contraction of muscular fibre by calling natural affinities into play. There is therefore nothing extravagant in assuming that the vascular nerves may cause an afflux of blood by exciting an increased exercise of the attractions and repulsions naturally and independently going on in the capillaries. Whether these molecular actions depend upon the conversion of blood into tissue, the separation of secretions in secreting organs, the change of arterial into venous blood, or, as is most probable, upon all these processes together, it is fully more philosophical to suppose that changes so extensive though so minute would be attended by some manifestation of attraction, than not. We have proof that these molecular changes, and the phenomena of attraction which attend them, can be affected in various ways. The elaboration of chyle and its conversion into blood take place doubtless without any assistance from the nerves. The constancy of such an arrangement as shall insure the passage of the chyle through numerous minute vessels before its reception into the blood, certainly implies that some kind of influence is exercised upon the chyle through the walls of the lacteals, especially in the mesenteric glands. There is no reason, however, for ascribing this influence to the nerves. With more probability it may be considered analogous to the changes occurring in the placenta between the impure fœtal and the purer maternal blood. The effect of animal poisons, and the alteration in the relative amount of the different constituents of the blood under various forms of diseases, the sudden augmentation of fibrin in sthenic inflammations, for example, evince a susceptibility to be readily affected in undergoing their changes, on the part of the blood-molecules. Similar facts occur in the vegetable kingdom. Humboldt noticed that, in a lettuce or euphorbium destroyed by a lightning, there is no such oozing out of milky fluid from the cut stalks as otherwise takes place. Here electricity instantly destroys vital molecular changes analogous to those presumed to occur in the capillaries of an animal. If the electric agent can do this, surely the equally subtle nervous force must have a similar power. The abolition of muscular contractility, the cessation of the circulation through the capillaries, and the non-coagulability of the blood simultaneously and instantly induced in some cases of sudden death from shock, which could act only through the medium of the nervous system, prove that it has. If, acting in an extreme degree, the nervous system can instantly and completely put a stop to all the molecular actions of life, when acting in a less degree it must be capable of modifying them. As an hypothesis, therefore, capable of explaining all phenomena referrible to the nervous system, so far as physical action is concerned, and apparently open to fewer objections than any other, we infer that the nervous force can stimulate every living molecule endowed with a certain function, to the more active discharge of that function; that it can consequently excite, variously modify, or greatly derange, all vital actions; that muscular contraction, cell-metamorphosis, the evolution of animal heat, are influenced by the nerves in precisely the same manner, the difference in result being due to inherent difference of vital endowment in the molecule subjected to the nervous influence; that the varied fulness and therefore the calibre of the capillary blood-vessels is secondary to, and dependent upon, the activity of the molecular changes going on in their contents, and under the control of the nerves only in so far as these affect the vital actions of the blood.

The proofs that the ganglionic nerves are the organic nerves; the relation of the ganglia to other nervous centres; and the extent of their normal influence on the vital processes, remain to be considered.

Holmes Chapel, Cheshire,
May 16, 1846.

PART THIRD.

The ganglionic nerves are the organic nerves for all the tissues, excepting, probably, the nervous and the muscular.—We have proof sufficient that the nervous centres for intellect, sensation, and muscular motion, exist in the cerebro-spinal system. All the nervous centres, except one, have functions correctly assigned to them. All the known functions of the nervous system, except one, have their nervous centres ascertained. The exceptional function, (viz. the control and harmonization of the many and various molecular actions classed as the organic processes,) must belong to the exceptional nervous centre, (viz. the ganglia in the aggregate).

In this syllogism, however, as in the remarks which preceded, the following important physiological points are taken for granted. (1.) That the different portions of the cerebro-spinal axis really have the functions which physiologists *agree* in assigning to them. (2.) That the ganglia are in no way directly essential to the discharge of these functions. (3.) That the superintendence of the organic processes is a function of some nervous centre. (4.) That the ganglia are anatomical nervous centres, and taken collectively may be viewed as one great nervous centre, just as the numerous spinal segments are considered to constitute the spinal centre.

Of these, the first will be admitted, and the second and third have already been noticed. The fourth, although now very generally allowed, is by no means so firmly established as to render its discussion superfluous.

To decide whether a ganglion possess the anatomical characteristics of a nervous centre, we must ascertain the exact arrangement of nerve-tubes and cells in parts acknowledged to be sources of nervous power. The difficulty of doing this is due less to the minuteness of the objects, than to their great delicacy and softness, rendering the more common modes of preparation for microscopic examination unsuitable. After failure in repeated attempts on portions of nervous tissue treated with alcohol, diluted acetic acid, or saline liquids, the following plan was pursued with more success. The thinnest possible slice was carefully removed on the edge of a sharp razor from some portion of the nervous system of an animal *just killed;* always, in the higher classes, whilst the body was quite warm. This slice was placed on a piece of thin glass, and examined sometimes uncovered, sometimes covered by another piece of microscopic glass. To prevent the close adhesion of the nervous slice to the glasses, which occurs when there is great difference of temperature, and causes any movement of the glasses upon each other to distort the outline of the objects between them, the pieces of glass were previously dipped into warm water and then wiped quite dry. Occasionally, by gently moving the upper glass upon the lower one, appearances were made out with greater distinctness, and observations, which would otherwise have been erroneous, corrected. Isolated objects displaced around the margin of the rest often presented a well defined outline. Nervous tissue removed before the animal heat is dissipated, for a short time remains more translucent and cohesive, and may be compressed with less separation of its constituent parts than that which by delay has been allowed to "set" before examination. Still, even when quite fresh, if suddenly and forcibly squeezed between the glasses, too considerable a disruption ensues for the observation to prove satisfactory.

To ascertain the relative size of the different objects without measurement, the same power of 300 lin. diam. was used invariably. The figures cannot be trusted as representing the *actual* size, but I believe the relative proportion of the objects is tolerably correct. The greatest care was taken to give the outline of every object with accuracy.

A portion of cerebrum, cerebellum, spinal chord, spinal ganglion, or sympathetic ganglion thus examined, furnished the following objects;

1. A straw-coloured oil-like fluid, forming, under compression, a liquid boundary around all the rest.
2. Semi-opaque white cylindrical nerve-tubes; largest in calibre.
3. Translucent tubules, not varicose; smallest in size.
4. Translucent varicose tubes; intermediate in size.
5. Regular-shaped cells, more or less spherical or ovoid; some nucleated; some without visible nuclei; of all sizes.
6. Irregular-shaped cells with projecting processes, (caudate vesicles).
7. Occasionally, cells with pigment spots.

The white nerve-tubes appear to be almost uniform in size where they leave the sphere of the grey matter, as at the margin of a ganglion, or where the grey joins the medullary matter in the encephalon; also, whenever they can be distinctly traced through all the grey matter of the object under examination. Some of these white tubes, however, in the midst of the nerve-vesicles, become manifestly smaller in calibre, and more delicate in their walls; these are either lost to view amongst the grey cells, or otherwise are seen to be continuous with the varicose tubes. This direct continuity of the straight with the varicose nerve-tubes is not always to be readily made out, owing chiefly to the readiness with which the latter break under manipulation.

The varicose tubes are smaller in calibre in the undilated portions than the straight nerve-tubes, and present, at distances somewhat equal, more frequently otherwise, flask-like dilatations resembling in outline a number of small eggs strung on a string, or a portion of the *Fucus vesiculosus.* The dilatations are often precisely similar in size on the same tube; but not always so. In shape ovoid, their long axis corresponds with that of the tube. Ehrenberg, who first described these under the name of articulated tubes, is understood to have renounced his first opinion that the arrangement is normal, and to now consider the appearance as the result of either *post mortem* change or of manipulation. Even in this case, it has been justly remarked,* the proneness to assume the varicose disposition is a distinguishing characteristic of these tubes.

The following reasons induce us to doubt whether Ehrenberg was not most correct in his original opinion. As these varicose tubes can be seen immediately after death, they are not the result of decomposition; as they can be rendered visible, particularly in the spinal chord, by mere scratching with the point of a fine needle, they are not produced by compression; as smaller and probably more delicate tubes than they, and larger and probably less delicate tubes, maintain a straight cylindrical appearance under precisely the same circumstances as to exposure and manipulation, the varicose appearance cannot be due to greater or less delicacy of texture; as there is no thinning perceptible in the walls of the dilated portion at its greatest circumference, the enlargement cannot be due to mere expansion of the tube from pressure; moreover, by the compression of a varicose tube accidentally isolated, we occasionally produce an irregular-shaped tube, very different from the regular-shaped varicose one; lastly, as Ehrenberg himself remarked, the appearance cannot be due to mere elasticity, since stretching one of the tubes, (which may sometimes be managed rather by accident than design,) will break it, but not cause any alteration in its varicosity.

* British and Foreign Medical Review.

Remak ascribes the varicose appearance to the contraction of a longitudinal central band in the interior of the nerve-tube, but does not explain how this can occasion such regular and uniform dilatations as we actually find. Any alteration so originating would cause an irregular and puckered appearance only. Ehrenberg considered that the nerve-tubes were filled with soft medullary matter, and that the articulated appearance was restricted to the nerve-tubes appropriated to sensation. Remak goes further, and attempts to distinguish sensational and motory nerve-tubes from each other, by anatomical characteristics. According to him, a sensational nerve-tube is minute, has its walls excessively thin, and appears flat, transparent, and varicose ; a motor nerve-tube is larger, thicker, has its walls more resistant, and appears opaque, cylindrical, and merely rugous, not varicose. Remak is peculiar in holding these opinions, which are quite unsupported by microscopical observation. The varicose tubes are found wherever grey nerve-cells exist, in the convolutions of the brain and cerebellum, in the centric and basic grey masses of the encephalon, in the olfactory, optic, and auditory nerves,—which are rather processes of brain than strictly nerves,—in the spinal chord, and in the ganglia. They are never found in the purely white part of the nervous centres, nor in the nerves, with the above exceptions.

In addition to the larger straight nerve-tubes, and the varicose tube, there are innumerable tubules smaller than either of the others, but nearly uniform in size amongst themselves. These are enveloped amongst the cells and granules, appear on the surface for a short distance, and then sink down again, and are so delicate that they break on applying sufficient compression to expose a single layer of them. On this account their examination is difficult. I have traced some of them into a caudate vesicle, but I could never succeed in making out their connection with either straight or varicose nerve-tubes.

The regular-shaped cells are met with of all sizes ; they are either spherical, ovoid, or pyriform in shape ; most commonly the first. The greatest variety as to shape, size, and arrangement is to be seen in the grey portion of the pituitary body, just where it is joined by the infundibulum. Here the number of nerve-tubes is comparatively small, and the vesicles are therefore less obscured than elsewhere. The nucleus often appears to project at one portion of the parent cell, rendering the outline that of two very unequal circles, like a section of the human eye through the cornea. When two nuclei exist, they generally form two prominences at opposite points of the cell. Some cells, which are yet not caudate cells, present very irregular shapes, as if one end had been pushed out into a pouch-like process more or less elongated. Occasionally an object is presented, which looks as if it had been made by two cells becoming joined together by such a process from one cell having opened into another cell, producing a sort of "dumb-bell" appearance. Here and there may be noticed a pyramid of cells, progressively diminishing from the basement large cell to the small one which forms the apex. On gently moving the glasses, the pyramid of cells is found to move altogether, as if some bond of union existed between them, but this may be accidental, or due to common physical attraction only. The smaller cells are frequently arranged in lines, like a row of beads; or in clusters around the nerve-tubes, like the grains in an ear of Indian corn.

The nuclei vary greatly in size. When sufficiently developed, and viewed in an isolated cell, the projecting nucleus appears to be itself a distinct cell, the outline of one segment of its sphere being visible through the wall of the parent cell, whilst the remainder is external. In some cells there is no projecting nucleus, but one or more round bodies are seen in the interior of the parent cell, which then, except as regards the number of the contained bodies, somewhat resembles the common *volvox globator*. As these internal nuclei are motionless under examination, it is difficult to decide whether they are free or not. But since they present an unbroken spherical contour when viewed through the wall of the parent cell, they probably are free and unadherent. I have never noticed more than three of these secondary cells in one parent cell.

The pigment cells keep together in little clusters when the upper glass is moved upon the lower, in examining the specimen between two glasses; but it is difficult to infer what may be their normal arrangement and relative position to the other parts in a nervous centre. I think, however, that they abound most where the white nerve-tubes separate from each other, as at each end of a spinal ganglion. They are abundant in the *locus niger* of the *crus cerebri*. The pigment spots bear some analogy to the dark granules in vegetable spores and pollen-cells.

The small granules, which are probably minute cells, encrust the tubules, forming a complete bed for them, and filling up the interstices of the other tubes and cells.

The most interesting objects are the irregular cells with projecting processes, appropriately designated by Todd and Bowman "caudate vesicles." In size, shape, and number of processes, they vary greatly. They are large in the spinal chord, and in the ganglion of the vagus, small in the cineritious substance of the brain. The size of the vesicle appears to bear a direct proportion to the number of processes connected with it. The processes seem to be small tubes, resembling the tubules above referred to, which they probably are. Sometimes one or more processes may be distinctly traced from one caudate vesicle to another, being then intervesicular, or merely commissural as regards the vesicles. Another process may be seen to pursue a longer course, and then to become varicose. I have never happened to see more than two processes which thus became varicose connected with one caudate vesicle; this may indicate the truth, or may be owing to the difficulty of following the tubules for any distance, since when a caudate vesicle is isolated, its processes are broken off at various lengths; and when surrounded by other cells, its processes are readily lost to view by dipping amongst the rest. These varicose vesicle-processes do not differ in size, or in any other obvious respect, from the varicose tubes. In ganglia I have clearly distinguished direct continuity between a nerve-tube emerging from the ganglion, and one of these varicose tubules leading to a caudate vesicle. I have seen the same in the spinal chord between the caudate vesicles and the nerve-tubes of the spinal nerves; but I have not succeeded in detecting this connection in the grey matter of the cerebral convolutions.

The assumed discrepancy in the observations of the older microscopists was less owing to actual error than to a spirit of exclusiveness which would not acknowledge the co-existence of a variety of appearances in the same object, certain of which proved most striking to one observer; certain others to another. Thus the thin, translucent, irregular-sized globules of Leeuwenhoek; the rows of granules of Della Torre, and of Prochaska; the roundish corpuscles lying amongst intestine-like convolutions of nerve-tubes, described by Fontana; the globules, fibres, and albuminous fluid of Bauer and Home,—are all to be seen, and are doubtless for the most part the same objects seen with various degrees of accuracy.*

In noticing the various appearances presented by the grey cells, it is difficult to avoid the conjecture, that we are viewing nerve-cells in all stages of growth; that the mere granule is the early stage; the large cell with its contained nuclei, or its pouch-like bulging, the mature stage. That nerve-cells are generated in the two ways so universally manifested in cell-life, viz. by budding from the side of a matured cell, and by the rupture of a parent cell setting free the lesser cells previously contained within it. Certain longitudinal loop-like arrangements, met with especially in the ganglia of the fœtus, lead us to admit the conclusion of Schwann, that the tubules originate in the linear apposition of cells, which afterwards open into each other, as in the genesis of the vascular tissue in vegetables.

The grey part of nervous tissue is now admitted to constitute

* See an Analysis of Ehrenberg's Views by Dr Craigie, Ed. Med. and Surg. Journal vol. xlviii. p. 257.

the force generating, the dynamic apparatus. How is the *vis nervosa* transmitted from the grey cells into the white tissue? Those who believed that no direct communication could be made out between nerve-tubes and nerve-cells, but that the sole relationship consisted in the close apposition of the two kinds of nervous tissue, must have assumed that the nervous force passed through the walls of the nerve-tubes, or else along the exterior only of these tubes. But if every nerve-tube terminate by opening into a caudate vesicle, there would in this way be a direct continuity of internal surface between cell and tube, (force-generator and duct.) And impossible though it is to demonstrate that all the white nerve-tubes open into vesicles, it is most probable that they do so. We cannot at least discover any other mode of termination for them in any nervous centre. By one physiologist, the nerve-tubes are stated to end in loops amongst the grey matter; by another, in bulbs; by a third, in division into smaller tubes or fibrils. Such appearances are easily seen, but are in reality, I believe, fallacious. All nerve-tubes that can be distinctly traced to their natural termination,—and they are very few,—open into caudate vesicles. A nerve-tube is never seen to join another without the existence of a dilatation at the point of junction, constituting an irregular-shaped cell, larger or smaller, according to the number of tubes joining; hence the caudate vesicle is the only medium of communication between the nerve-tubes. Still the great number of regular-shaped grey cells into which no tubes can be traced, their close application and intimate connection with the nerve-tubes, and the translucency, greater delicacy and smaller calibre of the tubes themselves whilst surrounded by the grey vesicles for some distance after their connection with caudate vesicles, render it extremely probable that the regular-shaped cells of all sizes generate nervous force, which passes through the walls into the interior of the nerve-tubes. There is good reason for considering that the white matter of Schwann, (the white coat of the larger nerve-tubes), acts as a non-conductor, obstructing the transfusion of nervous force during its passage along the interior of the nerve-tube. If this be granted, it is a fair assumption that the grey tubes, tubules, and caudate vesicles, as they do not possess this white coat, will allow the force generated by the cells around them to permeate their walls. The varicose tube has no white coating, and is found only amongst the grey cells. May not the flask-like dilatations be a normal arrangement for the purpose of exposing at different points a greater extent of surface to the surrounding grey cells, than the mere ordinary calibre of the nerve-tube would permit? Are not the caudate vesicles and varicose tubes permanent structures; whilst the nucleated cells are temporary, and evolved rapidly during the functional exercise of nervous tissue? The caudate vesicles may perhaps be compared to central termini, where different lines join, and where the chief supply of power is furnished; the varicose dilatations to side stations where additional force may be obtained.

The larger nerve-tubes have been characterized as semi-opaque and white. It would be more correct to say that they have a great tendency to assume these peculiarities, since when perfectly fresh, they are neither white nor opaque, but become so even whilst under examination,—just as the retina, though perfectly transparent during life, becomes white and opaque after death.

On compressing a portion of any white nerve-cord, the cut ends assume the appearance of a woolly mop. This is owing to the squeezing out from the white nerve-tubes of innumerable small granules, not distinguishable by myself from the gray granules so abundant in the nervous centres. Is the central band or axis of a white nerve-tube made up of these granules linearly disposed? And, is each granule itself a minute nerve-cell? On examining a nerve-cord in a living animal, (in the axillary or inguinal regions, for instance,) or in one just killed, before the neurilemma has lost its transparency, each nerve-cord is seen to consist of the nerve-tubes invested with a finer and inner membrane, forming a longitudinal fasciculus, which is either bent upon itself in a zig-zag manner, or otherwise coiled round in the canal of the denser outer neurilem, with its spirals so close as to present a zig-zag appearance. The light is so much refracted by the glistening surface of the object under a lens, that I could not satisfy myself which was the true arrangement, *i. e.* whether the angles of flexure were sharp or obtuse. When a nerve-cord is about to divide into two or three smaller ones, the requisite number of fasciculi first appear by the nerve-tubes separating into bundles, which are at first intertwined altogether, but by degrees become distinct, lying side by side, and each presenting the zig-zag arrangement. Hence we may see one larger line of zig-zag flexures splitting into three smaller lines of zig-zags, each of which presently obtains a distinct outer neurilem, and is then a distinct nerve. If one of these nerves has its outer sheath scratched through, and its zig-zag nerve-fasciculus drawn out, the latter remains elongated, and looks opaque and fleecy, the zig-zag appearance being lost. Hence the arrangement is not due to elasticity of the inner sheath. As this zig-zag arrangement allows at least three lengths of nerve-tube to be contained in one length of the external neurilem, it must be subservient to some other purpose besides that of obviating injury from sudden stretching of the nerve. Like the convolutions of the cerebrum, the laminæ of the cerebellum, the striæ of the *corpus striatum*, the curl of the *corpus rhomboideum*, or the lobules of a gland, these flexures will permit of a greater extent of surface in a given space, than could be otherwise obtained. The interior surface of each nerve-tube is thus rendered very extensive, whilst the tube itself is most conveniently and safely packed. If we decline to admit that the minute granules contained in the nerve-tubes do of themselves generate nervous force sufficient, speaking metaphorically, to change the nerve for conduction, we must allow that, by the arrangement described, a certain accumulation of nervous force is favoured.

The zig-zag appearance being invisible as soon as the outer sheath has become opaque, is not to be seen in the ordinary dissection of the human body, but it is distinct in the nerves of a limb just amputated. I have found it to be presented alike by spinal and cerebral nerves, with the exception of the olfactory, the optic, and the auditory; by sensational and motor nerves, when not so large as to preclude it by their density; and by the roots of all the spinal nerves. It is met with in the calf, sheep, dog, cat, fox, horse, ass, hare, rabbit, guinea-pig, hog, rat, mouse, and weasel; in the pigeon, owl, rook, duck, goose, and fowl; in the frog, and water-newt; in cod fish, skate, trout, carp, and eel; and may therefore be considered constant in the vertebrata.

Valentin doubts whether the inferior ganglion of the vagus be really ganglionic at all. In the young rabbit, I have found it a very good source for furnishing characteristic specimens of the general structure of a ganglion. Slices suitable for examination between glasses are conveniently obtained from the spinal ganglia in the frog, from the sympathetic near the psoas-muscle in any small young animal, and from the ganglion of the vagus in the eel, and in fish generally. In water animals the connecting tissue seems looser, and the nervous elements separate on the slightest pressure. The apparent anatomy of the Gasserian ganglion gives a good idea of the minute arrangement in a spinal one. The white nerve-tubes of the posterior roots of the spinal nerve separate immediately on entering the ganglion, and cross each other at an acute angle. After passing through the substance of the ganglion, they come together again, and, accompanied by additional nerve-filaments from the gray cells of the ganglion itself, emerge in as many fasciculi as there are primary divisions of the compound nerve formed subsequently by conjunction with the anterior root. The nerve-tubes of a given fasciculus come out of the ganglion at different points; so that, dividing the anterior margin of the ganglion into upper, middle, and lower portion, a fasciculus which leaves the lower part derives nerve-tubes from the upper and middle divisions as well, and *vice versa*, producing in this way a crossing of nerve-tubes, intricate in proportion to the number of fasciculi. Some nerve-tubes pass round the sides of the ganglion in a curvilinear manner, but not, as far as I could ascertain, so as to form any regular boundary. When compressed, the larger nerve-tubes keep together in bands, leaving the other parts of the ganglion in the interspaces, and hence the normal arrangement cannot be thus ascertained. Enough, however, may be distinguished to justify the statement that the nerve tubes are closely connected with, and imbedded in, a nidus of cells, granules, and caudate vesicles, or, in other words, of cells of various kinds. A nerve tube accidentally isolated is often seen to have a string of cells applied along its walls.

I have thought that the nerve-tubes appeared rather smaller in calibre, and their walls thinner whilst passing through the ganglion; but I am not satisfied of this, and cannot trust my own attempts at measurement. I have never seen a white nerve-tube terminate in a ganglion, either by opening into a vesicle, or in any other way. If not broken under manipulation, nor lost by its disappearance under other objects, every nerve-tube entering from the spinal cord could be traced through the ganglion without interruption of its continuity, and without becoming varicose. The varicose tubes are less numerous in the ganglia than in the brain and spinal chord, and are never noticed beyond the extent of the grey ganglionic matter. Small non-varicose tubules are seen running in every direction, but to the greatest extent across the course of the larger nerve-tubes. Thus, whilst the latter pursue for the most part a longitudinal course through the ganglion from end to end, the former chiefly pass transversely from side to side. I have never seen these tubules become continuous in the ganglia with the larger nerve-tubes. When traceable at all, they have terminated here as elsewhere in caudate vesicles. Irregular ring-like arrangements of caudate cells and their intervesicular processes, are occasionally observed. Examples are figured from the cœliac ganglion of the kitten, and from the Gasserian, vagus and spinal ganglia, and from the brain in the rabbit.

Some stress has been laid on the obvious difference in external character between the spinal and the sympathetic ganglia.* The spinal ganglion is regular and uniform in shape and size, and constant in its relation to its afferent and efferent nerves. The sympathetic ganglion is irregular and variable in shape and size, and inconstant in its relation to the nerves connected with it. Processes of grey semitransparent nervous tissue are seen emerging from a sympathetic ganglion; in a spinal ganglion no grey fibres leave separate and distinct from the fasciculi of white nerve-tubes. Microscopic examination proves that whilst in a spinal ganglion the white nerve-tubes are arranged with regularity—a given number entering at one extremity, and leaving at the other; in a sym-

* Procter on the Sympathetic, p. 29.

pathetic ganglion, the white nerve-tubes enter and leave in any and every direction; some passing straight through several ganglia in succession before they are finally distributed; some leaving every ganglion immediately for their destination. The sympathetic ganglia anatomically differ from the spinal, therefore, in the less regular course of the white nerve-tubes through them, and in the greater predominance of grey cells and tubules. The white nerve-tubes transmitted have no closer connection with the grey cells than in the spinal ganglia; they never terminate in the sympathetic ganglia. The fibres of the sympathetic grey nerves, gelatinous fibres as they have been termed, differ from the white nerve-tubes in the following respects. (1.) They are smaller in calibre. (2.) They have occasionally flattened bodies here and there in their course. (3.) They are translucent, and of a yellowish grey, or pale straw colour. (4.) They do not present a double outline of walls. (5.) They are straight in their course, and are not arranged in a zig-zag manner.

It is difficult to decide whether these fibres are tubular or solid, since their small calibre, their delicacy and translucency, prevent the defined double outline of the larger white nerve-tube. It may be that the ganglionic nerve-fibre is not essentially different from the white nerve-tube, excepting in the non-possession of the white matter in its walls. We may conjecture that the white nerve-tube insulates the force it conducts; whereas the grey one does not; that the white allows, from its flexions, of more accumulation than the grey tube. The nerves of animal life must act with suddenness and intensity. The organic processes require a more gentle, gradual, but persistent supply. To perceive a pin's breadth, or the traction of a single hair, a sensational nerve-tube must have its action insulated; and to convey commands to a given muscle, the motory nerve-tube must be capable of acting singly, or almost so. But there appears no such necessity for the purposes of an organic nerve. In health, uncontrolled by sensation, not necessarily affected by voluntary movement, a secreting surface does not require that one point only shall be influenced at one time by its organic nerves. All the nerves from the same ganglion supplied to it may act in concert without inconvenience. If one is required to act, all may act. Hence, not only is insulation of the organic nerve-filaments not required, but the absence of it is possibly a means of ensuring regularity and consentaneousness of action.

Distribution of the ganglionic nerves.—Whenever a ganglion is situated near to an artery, its nerves apply themselves to the coats of the blood-vessel, intertwining around it "like ivy round the oak." Hence, Soëmmering termed the sympathetic, par excellence, the nerve of the arteries. But the general fact of anatomical connection is no proof of this, since the nerves might attact themselves to the arteries merely as furnishing them convenient guides and supports to their common destination. Nor can any direct argument as to function be drawn from the fact, that "the great sympathetic bears a strict relation in its development, to the activity and force of circulation in the four classes of vertebrata, in whom alone a red-blooded circulation exists,"* since such increase of energy in the vascular system is always accompanied by a corresponding augmentation of the sensorial and the other higher endowments. But when we find that wherever any additional vascular apparatus exists, it has invariably a corresponding supply of ganglionic nerves, *e. g.* the free distribution of nerves to every *rete mirabile*, whether in the neck, as in ruminants, in the spinal canal, as in cetaceæ, or in the thorax, as in the porpoise, there appears to be some ground for assuming a functional relationship between the ganglia and the blood-vessels. The sympathetic and the ganglionic system in general, throughout the vertebrate series, are not developed in accordance with mere activity of nutrition, but in exact proportion to the degree in which organic activity requires to be varied in response to the wants of the system. This coincidence is so universal that it must point to the truth. And when we find, moreover, that in each individual animal, the situation and connexions of the ganglia correspond to the same anatomical law, we have particular instances to confirm the general observation. The secretion of hair requires greater nutritive action than the ordinary performance of the other functions of the integument; yet the scalp has no extraordinary supply of ganglionic nerves. The formation of scales must demand considerable organic activity in the outer covering of the fish, yet so small are the spinal ganglia in osseous fishes, that their very existence has been questioned. They are more developed in the sharks and rays, which must be considered as decidedly the highest of the fishes. In craftiness, courage and determination in the pursuit of prey, they clearly evince superiority of mental endowment. They have the integument covered here and there with irregular rough scales, or with pointed tubercles, but are not, like osseous fishes, completely enclosed in a scaly coat of mail. Hence, the surface is more impressible, and the dermoid mucous secretion more under the influence of external impressions. In the crocodile, tortoise, and snake, covered in as they are with scales, horny shields or bony plates, the spinal ganglia are small in comparison with what we meet with in the naked amphibia. In the toad, frog, and water-newt, the delicate, sensitive, and vascular skin is largely supplied with glandular follicles. The spinal ganglia in these reptiles are very large. The acrid nature of the secretion on a toad when

* Langston Parker.

alarmed or irritated, may exemplify altered organic activity produced through the medium of the spinal ganglia. The transition stage of Batrachian reptiles is the analogue in vertebrata of insect metamorphosis in invertebrata, and furnishes equally interesting additions to our knowledge of the nervous system. In confirmation of the above, we have the spinal ganglia proportionably more highly developed in the reptile stage (full grown frog), than in the fish-condition of the same animal (tadpole). Ganglionic plexuses accompanying the visceral arteries in fishes are most distinct on the stomach, generative organs, and swimming-bladder. The functional activity of the two first is manifestly subject to frequent variation. That of the swimming-bladder is probably equally so. Whether it be subservient or not to the aëration of the blood, this viscus is unquestionably a floating or sinking organ under the control of the animal, which by muscular compression can at will increase the density, or, where the existence of a valvular opening into the gullet permits it, cause the expulsion of the contained gases. The refilling of the bladder, or the rarefaction of its contents in consequence of diminished pressure, by which the fish is enabled at pleasure to lessen its specific gravity, and thus rise to the surface at a small expenditure of muscular power, necessitates a consciousness on the part of the animal of the existing state of the swimming-bladder. Hence nerves of sensation from the vagus are furnished. A beautiful network of arteries and veins ramifies between the coats either over the whole of the bladder, or otherwise, is collected in the form of a vascular mass at one spot. In either case, ganglionic nerves proceed to this vascular apparatus. Acting, as it were, under the dictation of sensation, or, if not that, at least of spinal perception, the nerve-tubes supplied by the vagus pass through the ganglia which furnish the ganglionic filaments. In the same way ciliary twigs from the third nerve pass through the minute ganglion, which constitutes the bell-shaped nodule known as the *Campanula Halleri*, on the vascular falciform process in the eye of the sturgeon, and of some osseous fishes. Birds cannot have any great amount of cutaneous sensibility, yet their spinal ganglia are large in proportion to the size of the body. When we consider, however, the periodical variations in the state of their plumage, the half-moulting in spring, the entire moulting in autumn, and the extent to which experience shows the appearance of the bird is affected by its general health, there is sufficient reason for concluding that the highly organised feather-bulbs are materially influenced by the state of the internal organs. Besides this, several portions of the surface where much friction takes place have no feathers, but are soft, moist and covered with down. Here the integuments may differ but little from those of man in their functional endowments. The complexity of the structural arrangements for the formation of feathers should not of itself, if the principle laid down be correct, require any additional development of the inter-vertebral ganglia, and cannot therefore be an explanation of it. There is no stronger anatomical argument against the view that nerves are essential to extensive nutritive actions, than the comparative paucity of ganglionic nerves furnished to the organs of generation in the female of all vertebrate animals. These organs are endowed with ganglia sufficient to subject their nutritive processes to the influence of the rest of the economy, but in no degree adequate to superintend the minute atomic changes going on, for instance, in the myriads of ova contained in the ovary of a cod-fish or a herring. If this be true, what purpose could be subserved by the ganglia of the gravid uterus enlarging during gestation in mammalia? They have not to furnish the power, the *vis formativa*, required, but merely to be the media through which vascular activity may be modified. For this, their normal size and relation to the blood-vessels would, theoretically, appear sufficient. I have dissected an ape, whose uterus contained two full grown fœtuses, without being able to perceive any increase of size in the ganglia supplying the parts. The spermatic nerves of the common sparrow undergo no apparent change during the excessive alteration in the magnitude of the testes, which takes place in the spring. In January the testes are the size of pin-heads; in April they are as large as small marbles (Hunter).

In the common fowl, during the period of laying, the transparent membranous connections of the left generative organ permit the nerves to be easily made out immediately after death. The number of ova of all sizes from the grain-like ovulum to the perfect egg, the great vascularity of the outer membrane of the larger ovisacs, the injected vessels in the ruptured calyces which are undergoing absorption, the secretion of albumen by one portion of the oviduct, the deposition of shell by another, and the constant production of lubricating mucus by the whole, sufficiently evince how extensive must be the organic processes constantly proceeding. Yet the ganglionic supply is not large: nor to common observation is it at all greater than when the ovary is inactive. White nerve-tubes are sent to every part, but most freely to the oviduct. A small ganglionic mass connected with the semi-lunar ganglia furnishes the grey nerves, which radiate towards every portion of the oviduct, but are chiefly distributed to the grape-like ovarium. The numerous white nerve-tubes are also derived from fasciculi which had previously passed through the semi-lunar ganglia. They all pass through the ovarian ganglion before diverging, like the intestinal nerves in the mesentery, in their course between the layers of the musculo-membranous mesometry which ties down the oviduct. The lowest portion of the duct, viz. that between the calcifying dilatation and the cloaca, has in addition white nerve-tubes from the lumbar nerves which do not pass through any ganglion. The most important part of the generative organ, the ovary, in which the first step towards the development of the future animal takes place, is more influenced than the rest by other organs. It has therefore a larger proportion of ganglionic nerves, through which its organic actions may be affected. Having no muscular power, it requires no motor nerves; but in order to communicate its own state to the rest of the system, percipient nerves are necessary; hence it possesses some white nerve-tubes. As any excitement of the ovary requires increased nutritive activity of the part, the white nerves pass through the ovarian ganglion in order to call into co-operation the organic nerves on every occasion. The involuntary movements of the oviducts require a large supply of motor nerves. There are, therefore, white nerve-tubes in greater quantity; and as in proportion to the necessity for active muscular movement will be the necessity for liberal secretion of the required products, so also do the motor white nerves pass through the source of the ganglionic nerves of the oviducts. But as the final expulsion of the egg when perfected may be conveniently left to the will of the animal, the lowest portion of the expelling tube is furnished with non-gangliated nerves, which we may assume to be nerves of voluntary motion. It is obvious that if the ganglia supplied nerves for involuntary muscular motion, the arrangement here would be misplaced. More grey nerves should have proceeded to the muscular parts, and fewer to the non-muscular, which is the reverse of the fact.

From the general distribution of the ganglia we may justly infer that some very intimate functional connection subsists between these nervous centres and the blood-vessels, yet to define the precise nature of the relation we require to know the exact termination of each portion of the compound ganglionic nerves. Our information on this point is at present very imperfect, but as far as it goes, it supports the supposition that purely ganglionic nerves are never destined for muscular fibres, but terminate exclusively in capillaries or secreting structures. By the use of diluted acetic acid, Purkinjé has succeeded in rendering the pia mater of the spinal chord so transparent, that its nerves become visible to the naked eye. "A most beautiful network of the finest nerves" presents itself, the filaments of which belong to the vegetative system. Their discoverer has not been able to find any connection between these filaments and the roots of the cerebral or spinal nerves, though if any such existed, it would be easily discovered, from the greater size of the nerve-fibres of the cerebro-spinal system. " A part of these nerves are connected with the delicate coverings of the spinal chord by the anterior, and others by the lateral spinal arteries which pass in pairs through the spinal (intervertebral) foramina. In both cases they appear to arise from the sympathetic system." In the cranial dura mater, " the largest collection of these nerves are to be found close to the anterior, middle, and posterior arteries where they enter this membrane, and it is not very difficult to trace them running with the arteries back to their origin in the sympathetic system. In the dura mater of the spine I have not found a trace of nerves." The Professor, however, proceeds to explain that this remark applies only to the dura mater proper, which separately surrounds the chord ; whereas the outer of the two layers into which the cranial dura mater splits at the *foramen magnum*, and which is applied to the walls of the vertebral canal as a periosteum, is largely supplied with fine nerve-filaments, which appear to communicate with the sympathetic system through the intervertebral foramina. The cornea, the periosteum of the tibia, and several other non-muscular tissues were found to be furnished with similar nerves.* Purkinjé has not at present detected them in serous membranes; but Bourgery states, that " he has observed in great abundance the nerves of serous and synovial membranes ;"† and Mr Rainey believes that he has detected not only filaments, but ganglion-globules also, in the arachnoid. He considers, moreover, the supposed epithelial cells situated on the choroid plexuses to be in reality ganglionic vesicles. The choroid plexuses are, unless Mr Rainey's observation be correct, a remarkable instance of *retia mirabilia* unsupplied with nerves. I have failed in my attempts to distinguish either nerve-corpuscles or filaments in the choroid plexuses, and Purkinjé states that no trace of nerves can be found in them ; notwithstanding, therefore, the superiority of positive over negative evidence, to my own mind the question is undecided.

Whether the ganglionic nerves end by forming loops, in free extremities, or in bulbous enlargements, is entirely unknown. But whatever may be the precise mode of their peripheral termination, it is quite certain that, in common with all other nerves, they must exercise an influence beyond the absolute extent of their nervous filaments. To doubt this is as unreasonable as it would be to question whether the organizable constituents of the blood extend beyond the limits of the vessels which convey them. As the nerves have no other object but that of affecting non-nervous textures, the nervous force must of necessity be imparted to other tissues than the nerve-tubes which conduct it. And if communicable to one living molecule, it may be to many. Hence,

* Dr Gull's Translation, Medical Gazette, 1845.

† Ranking's Abstract, vol. xi.

Reil's idea of a "nervous atmosphere" is far from absurd. Bichat objects that it is vague and indefinite. It is so as regards our knowledge of its extent of operation, and of its possible variation. But there is little to cavil at in the expression, and nothing vague in the thought. Without emanation of influence of some kind, the ascertained power of the nervous system would be inexplicable. How could a motor nerve affect muscular fibre unless its energy, whatever its nature, proceeded out of the nerve to the muscle? How could an organic nerve affect a cell unless its force were communicated by the nerve to that cell? The nature of the force is unknown. So is the nature of light and heat. But as matter cannot be illuminated or heated without the communication of these, so it is impossible for a gland or a muscle or a secreting membrane to be influenced in the least by the nerves, unless the nerves can send out from themselves the force they convey. It would be interesting to find that all nerves, cranial, spinal, and ganglionic, are alike divested of their insulating walls at their ultimate terminations. The incomplete information at present possessed certainly favours the supposition. Hannover and Kolliker state that the peripheral filaments of the encephalic and of the spinal nerves become so much finer as to be with difficulty distinguished from grey ganglionic nerve-fibres. In the Pacinian corpuscles, the entrant nerve loses its double contour and white wall the instant it reaches the inner capsule, and is thenceforth a grey fibre. In the cutaneous and lingual papillæ the nerves are seen to become grey ere they are lost to view. In the superficial follicular bodies discovered by Savi in the electric torpedo, the sensational nerve-twig is stated to enlarge within the follicle, to supply filaments to the contained granular matter, "which nearly resembles the amorphous grey matter of the cerebral hemispheres," and to emerge much reduced in size; but whether or not it is divested of the white matter of Schwann is not remarked.*

The final loops of muscular nerves are not stated to be deprived of their insulating walls; but from Mr Bowman's researches we glean the important fact, that mere areolar tissue can offer no obstacle to the passage of nervous influence, since the sarcolemma in every instance separates the muscular from the nervous fibre. Unless the *vis nervosa* can pass from the generating nerve-cell into the nerve-tube, we can understand nothing of the origin of nervous force; and unless it can pass out of the peripheral portions of the nerve-tubes, the undoubted effects produced through the medium of the nerves are unaccountable. We can demonstrate neither; but we must admit both. If, in addition, there be no reason to doubt that the *vis nervosa* is one and the same kind of force by whatever centre generated, it is fair to assume

* Art. Pacinian Bodies: Cycl. of Anatomy and Physiology.

that all delicate tissues in immediate contiguity to grey nerve-vesicles will be more or less under the direct influence of those vesicles. Hence the non-necessity for ganglionic nerves in the *plexus choroides.* It is no refutation to assert that this is mere conjecture. It is not open to positive proof, and should be estimated solely by the reasonableness or groundlessness of the argument.* It would also result, that although the ganglionic nerves be especially the organic nerves, yet their presence is unnecessary for the purpose of regulating nutritive activity where any other kind of nerve exists divested of its insulating white matter; provided no very intimate consent of action with other tissues supplied with ganglionic nerves is required. The molecular changes of nutrition in muscle may therefore be modified directly through the medium of the muscular nerve; the nutrition of sentient papillæ in the tongue and skin, and of the tissues of the Pacinian bodies, through the sensational nerves. The nutrition of these parts needs modification in accordance with the discharge of their respective functions only. It is quickened in activity when the muscular nerve excites contraction, or when the sensational nerve fits the papilla for receiving impressions. It is not susceptible of frequent alteration independently of these nervous actions, as the secretions of mucous surfaces are, *e. g.* the tongue. If it were, according to theory, ganglionic nerves should exist.

Of the exact mode in which the blood-vessels are supplied with nerves, whether their nerves are cerebral, spinal, or mixed, how they terminate, and where, we are quite ignorant. In the extremities, twigs from the cerebro-spinal nerves which accompany the arteries may be traced into the coats of the vessels, but their actual termination is not known. An anatomical connection between the nerves and the smaller vessels "has been proved by Purkinjé, Valentin, Remak, Henle, and others, who have seen the finest nervous filaments on the wall of the cerebral and other blood-vessels, of less than one-fiftieth of an inch in diameter."†

We find but few simple unmixed ganglia for our notice, but wherever these do exist, their nerves invariably supply either secreting membrane, or vascular tissue; never muscular fibre. Remak has observed purely grey ganglia on the surface of the heart, in the posterior pulmonic plexus, and on the walls of the urinary bladder. Müller and more recently Purkinjé describe similar ganglia in the *corpora cavernosa penis,* where they cannot supply any thing but vascular tissue. Connected with the descending grey fibres from the spheno-palatine ganglion in the sheep, calf, and probably in other herbivora, we may frequently meet with minute, oval, round or fusiform enlargements; grey, translucent,

* See a note in the Lancet for 1846.

† Paget's Report. British and Foreign Medical Review, No. xxvii. p. 288.

and unmixed with white nerve-tubes. The aggregate of the efferent fibres from one of these simple ganglia exceeds in quantity the gray nerve on which the nodule is placed. The purely gray nerve-filaments are distributed to the well-developed follicles on the soft palate.

In the few instances in which supernumerary ganglia have been discovered in unusual situations, they have never been found connected with the filaments of a motor nerve. Mr Swan has occasionally detected a ganglionic enlargement on the branch of the spiral nerve which lies beneath the extensor tendons of the wrist,—a cutaneous nerve. In two subjects,* Mr Pilcher met with "a gangliform enlargement on the internal nasal nerve, where it is lodged on the œthmoidal bone," a sensational nerve.

If the ganglia do exert an especial influence on the organic processes, inasmuch as these are in action whilst sensation and muscular motion are yet scarcely exercised, we should expect to find the ganglia fully developed earlier than either encephalon or spinal chord. Arnemann and Beclard assert that the intervertebral ganglia are the earliest of all the nervous centres in their appearance, at least in birds. This is probably erroneous, but there can be no question that the ganglia generally are proportionably larger than the other centres, in the fœtus. And if essentially independent of both brain and chord, the ganglia will occasionally be present, where, from arrest of formation, both the other great nervous centres are absent. Accordingly, in anencephalous and arachidian fœtuses, we find the ganglia where there is neither brain nor chord.

The anatomical grounds for deciding, first, that the ganglia superintend and regulate the activity of the organic processes; and, secondly, that they do not in any muscle excite contraction; may be summed up as follows. (1.) The ganglionic nerves possess special centres of origin distinct from those which are known to preside over the other functions of the nervous system. (2.) Nerves from other centres (with the exception of a few communicating gray filaments which connect the gray cells of one centre with those of another in some instances) do not terminate in the ganglia, but merely pass through them, and afterwards supply compound tissues in common with the purely ganglionic nerves. This would have been needless if the ganglia themselves were so related to the tissues supplied, that they could ensure perception, sensation, and muscular action. (3.) In their course, the ganglionic nerves are intimately related to the arteries, the carriers of the matériel on which the organic nerves must work. (4.) By their termination, so far as this is known, they are fitted for influencing capillary actions, and the atomic changes in non-nervous

* Grainger in Cycl. of Anatomy, Art. Ganglion.

and non-muscular tissues. (5.) Developmental and abnormal anatomy support these conclusions.

On the other hand, certain recent experiments of Volkmann are considered to have proved that the heart, and the muscular viscera of the abdomen, contain within themselves nerve-centres of muscular motion. Such centres, if they exist, can be no other than the ganglia.

Experimental evidence concerning the alleged motor-power of the ganglia.—By employing the continuous current of an electro-magnetic apparatus, Volkmann believes that he has established the following laws :—

(A.) When an excitor nerve only is electrified, any muscular movement which results is intermitting and orderly, the muscle contracting and relaxing alternately. This kind of muscular contraction may be distinguished as alternating contraction.

(B.) When a muscular nerve is electrified either at its origin, or at any part of its course from centre to muscle, the resulting contraction lasts during the continuance, but ceases on the cessation of the stimulus. Volkmann terms this form continued contraction.

(C.) But when the stimulus is applied to the centre in which the motor nerve arises, the muscular contraction not only continues during the application of the electric force, but persists without remission for some time afterwards. Persistent contraction.

It is very difficult to elicit excito-motory action in any other way than by stimulating the peripheral terminations of the excitor nerves. Todd and Bowman illustrate this by the great excitability of the skin of the thumb of the male frog. On shaving off the papillæ at this part, the susceptibility is lost, and irritation, which before would have caused the animal instantly "to assume the attitude of grasping," is now of no avail. The same fact may be exemplified in another way.

Experiment XXV.*—A large frog was pithed in order to remove the influence of sensation. The skin was stripped for an inch off the right side of the back, so as to expose three cutaneous spinal nerves passing transversely towards the abdominal integuments. A longitudinal incision through the skin in front of the abdomen prevented any interference from the cutaneous nerves of the left side.

134. Irritating with a needle, and twitching the exposed nerve-trunks produced no effect.

135. Tickling and pinching the skin adherent to the abdomen on the right side of the longitudinal incision, and opposite to the reflected flap of thin integument, caused motion of all the extre-

* Whilst these pages were passing through the press, I found that this experiment was almost identical with one of Dr Marshall Hall's. I was not aware of this at the time.

mities. After the lapse of eighty seconds no effect could be produced. Hence irritation of a coarse mechanical kind applied to the nerve-terminations fitly organised to receive such impressions, caused excito-motory action until the nerve-trunks had, by exposure probably, become incapable of conduction; but similar irritation of the nerve-trunks, though applied first, had no such effect.

Where is there a purely excitor nerve which is unconnected from its origin to its termination with motor fibres? The physiological evidence of the existence of excitor fibres is founded on the results of stimulation of surfaces, which could not directly excite motor fibres. But a continuous current of electricity passed along a cutaneous nerve, before it arrived at the central origin, would come in close contact with motor fibres. What proof have we that it affects the nerve-centre at all? It may react along the muscular nerves, to which the excitor fibres of necessity first convey it. The posterior roots of the spinal nerves alone would offer an exception. In applying a continuous current to them, it would be difficult to restrict its influence merely to the short portion of nerve-root. But assuming that the electric current does act through the medium of the nerve-centre, how can we prove that it does so by calling forth the normal action of the dynamic grey cells, and of the motor nerve-tubes to which they give origin? And unless this be established, any result is worthless as regards the function of the nervous centre. It is stated that if the magneto-electric stimulus is applied to the brain or spinal chord, persistent contraction of the voluntary muscles results. For how long a period after withdrawal of the stimulus is not mentioned. I have made many experiments with a rotating magnet, of the power usually employed for hospital patients. So long as the electric influence was carefully restricted in its passage to the grey portions of the encephalon, no muscular motion in any instance resulted. When applied to white matter any movement resulting was alternating or continued, according to the amount of electric force, and the care with which the instrument was kept applied, and the state of muscular irritability of the animal; never persistent. But supposing the fact to be as stated, that a continuous electric current applied to the brain or chord will occasion contraction of some voluntary muscles which lasts for a certain time after ceasing to apply the electricity, this is no proof that the centre itself is acting in a similar manner to its normal mode in the motor nerves. It may be that a greater number of motor fibres destined to a given muscle have been subjected separately to the stimulus, than can be the case where an excitor or a muscular nerve, or, as must usually happen, where a compound nerve alone is stimulated, and thus that the amount of stimulus is greater.

The heart, stomach, and intestines do not present continuous contraction in answer to stimulation of the brain and chord. Volkmann hence infers, that these organs derive no motor fibres from either brain or chord. How much this is opposed to anatomy need scarcely be noticed. Direct irritation of the motor nerve of a volunary muscle causes alternating contraction only, unless the irritation be applied without intermission by means of the electro-magnet. And even with this instrument, when the power is feeble, the muscular contraction, though irregular in its duration, is not uniformly continued as Volkmann asserts. The continuousness of the muscular contraction, therefore, depends not upon any property of the motor nerves, but, *cæteris paribus,* upon the degree and continuousness of the stimulation. At the utmost, then, if well-founded, Volkmann's laws could be useful merely as tests for different nerves, whether excitor or motor, but would add nothing to our knowledge of the normal influence of the nervous centres. They would prove that excitor nerves pass into centres, and motor nerves pass out, and that the entrant nerves of the viscera pass into the visceral ganglia; none of which stands in need of such support. They would furnish new facts as to the behaviour of these several kinds of nerves under the physical stimulus of electricity, but no evidence as to their comportment under the natural stimulus of nervous force. Until excitation of the dynamic nervous tissue by the electric stimulus after death has been established, we have no foundation for assuming that there exists the slightest analogy in the mode in which the nerve-tubes are affected by the two forces. The nervous force travels along the interior of the nerve-tubes, and its transmission is at once stopped by placing a ligature around the nerve. The electric force travels along the outer surface of the nerve-chord, and receives no obstruction from such a ligature. The circumstance of the involuntary muscles, therefore, presenting alternating contraction only, in answer to electrifying the brain and chord, is, if correct as to fact, no proof that the ganglia are motor centres to the viscera; it is a proof merely that the ganglia have a similar relation to the passage of the electric force along the nerves connected with them, to that of the brain and chord in reference to the nerves connected with them. But even this is questionable. The peculiar characteristics of the muscles must be borne in mind. The muscles supplied with nerves connected with ganglia, and the muscles supplied with cerebro-spinal nerves, are themselves different in both structure and endowment. Mr Bowman's admirable researches have proved that striped muscular fibre, when isolated from every vestige of nerve and blood-vessel, will itself contract under irritation; that unstriped fibre will also contract on stimulation, but not precisely after the same manner, although, as far as is known, there is no difference in the kind of molecular change essential to the act of contraction. "Wherever the striated structure occurs, we witness an aptitude for quick, energetic, and rapidly repeated movements; while, where it is deficient they are sluggish, progressive, and more sustained."* The electric force applied to nerves has a two-fold action according to the mode in which it is used. When strictly confined in its course to a small portion of nerve isolated from all the surrounding tissues, it can affect the part to which that nerve is distributed only by stimulating the nerve-tubes to give out their nervous force. But unless great care be taken, the electric force is itself conducted to the distant part, where it acts as a direct stimulus. If we can prove that all the effects on muscles obtainable by the operation of electricity in either of these ways, may likewise be produced by mechanical irritation of the muscles themselves, under circumstances which preclude the possibility of the intervention of any nervous centres, it is manifest that the results arrived at by Volkmann are due entirely to the degree and extent of action of the stimulus, the mode of its application, and to the difference of endowment in the muscles experimented on. Pathology furnishes numerous instances of every variety of muscular contraction suddenly induced by irritation of excitor nerves; from the momentary twitches of the face, (alternating contraction,) to rigid tonic spasm, (continued and persistent contraction.) If the *vis nervosa* and the electric force acted alike on the nervous centre, we ought never to see more than the alternating kind. As we can induce all the three kinds of contraction in a living muscle separated from its nervous centre, the influence of the nervous centre cannot be essential to the production of any of them; and consequently the existence of any one is no proof of either the exercise or the non-exercise of the normal force of a given nervous centre. In this case, Volkmann's inference that the hollow viscera derive their nervous stimulus to contraction from the ganglia exclusively, is unsupported by his evidence. In observations which follow, will be found facts to show that the behaviour of different kinds of muscle *per se* must be taken into consideration. But there are some of Volkmann's inferences in which the relation to his own (assumed) laws is not very clear.

After establishing a law on the logical error that because all reflected movements are alternating, all alternating orderly movements must be reflex, it is inferred that the ganglia are the motor centres to the heart, stomach, and intestines, and that the vagus, spinal chord, and sympathetic furnish excitor fibres to the ganglia, because electro-magnetic stimulation of these occasions "orderly movements of alternate contraction and relaxation," (such move-

* Todd and Bowman's Phys. Anatomy, vol. i. p. 185.

ments, however, bearing no resemblance to the alternating contraction of voluntary muscles.) Then, as regards the iris, because stimulation of the third nerve causes contraction of the pupil, which is sometimes prolonged after withdrawal of the magnetic stimulus, it is deduced that the ophthalmic ganglion is the motor centre to the iris, and that the trunk of the third nerve conveys excitor fibres to the ganglion. Thus the cardiac ganglion is proved to be a motor centre receiving excitor nerves, because persistent contraction cannot be induced; whilst the ophthalmic ganglion is proved to be a motor centre receiving excitor nerves, because persistent contraction can be induced! And as to the excitor fibres, the spinal excitors are those between surface and centre; Volkmann's centripetal fibres are those between centre and centre, chord and ganglion. Hence there is no parallelism between them. Again, it is inferred that "the motor nerves of the anterior, but not those of the posterior extremities (of the frog), arise from the uppermost part of the spinal chord. For if the anterior part of the chord be electrified, the contraction of the anterior extremities is often prolonged after the withdrawal of the stimulus; but that of the posterior extremities ceases with the cessation of the stimulus. Now, if the motor nerves of both extremities arose in the brain, this difference would be unaccountable; and as, according to the preceding rule, it is stimulus of the central organs alone which induces prolonged contractions, it follows that the upper part of the chord is a centre to the brachial, but not to the sciatic plexus (of the frog)."* There is an important omission here. Volkmann found that persistent contraction of the lower extremities of the frog occasionally did result from applying electricity to the upper portion of the chord. As one instance of success should annul all cases of failure, this exceptional occurrence must not be slurred over. In reality, according to the principles laid down, it would prove the reverse of the conclusion drawn. Volkmann wishes it not to be considered as militating at all against his views, and accounts for the fact by assuming that the electricity was too powerful, and produced persistent contraction of the muscles of the posterior extremities by reflex action! In that case, what proof that the brachial nerves were not excited in a similar way; and what becomes of the law that all movements excited by electro-magnetism in the reflex manner must be of the alternating, never of the persistent kind? A natural law must have no exceptions. I believe it may be objected to Volkmann's laws, that the facts on which they are founded are not sufficiently constant and uniform to sanction their generalization into laws at all. But waving this as being mere matter of opinion, there are several reasons why we must reject the inferences, even if we admit

* Paget's Report, op. cit. No. xliii. p. 279.

the correctness of the laws. (1.) As the muscles which are supplied with gangliated nerves cannot be made in any way to present alternating contraction resembling that of the voluntary muscles, the non-presentation of it under the stimulus of electricity proves nothing *pro* or *con* with respect to the assumed motor influence of the ganglia. (2.) As every possible variety of contraction presented by voluntary muscles may be elicited without the intervention of nervous centres at all, the production or the non-production of a given kind of contraction through stimulation of the nerves, proves nothing with respect to the manner in which motor influence is normally exercised by the chord or brain over the voluntary muscles. (3.) As the gangliated muscles can be made to present both continued and persistent contraction by stimulating sufficiently their spinal nerves, spinad to the ganglia, if it were true that the occurrence of these kinds of muscular contraction is a decisive proof of the motor nerves having already departed from the centre which supplies them with motor energy, we should arrive at the reverse of Volkmann's conclusion, and infer that the ganglia are not motor centres. (4.) As all the phenomena elicited, together with their variations, can be reasonably explained by referring them to the special properties of muscular fibre, under different degrees of stimulation, and as they cannot be satisfactorily accounted for by reference to any known properties of the nervous system, the former is probably the correct explanation.

The following experiment will exemplify several of the statements advanced.

Experiment XXVI.—A large kitten was bled to unconsciousness, that appearing to be the best mode of producing insensibility without occasioning great interference with the nervous and muscular systems. A sharp small blade was pushed behind the cervical vessels on the right side, so as to divide the carotid artery, jugular vein, and vagus and sympathetic nerves. As the blood flowed freely, the animal became faint and still, but its heart continued to beat rapidly and feebly.

136. In five minutes the animal appeared to be unconscious. The abdominal viscera were exposed. The stomach was distended with food; the intestines motionless. It is supposed by some that the vermicular movement of the small intestines is constantly or almost constantly going on. This appears to be an error. The muscular coats act so as to produce motion only when stimulated by the presence of contents or by the nerves.

137. The diaphragm was at rest, except that at each stroke of the heart against its upper surface, the muscular fibres nearest to the part struck became firmly contracted for the instant. This contraction extended through the entire length of the fasciculi af-

fected, but did not spread to the rest of the diaphragm. Here was continued contraction of muscular fibre produced by the mechanical irritation of the heart-stroke, and not spreading to neighbouring fibres, because the diaphragm is made up of the striated muscle, and has its fasciculi separated from each other by septa of areolar tissue.

138. The elongating effect of the arterial wave on the mesenteric arteries was very apparent; but it was not perceived that the calibre of the vessels underwent the slightest change.

139. On touching any part of the small intestine, contraction of the part touched occurred instantly, increased for some time after removing the contact, spread along the intestine in both directions, upwards as well as downwards, and finally left the part touched in a medium state of contraction, its calibre being greater than during its active contraction, but less than before it was caused to contract at all.

140. In no case would this local irritation, if applied so gently as not to affect other portions of the tube mechanically, cause movement of a distant portion of the intestinal canal immediately; but it sometimes did this—after the primary contraction by spreading from fibre to fibre had implicated so much of the intestine that its coiling movement could not do otherwise than drag the mesentery and its nerves.

141. The contraction resulting from a gentle touch, together with that which spread from the point touched, was evanescent. But not so if a scratch with a sharp instrument or a pinch with the forceps were inflicted on the bowel in place of merely touching it. The contraction at the point irritated was considerable in its degree and in its length of duration in exact proportion to the amount of irritation inflicted. Thus, whilst mere touching of the peritoneal coat of the intestine produced a dimple which remained for 50 or 60 seconds only, a rough scratch along the length of the bowel caused instant and strong contraction; the irritated fibres becoming firm, prominent, and standing out from the surface of the intestine; and, by contracting much more suddenly and forcibly than the neighbouring fibres, causing a longitudinal crescentic depression, which remained for from five to ten minutes. In similar manner a scratch across the tube of the intestine produced a ring-like constriction which lasted equally long. Gentle vermicular action spread along the bowel from the point irritated, as in the previous observation (§ 139), where the irritation was slighter; and this spreading contraction subsided equally soon, leaving one portion of the intestine as it implicated another. Here we see continued and persistent contraction of unstriped muscle produced by direct irritation of the fibres themselves. The nerves had probably no share in producing the phenomenon; cer-

tainly there was no direct excitement of any nervous centre; hence the occurrence of this form of muscular action is no proof that the nervous centre in which the motor nerves of the part under examination arise, is acting strongly, or indeed acting at all.

142. Scratching the cœliac ganglion had no effect on the distended stomach, but produced vermicular movement of various portions of both large and small intestines simultaneously.

143. Pinching the nerve-trunk accompanying a principal mesenteric artery caused immediate vermicular action of the portion of intestine to which the peripheral filaments of the irritated nerve were distributed; but no further movement of the rest of the intestine than what proceeded from an extension of the primary muscular contraction. Hence, there was no excito-motory action induced.

144. Scratching the surface of the stomach produced contraction at the irritated part, but no general muscular action of the stomach. It never occasioned motion in any distant part. The over-distension of the viscus, however, would lessen the irritability of its muscular fibres, and probably impair also the excitability of the surface.

145. The gall-bladder and the biliary ducts were quite full. Scratching the first caused a slight rugous dimpling of its coats, but no such prominent appearance of the fibres in action as the stomach and intestines presented. No manifest effect resulted from irritating the hepatic and the gall-ducts.

146. The spleen was moderate in size, and resembled a flattened, elongated raspberry. Irritation of its surface had no effect. On cutting it half through, no blood flowed; on dividing its vessels in the hilus, blood flowed freely.

147. The kitten had appeared quite insensible and motionless all this time; it inspired at intervals, and its heart beat rapidly and feebly. The abdominal aorta was now divided; a sudden gush of blood instantly stopped the action of the heart; a single deep inspiration was drawn; the pupils, previously small but sluggishly responsive to the light of the sun, suddenly enlarged to their utmost, and the animal was dead. Thirty-six minutes had elapsed since the division of the cervical vessels.

148. The front of the chest was removed without injuring the pericardium, the transparency of which permitted the action of the heart to be distinctly seen. The right auricle and ventricle were contracting vigorously and in regular order. The left ventricle appeared small, firm, and motionless, being moved at each systole of the right ventricle, but having no independent motion of its own. The left auricle contracted feebly but distinctly, synchronously with each systole of the right auricle. The action was

rather a sudden quivering of the appendix of the left auricle than general contraction of the auricle. The auricles always moved together; were equally motionless when the ventricle contracted; and usually contracted twice for one systole of the right ventricle.

149. The diaphragm was convex towards the thorax. On gently pinching the left phrenic nerve, the left moiety of the muscle contracted; the right portion remaining quiescent. The heart's action, which had become more tardy, was accelerated. After these effects had subsided, on strongly pinching the phrenic nerve lower down than the seat of its former irritation, the left half of the diaphragm contracted suddenly and firmly, and *its muscular portion remained flattened and rigid for eight minutes.* Division of the phrenic nerve did not interfere with this state of persistent contraction, which was thus proved not to be dependent on any given influence of a nervous centre. On mechanically irritating the central portion of the divided phrenic nerve, no movement of the heart whatever resulted. The acceleration of the heart's action noticed on irritating the nerve before its division was not due, therefore, to any excito-motory influence through the medium of the phrenic nerve, as in similar experiments some have erroneously supposed, but probably to the effect of the contraction of the diaphragm in disturbing the position of the heart.

150. The right ventricle had not moved for two minutes; on pinching the left vagus at the root of the neck, the right ventricle contracted four times and then ceased. In performing this, care was taken not to move the heart or pericardium by any traction of the nerve.

151. The pericardium was now opened, and the surface of the heart exposed. The auricular appendices twitched slightly, but the ventricles were motionless. The contact of the air appeared to have no effect; but the irritability might have been becoming exhausted. Scratching the left ventricle produced no general action in it, as it had remained contracted from the first (*persistent* contraction without direct irritation either of nervous centre, or nerve; due possibly to the sudden removal of the contents of the left ventricle when the aorta was divided having occasioned an extreme contraction of the muscular fibres); but there was slight elevation of the muscular fibres at the part irritated. When the left ventricle was so pressed as to communicate movement to the rest of the heart, the right ventricle and both auricles contracted slightly; but irritation of the left ventricle without pressure had no effect on the rest of the organ. Pinching the right ventricle caused its contraction, followed by that of both auricles. Pinching the right coronary vessels and nerves in the right auriculo-ventricular groove, caused contraction first of the ventricle, and afterwards of both auricles.

152. All the vessels were cut through close to the base of the heart, and the organ removed. Slight irritation of the right ventricle caused slight contraction of the fibres irritated, but nothing more. Stronger irritation of the ventricle induced more extensive action of the right ventricle followed immediately by contraction of both auricles. After the lapse of five minutes from the time of removing the heart, irritation failed to induce any muscular contraction.

153. Six minutes after dividing the aorta, the whole of the abdominal viscera were removed. There could now be no spinal action. Irritation of any portion of the intestine occasioned local, and spreading muscular contraction; but no contraction of any distant portion of the alimentary canal.

154. Two feet in length of small intestine were separated from their mesentery, which was cut off close to its attachment to the bowel. This portion was loosely spread out on the table, being still connected with the rest of the intestines at each end. As soon as the contraction produced by the manipulation had quite subsided, a single point of the loose intestine was scratched with the scalpel. At the part irritated, strong contraction ensued, and spreading from this, a twisting and coiling movement of the intestine gradually extended in each direction until it implicated the bowel to which the mesentery was still adherent. Here the ganglia being removed, no central nervous influence could operate, yet the effect as regards muscular contraction was as considerable, excito-motory action excepted, as that which results from similar irritation when the viscera remain *in situ.* The proof that muscular contraction is independent of innervation both in the power of contracting, and of communicating that contraction from fibre to fibre, cannot be carried further by experiment. Certainly some nervous tissue still remains in the terminal filaments distributed amongst the muscular fibres; but, if all nerve-tubes are independent of each other, and never anastomose after leaving their origins, whether they can themselves generate force, or whether they be mere conductors, they cannot certainly combine actions without the intervention of centres of some kind. After separation of its mesentery nothing but cut nerve-ends remain in the bowel. Notwithstanding the high authority of Müller, it seems impossible that these can exercise any re-action on the muscular fibre adequate to transferring irritation from one point to several distant points. If, indeed, the peripheral nerves were so joined together, and were so organised, as to constitute a kind of expanded nerve-centre capable of re-action on the tissues in which it lies, the question would be undecided; but such an arrangement of the muscular nerves at least is quite opposed to anatomy.

Anatomically speaking, all the known forms of muscular tissue may be reduced to two, the striped and the unstriped; but physiologically it is convenient to distinguish several varieties according to the mode in which they respond to irritation. The lowest variety is presented in the skin, where the contractile tissue is so diffused as not to be clearly demonstrable except where it exists in greater quantity, as in the dartos. To this the natural stimulus is cold. It may be questioned whether the effect of mental emotion in producing *cutis anserina* is not in part due to the actual diminution in the heat of the surface; witness the chilliness which accompanies that condition. The final cause may be that of checking further evolution of animal heat from the surface, by lessening cutaneous transpiration. It is interesting to find that mere exposure to cold will directly induce contraction of unstriped muscular fibre. Volkmann considers that he has proved this by laying bare the urinary bladder of a living dog, when that organ immediately contracted and expelled its contents. But this experiment is not satisfactory. The pain and the fright might have caused micturition. The occurrence of contraction when the animal is insensible is a better proof. The contraction induced by cold in the diffused contractile tissue of the skin is persistent. It is not known that similar action can be induced artificially by experimental irritation of any part of the nervous system.

The next remove, perhaps, is seen in the muscular walls of ducts and vessels. Their contraction during life is probably of that continued, regular character which accommodates their calibre to the distending force of their contents. When they do respond to mechanical irritation at all, the fibres in the neighbourhood of the part irritated contract and retain their contraction for some time; they never present waves of contraction, like the intestines; nor usually do they furnish a series of rhythmical movements, like the heart. Dr Procter, however, states that he transmitted galvanism from "the branch of the sympathetic which joins the ischiatic," to "one of the arteries in the leg" (l. c. p. 33), with the effect of reproducing pulsation in the artery; but nothing is mentioned concerning the heart, whether it was passive or otherwise at the time. Good experiments are wanting to decide on the extent to which irritation of the nerves can affect the arteries, the heart being quiescent.

The muscular coats of the alimentary canal consist of unstriped fibres not separated from each other, and bound up into distinct bundles, but devoid of areolar tissue, and freely intermixing amongst themselves. The unstriped character of the primary fibril confers the peculiarity of gradual rather than of sudden contraction; whilst the non-isolation of bundles, and the intricacy of the mutual connection of contiguous fibres favours the spreading of contraction from one fibre to those around. The alternating contraction which we notice in a voluntary muscle, viz. a succession of equal contractions and relaxations of the same fibres under slight but continuous irritation, cannot be induced in any way. By irritating the spinal motor nerves spinad to the sympathetic ganglia, Valentin induced ring-like constriction of various portions of the alimentary canal, *i. e. persistent* contraction. By irritating the ganglia themselves, and their nerves both spinad and viscerad to the sympathetic centres, I have found spreading vermicular motion, which extended from the several points, or the single point, at which it commenced along the contiguous fibres; but never anything like alternating contraction. From direct irritation of the muscular fibres *persistent* contraction always resulted, and lasted long in proportion as the irritation was considerable. Unstriped muscles respond more readily to direct irritation of their fibres; less readily to irritation of their nerves, than voluntary muscles.

The striped fibres possess energy and rapidity of action, and aptness for excitation through their nerves, in virtue of their special organization; and a tendency to act in portions without the general spreading noticed in the intestines, in virtue of their arrangement in fascicles and their possession of distinct sheaths. This is easily observed in the thin fasciculated muscles of the neck in a recently killed ox after removal of the head. On pinching a single fasciculus, that alone will be retracted; a sharp twitch which pulls the entire muscle will cause all of its bundles to be drawn up, but unequally. Sometimes the irritation arising from cutting through the neck will cause one of the thin muscles, a hyoidean muscle for example, to alternately retract and elongate for a considerable time, no other source of irritation being present except exposure to the atmosphere. I have seen this spontaneous alternating contraction continue for ten minutes after the butcher had suspended an ox's head. In a leg just amputated, pinching the nerves will cause vigorous contraction at the instant; and tremulous vibratory contractions several times repeated after ceasing to irritate the nerve. Great irritation of a motor nerve will cause firm contraction, which sometimes ceases with, and sometimes outlasts the removal of the irritation. Hence, we can produce alternating, continued, or persistent contraction of voluntary muscles, according to the degree and kind of irritation, without such irritation acting through a nervous centre at all. But we cannot in any way induce either spreading or rhythmical contraction of voluntary muscular fibres.

The heart is a compound variety of muscle. With the striated arrangement, it has all the energy of voluntary muscle; whilst the absence of areolar tissue and of sarcolemma, and the intermixture of its fibres with each other, confer the power of endurance and of spreading contraction of involuntary fibre. The alternate contraction and rest of the heart have been variously explained. This peculiar kind of muscular action is not due to any influence derived from the brain, nor from the spinal chord, since it outlasts the destruction of both. Nor is it owing to any especially stimulating quality of the blood, for it continues after the heart has been removed and placed in water. Nor to contact of liquid at all, for it occurs when nothing but air surrounds the organ. Nor to the stimulation of the air, for it continues in vacuo. Is it due to the cardiac ganglia? Not unless these ganglia exist to an adequate extent in every portion of the heart, since every portion of heart sufficiently large to contain the terminations of a sufficient number of muscular fibres, to furnish fixed points for the acting ones, will spontaneously present rhythmical movement, when separated from the rest. That this experiment often fails, is no objection. Volkmann considers the fact of some portions of a frog's heart, which has been cut up into separate pieces, continuing to present these actions, whilst certain others do not, a proof that the contraction where it is presented depends on the influence of ganglionic centres. Not to insist upon the want of proof that any more ganglia exist in the contracting than in the motionless portions of heart, how does the assumption of ganglionic influence lessen the difficulty? What confers upon the ganglion the power of acting periodically and regularly, so as to stimulate the muscular fibres at one moment, and not at the next? To invest the ganglion with any such power, is merely to remove from muscle a peculiar endowment, because we cannot explain it, to nervous tissue, where we can explain it just as little.

Nor by ascribing the periodical activity of the heart solely to muscular fibre, shall we violate anything we know of the characteristic properties of other living tissues. Alternate action and apparent rest are presented alike by all. The comparative duration of each condition is but a difference of degree. But when we examine more closely we find that the apparent rest is not perfect repose; it is merely lessened action, gradually to be augmented, until sooner or later it becomes manifest by its obvious effects. The obvious manifestation we consider alone the state of action; the preparatory process, that of rest; the succession of the two, an alternation of excitement and quiescence. From the evolution of the first embryotic cell to the last vital change of dying tissue, life pursues one never-ceasing round of activity; perpetually varying in amount, observing definite laws in every variation, this activity is never for a moment entirely suspended; it ceases only with life. The changes of nutrition are never at a stand. During emaciation they are even more active than when the presence of surplus material combined with small energy occasions extra-deposit. But the material is bad, not fully elaborated, its change into tissue rapid and imperfect, its existence short, its removal early. Still, whether sound or imperfect, leading to the fulness of health or the wasting of disease, quick or tardy, the conversion of organisable matter into tissue is unceasing. In mere nutrition, the molecules having played their part, are reduced into such matter as can be taken up by absorption, and conveyed elsewhere. In secretion, under whatever form, the abstract difference in the process consists chiefly in the fact that the residue of the molecular changes is not absorbed immediately, or, when not absorbed at all, received by excreting tubes which procure its removal elsewhere. The exhalation on the free surface of a secreting membrane may be uniform as regards quantity, the secreting activity experiencing no variation. Even this is doubtful; the pleural and peritoneal halitus may be increased in precise accordance with the movements of the viscera; the serous exhalation in the encephalon and spinal chord is presumed to vary in quantity as more or less pressure on the nervous centres is required; and there is little doubt that synovia is abundant in proportion to the exercise of the joint. Mucus is furnished freely in exact ratio to the exposure of its secreting membrane to irritation; but more or less it is always being secreted. In the production of specific secretions, such as the gastric juice, bile, semen, and the rest, the constancy of their production is less obvious. Under circumstances of excitement saliva or tears are immediately secreted copiously, but that the gentle action of the salivary and lacrymal glands is always going on, needs no argument. Just so with gastric and pancreatic juices, bile &c., secreted more copiously under the stimulation to which they are periodically subjected, it is probable that they still continue to be secreted after that state of extra-excitement has passed by. We know that semen is formed and stored up for use, whilst its organs are unexcited. This is true as regards man; but it is more obvious in other animals, in which procreative energy is required to be greatly exercised. In the male guinea-pig the *vesiculæ seminales* are often immense and full of semen. We know that the kidneys are never idle; and unless the same be true of the liver, the gall-bladder would be without a purpose. It is objected that Dr Beaumont has satisfied himself that true gastric juice only flowed during the process of digestion (Grainger on the Spinal Chord, p. 141). But that Dr Beaumont himself thought the gastric juice was accumulating in the absence of digestive activity, though not poured forth, is evident from his ascribing the sense of hunger to the distension of the follicles prior to the effusion of gastric juice. Be this as it may, the admission of air through the perforation into St Martin's stomach might modify the natural condition of the follicles and lining membrane.

Nervous power is ever ready, is exhaustible, and reproducible; is considerable or deficient in proportion to previous excitement or otherwise. We find structures fitted for its production, accumulation, conduction, and distribution. Is it not being constantly formed, accumulated, and expended? The functional manifestations of nervous tissue depending upon and corresponding to the energy with which its nutritive changes are performed, vary with, and are affected by this. But though subject to the greatest difference in amount, they can be elicited at any moment. Excitement—*i. e.* undue expenditure of nervous power—is invariably followed by exhaustion. The suspension of extra-excitement for a time invariably leads to the increase of nervous energy. We have proof that the spinal chord is active during sleep; and doubtless the ganglia are equally so; but how can we imagine the brain to be otherwise than at rest, when no evidence of its functional activity is presented? Some metaphysicians assume that the mind is ever active, even when the tired body seeks repose; that we are in reality always conscious whilst asleep, but as constantly forgetful of our sleepish imaginings in our wakeful moments. Without any such gratuitous assumption, however, there is no real difficulty. When a body feels cold, it is not really devoid of heat. When it ceases to manifest apparent electric phenomena, it is not really deprived of electricity. So also when the brain sleeps, it continues to perform its nutritive molecular changes, but with an energy too feeble to permit of mental manifestations. At any time, what will lower nutritive action in the brain will induce sleep; what will excite it, awakens. Tardy circulation from a hearty meal, or apoplectic congestion, causes stupidity and sleep. Energetic circulation from wine, or in the first stage of encephalic inflammations, causes vivid intellect and watchfulness.

Many object to the use of such words as accumulation, conduction, transmission, when applied to the nervous energy, because we know nothing as to the nature of that force. On the same ground such terms should be discarded from physics, because the exact nature of the non-vital imponderables is not ascertained.

Nor, with respect to the muscles, will the assumption of a similar accumulation of muscular force presuppose any undue expenditure of resources, an error unknown in nature's works. To those who object to speak of muscular force as a distinct entity, the argument will be unaltered, if we consider that, during the apparent rest of muscle, the sarcous elements are gradually acquiring that condition which fits them for the highest manifestation of their property of contractility; this is really tantamount to accumulation of power. And the same, *mutatis mutandis,* of other tissues. If their product be not expended in due time, in the normal manner, molecular changes do not proceed unchecked and extravagantly, but are performed more and more feebly, until, by prolonged disuse, a part will waste and lose its capacity for responding as before, even to its natural stimuli. Machinery rusts by standing still. On the other hand, we have some evidence of accumulation of muscular power in the restoration of vigour by rest, and in the increased action of the sphincters during sleep. It is difficult to appreciate any change in the degree of contraction of most of the sphincters during sleep, but we have an index in the state of the iris. It is generally asserted that in sleep the eyeball is turned upwards and inwards, and the pupil contracted. This, however, is not unconditionally true. After sleep has lasted for some time, the eye is indeed in the state described; but the pupil does not contract in size immediately after sleep ensues, nor is the eye necessarily directed upwards and inwards. Of this I have convinced myself by repeated observations on infants. The pupil during sleep is at first of the medium size and by degrees only becomes smaller, but it never attains its minimum contraction. The eye is invariably directed out of the way of the light; the cornea may point upwards, or outwards, or downwards. It is only after sleep has been continued, and where the room is so darkened that light cannot approach more freely in one direction than another, that the eyeballs are directed upwards and rather inwards. The upturning muscles of the globe of the eye exceeding the depressing, and the inverting muscles, the abductors, in power, an augmentation of passive contractility proportionably equal in each of the orbital muscles, would lead to the upward and inward position of the cornea which we find. There is no evidence, as some contend, that this position is owing to the action of the *obliquus inferior oculi* alone, since we have no proof of that muscle being more active than its fellows during sleep. Its relationship to the lenticular ganglion is, if the views I am defending be correct, for the purpose of associating the action of the muscle during wakefulness with change in the vascular apparatus within the eyeball, and cannot confer any especial power of maintaining prolonged contraction on the *obliquus inferior.*

As regards the pupil, the degree of contraction which it acquires during sleep is just what we might expect from a gradually increased development of the passive contractility of the *sphincter iridis*, not passing the limits to which the antagonising elasticity of the iris restricts it. One phenomenon is very difficult of explanation. If we raise the eyelid of a sleeping person, and cast the rays of a candle on the eye, so long as the individual remains unconscious, the contracted pupil is unaltered; but on rousing the sleeper, the pupil first enlarges under the light; and as vision becomes more distinct, the pupil contracts. The ordinary effect of light being to induce contraction of the pupil, how does it in this case occasion dilatation? If, as I suppose, the previous contraction during sleep depended not on any nervous influence, the enlargement on awaking cannot be due to a sudden suspension of such influence. And if the passive contractility of the *sphincter iridis* do accumulate during sleep, the dilatation must be an active effort, or it would not overcome the increased tendency to contraction. Being active, elasticity will not account for the dilatation; nor will the assumption of a dilating nerve lessen the difficulty unless we admit that light stimulates the dilating nerve, and if it did so in this instance, how could we explain its more constant effect in producing contraction? No peculiar action of the fifth nerve, or of the ganglionic nerves alone will suffice, since the state of vision is essential. Pathology establishes this. In some cases of hydrocephalus, the child lies still with its pupils contracted, but on bringing a light near to its eyes, the pupils dilate and vision is dim. When the child is quite blind, this never happens; the pupils are then either dilated and motionless, or contract on the application of light. Hence the phenomenon in question is referrible in some way to the perception of light. Can it be that when the optic nerve acts too feebly to influence the centric connection of the third nerve, its effect on the retina is such as to abstract the blood from the vascular apparatus of the iris and thus produce expanded pupil by virtue of the contraction induced in the vessels of the iris; this effect being removed as soon as vision becomes clearer, the optic nerve then acting with sufficient energy to produce its ordinary influence on the *sphincter iridis* through the third nerve? I need hardly remark that this is intended as a mere conjecture.

As the best type of the true sphincters, we may take the *sphincter ani.* Its contraction is influenced by its inherent muscular force, by spinal action, by sensation, emotion, and volition. During deep sleep, of these the two first alone are operative. As we have no proof that the spinal chord dispenses its energy more freely during sleep, provided it be not more excited, it is quite as reasonable to conclude that if the sphincters do then act more completely, they do so in consequence of a gradual augmentation of their passive contractility. Dr Marshall Hall contends that the muscles in general derive their tone from the spinal chord; and refers especially to the action of the sphincters. But Dr Todd well points out that this theory is insufficient to explain all the phenomena of their contraction.

In grave lesion restricted to the brain, although spinal excito-motory action is everywhere proceeding, the *sphincter ani* is lax. As the spinal centre is active, why, if the state of the sphincter depends upon that, is it not close and contractile on being touched? The causes may be two-fold. It may proceed in part from the muscle being deprived of the physical re-action of sensational nerves, in part from the abolishing effect on muscular contraction always occasioned by great shock, and which always operates most considerably on parts supplied with cerebral nerves, and therefore is manifested more by the *sphincter ani* than by the purely involuntary muscles. In a similar way may perhaps be explained certain experiments of Dr M. Hall, in which sudden removal of the chord caused general muscular relaxation, without our admitting with that able physiologist, that they prove the entire dependence of muscular tone upon the spinal centre. The MM. Weber have found that a strong current of electricity transmitted through the cardiac nerves caused immediate cessation of the action of the heart by palsy; the texture of the heart being relaxed, and all its cavities full. A less strong current enfeebled the pulsations. A still gentler current accelerated them. In the last we have an exciting stimulus; in the first, overwhelming shock. The difference in the effect of severe injury inflicted suddenly, and the same amount inflicted gradually, is well known, though not always sufficiently borne in mind when performing severe surgical operations. Whatever kills instantaneously, kills by shock. A blow on the head, epigastrium, or testicle, intense emotion, electricity, and prussic acid, when they produce instant death, do so in the same manner, by shock. Every vital process is suddenly brought to a stand; the heart ceases to beat, the lungs to breathe, the alimentary canal to propel its contents, secretion stops, and the condition of the blood is altered. To what kind of influence can these effects be ascribed? As muscular contraction and secretion are essentially independent of innervation, the mere suspension of nervous influence should not instantly stop their exercise. If the blood derive no special endowment from the nerves, its state should undergo no immediate change from mere want of nervous supply. The first to suffer in shock is the nervous system; all parts of it, brain, spinal chord, and sympathetic, at once; the second, the vascular system. The blood is prevented from passing through the capillaries; and the arteries and veins alike contain blood. May it be that there is a sudden discharge of all their energy by all the nerves at the same instant; overwhelming and deranging all the atomic actions of life simultaneously? If the shock be recovered from there always appears to be great want of power in all the nervous centres; and in experiments in which the first effect of shock can be observed, it is always such as implies discharge of their force on the part of the nerves; for example, convulsions. Be this as it may, it will readily be admitted that such a considerable shock as that occasioned by suddenly removing the spinal chord may so far derange the elementary constituents of muscle as for a time to incapacitate them for performing their normal actions; but it never prevents the subsequent accession of *rigor mortis* contraction. The stiffening of the muscles after death is probably due to some such gradual accumulation of *vis insita* as that supposed, which leads at length to the last effort of muscular vitality, the *rigor mortis*. This view is supported by the fact that *rigor mortis* comes on earlier and lasts a shorter time in the more energetic muscles of warm-blooded animals; and in man, its occurrence in the different muscles, *cæteris paribus*, accords precisely with the irritability possessed; occurring early and soon over in the left ventricle of the heart; occurring later and lasting longer in the intestines. In this, the cause of *rigor mortis* exactly corresponds with the natural contractility of the different muscles. And have we not an analogy to such a gradual accumulation of force during the last moments of life, in other tissues? How else can we account for the increased clearness of mind which often immediately precedes death,—the brightening flicker of the expiring flame; or, for the occasional absorption of dropsical effusions in the last moments of life; or, for the strong convulsions which often wind up protracted dying?

The general harmonization and balancing of the action of antagonist muscles, which, without our attention, maintains steadiness of frame, and which is never entirely lost during life, is probably an excito-motory function, partly of the sensational centre, and partly of the spinal chord. Removal of the cerebro-spinal axis would annihilate this, and therefore, even if it had no effect in lessening the contractility of individual muscles, would destroy that firmness and determinate attitude of limb which results from groups of muscles acting consentaneously. It could scarcely be otherwise than that the nerves should have a great influence over the tone of muscle, when we consider that this phenomenon, under whatever name designated, whether tonicity, tonic force, insensible organic contractility, or passive contractility, is simply a low amount of exercise of that same muscular force, which, when so increased as to produce obvious motion, is greatly under the influence of the nervous system. But more than this is not proved; and if the spinal chord be not the source of tone to spinal-nerve muscles, there is no argument from analogy to sanction our supposing that the ganglia supply tonicity to ganglionic-nerve muscles.

Muscular tissue then offers no exception to the universal law of perpetual activity. The skin always accommodates itself to the surrounding temperature, or otherwise, (and virtually this is the same) it is altered by increased sensitiveness of its nerves. The hollow tubes are antagonised by the distending force of their contents, and never cease to oppose this. Voluntary muscles ever manifest the subdued contractility which enables them to antagonise each other. Now as the contraction of an entire muscle in action is not really, as it appears, uniform through the entire muscle, but consists of certain fibres contracting and others relaxing so generally, that by a resolution of forces the gross effect is an apparent contraction of all the fibres at the same instant, is there not evidence that muscular force is generated, accumulated, and expended, just as we have supposed every vital force of other tissues to be? If so, the peculiar modification of muscular contraction presented by a given type of fibre, will depend upon the fitness of the molecules of the fibres (" sarcous elements") for undergoing the requisite atomic changes more or less rapidly. Thus, if the sarcous elements of the tissue of the heart be such that they perform their atomic changes more rapidly and simultaneously than those of voluntary muscle, bearing in mind that the heart has not an equivalent antagonist to require the unperceived expenditure of its contractility, as each voluntary muscle has, some such series of spontaneous contractions as we actually have hypothetically should result. As we can disprove the dependence of the rhythmical contraction of the heart upon any portion of the nervous system, upon the blood, respiration, and every other extraneous influence; and as the possession of such an endowment by the muscular fibre, although unproved, is in strict analogy to the rest of the economy, and especially as it appears but a modification of contractility as witnessed in other muscles, we may conclude that the heart alternately contracts and relaxes in virtue of the special organisation of its muscular fibre *per se.*

The cause of the sequence observed in the contraction of different parts of the heart is a question perfectly distinct from, though not unfrequently confounded with, the last. The heart acts in the order in which the blood is received into its cavities; the auricles contract first, the ventricles second. As the heart presents a greater aptness to respond to mechanical impression than any other muscle, the sequence observed is undoubtedly owing to the order in which the blood comes in contact with the several component parts. But one phenomenon essential to the result cannot thus be explained. On removing and emptying a heart still irritable, after temporary quiescence, either ventricle may be the first to contract, or either auricle. When the irritability is great, the corresponding portions, the two auricles, or the two ventricles, invariably contract together; but as irritability departs unequally, at length the right ventricle, and last of all the right auricle will contract singly. Still under any circumstances the auricle and the ventricle never contract at the same instant. Either may contract feebly several times without the other, or the ventricle may contract once, and be followed by a single contraction of the auricle, reversing the normal order. The parts which contract simultaneously are not separated by any non-muscular tissue. The parts which never contract together are. On separating the auricles from the ventricles, all may still contract, but the order is destroyed. Observation of a portion of intestine in which the contraction spreads from one fibre to another, shows that the fibres first irritated excite those around them with which they intermingle by the traction produced through their own movement. In the same way, probably, will all the fibres of the auricle re-act upon each other, but being unmixed with the fibres of the ventricle, they affect these only through the medium of the traction exercised on the tendinous ring which constitutes the common point of junction between auricle and ventricle. This being a less rapid mode of transmitting irritation than that which exists between fibre and fibre, causes contraction of the ventricle subsequently to that of the auricle, and v. v. And if the movements of the auricle be too feeble, no contraction whatever of the ventricle results, until a series of auricular contractions have occurred to make up by number what individually they want in force. In support of this, it is much more common for the auricle to contract several times to produce one action of the ventricle than the converse. This is what we should expect. The ventricle being the stronger muscle will more readily re-act through the tendon upon the auricle than the auricle upon it. The great facility displayed by the fibres of the heart in responding to mechanical impression, and in re-acting upon each other, obviates a difficulty felt by some physiologists in explaining how the application of blood to the lining membrane of the cavities can instantaneously occasion contraction of the external fibres, unless through the intervention of ganglia. The instantaneousness of contraction is not real. The fibres of the heart contract as progressively as do those of the intestines; but the progression is much more rapid.

In reference to the *ultimum moriens*, it is interesting to remark that the part which is last to lose its irritability is the venous heart. Cold-blooded animals maintain muscular irritability the longest, but their muscular energy is weakest. Hot-blooded animals have greatest energy, but the smallest power of retaining muscular irritability. It is urged that we have no proof of the hot-blooded arterial heart being more energetic than the other. But as the ventricles go through the same amount of contraction in the same space of time, must not each fibre of the larger muscle possess greater energy than that of the lesser muscle to effect this? Has the nature of the blood constantly bathing the internal surface of the cardiac cavities any influence on the contractility of the walls? There is at least a coincidence in the fact of the slow-acting involuntary muscles being invested with mucous membrane, in which the minute veins exceed the minute arteries in a far greater proportion than elsewhere.*

If these views be correct, the action of the heart is essentially independent of every nervous centre. The facts cited to establish the contrary, merely prove that it is greatly influenced by any and every nervous centre; a truth of which every man's personal experience will sufficiently convince him. Take, for example, the experiment on which Brachet laid great stress, viz. that after removal of the cardiac ganglia the heart ceased to beat: from which he concluded that the normal action of the heart was due to an influence supplied by the ganglia. With equal justice might it be ascribed to influence derived from one of the extremities, because a suddenly crushed limb will occasionally induce a similar result. It is the commonest of all errors in experimental physiology to infer that because A can be made artificially to affect the normal action of B, of necessity A must furnish something essential to the normal action of B. In illustration we may refer to the experiments on the encephalon, particularly on the cerebellum.

The continued existence of frogs after total destruction of brain and spinal chord; and the extensive movements of the hollow abdominal viscera when removed, have been adduced as good examples of muscular motion presided over by ganglia. (Mr Paget). The first, like the nutrition of imperfect fœtuses, positively proves that the brain and spinal chord are not essential to the performance of the vital processes; it by no means proves that the ganglia are. The only indication of the influence of a nervous centre being exercised in producing muscular movement, consists in obvious motion of one part induced by

* Mr Turner of Manchester some years ago was in the habit of exhibiting engravings which demonstrated this anatomical fact very beautifully; and which I understood it was his intention to publish.

irritation of another and distant part, no direct and continuous muscular or other mechanical movement being communicated from the one to the other, nor any motor nerves destined to the moving part included in the portion irritated. Such an indication cannot invariably be obtained from either the heart or the abdominal viscera whilst *in situ ;* but it sometimes can. (§ 124). From these organs eviscerated it never can. Irritation of one portion of intestine, when the whole have been removed together, will by spreading contraction gradually implicate the rest; irritation of a nerve-trunk may affect simultaneously several distinct portions of intestine; and rough irritation, such as by pinching or pulling, may disturb and thus excite several distinct portions together; but these sources of fallacy considered, the fact is as stated.

The importance of deciding whether the ganglia are motor nerve-centres to the involuntary muscles; and the great preponderance of authority (Bichat, Müller, Volkmann, Paget, Grainger, and many others,) favourable to the affirmative, rendered it incumbent upon the holder of a different opinion to discuss the subject at length. I have therefore endeavoured to show that, from general considerations, (see last paper), it is improbable that the ganglia are motor centres for muscles; from anatomy, that they are not fitted for such a function; and from experimental physiology, that they have not been proved to possess it.

If then the ganglia be, as I believe, centres for presiding over non-nervous and non-muscular organic processes, and for these only, the investigation of the function of a given ganglion resolves itself into an analysis of the different nerves which enter into its composition, and of the tissues to which its nerves are finally distributed.

Holmes Chapel, Cheshire,
August 14th 1846.

PART FOURTH.

Relation of the Ganglia to the other Nervous Centres.

The term ganglion was applied by Galen to enlargements on the nerves, from their resemblance in outward appearance to small enlarged bursæ, which Hippocrates had designated ganglions. (Béclard.) Gall was the first to extend the application of the word to the various grey masses in the encephalon. Reil, Walther, de Blainville, Carus, and many others, sanctioned the innovation. Even the partial enlargements of the chord, where the nerves of the extremities are given off, and the entire mass of convolutions of the cerebral hemispheres, are termed ganglia. Such parts, however, are never considered to belong to the ganglionic system; each of them has, or may have, its own anatomical designation, and certainly possesses no claim to the title of ganglion, if used in its literal signification of nerve-knot. For the purpose, then, of excluding the various nerve centres of the encephalon and chord, a ganglion may be defined to be a nervous centre, possessing nerves of communication and nerves of distribution. All nervous centres, it is true, are connected together by some nerve-tubes; but if we consider the packing up of such filaments in a distinct sheath, essential to the constitution of a nerve, the ganglia alone communicate by means of nerves.

A ganglion consists essentially of nerve-cells connected with the terminations of grey nerve-tubes. Every other nervous centre requires the addition of the white nerve-tubes, to some of which, in all cases, it furnishes the centric attachment. A ganglion, with very few exceptions, likewise possesses white tubes, but it never gives origin to them. These white tubes pass through the ganglion without any interruption of their continuity; they neither join with each other nor with the grey ganglionic fibres, nor do they open into the ganglionic cells. The ganglia, as a class, present marked differences in the presence or absence of these white tubes, and in their kind and proportion when present. On these differences may be founded an attempt to arrange the various ganglia.

The grey enlargements on some gangliated nerves formerly referred to,* which, from not appearing to be traversed by any white nerve-tubes, may be considered as mere nuclei of augmentation for ganglionic filaments, are few and inconstant. The indubitable existence of one such simple ganglion, however, will

* Page 329, Edinburgh Medical and Surgical Journal for October 1846.

suffice to prove that, 1. the action of the white nerve-tube is not essential to that of the ganglionic cell; and, 2. that whether or not the grey ganglionic nerves of distribution can act centripetally, (ganglionad) they must be able to act centrifugally. It follows that the gangliated white tube is extrinsic, and possesses so intimate a relation to the ganglion only for the purpose of influencing its activity, not for that of conferring upon it the power of acting. There is nothing in the arrangement of the white tubes in different ganglia to favour the idea, that different nerve-tubes react variously on the ganglionic cells through which they pass; nor is there any adequate variation in the grey constituents of different ganglia to account for their peculiarities of function. For this we must refer to the difference of origin in the nerves transmitted.

Through one or other kind of ganglion, every variety of white nerve-tube is transmitted, excepting only that of voluntary motion. Indeed it is solely by inference that the volitional nerve is excepted, since voluntary muscles in some instances do certainly receive white nerves which have previously passed through a ganglion. The diaphragm, for example; *rectus capitis anticus major; longus colli; buccinator;* and perhaps some other muscles concerned in mastication; occasionally, the *obliquus inferior oculi*, if that be a voluntary muscle; and some of the laryngeal muscles. But as the sentient surface which the given ganglion supplies is physiologically related to the automatic and combined contraction of these muscles rather than to their voluntary action, there is no difficulty in conjecturing that the gangliated white nerve-tubes of voluntary muscles are spinal in their origin; or if in part cerebral, that they are sensational only, not volitional. All the muscles in question invariably receive other motor nerves which have no connection with ganglia, and these exclusively may be deemed to convey volitional influence. Although not proved, this is so probable that we might correctly predicate of a muscle which received none but gangliated nerves, that it could be neither completely nor partially a voluntary muscle. Strictly speaking there is no entirely voluntary muscle in the system; since every muscle receives spinal motor nerves which may cause its contraction independently of the will.

The posterior root of every spinal nerve contains spinal excitor nerve-tubes which end in the chord, and sensational excitor nerve-tubes which end in the brain. The two kinds are not anatomically distinguishable; they pass together through every compound ganglion; probably react alike on the ganglionic cells during their passage; and though disproportionate in their distribution, they terminate peripherically together. It would be convenient to employ some common designation to signify this constant anatomical and functional combination. The term "afferent" has been adopted as regards the nerves of the spinal chord; but in reference to the nerves of the ganglia, it is exceptionable for the same reason as the word "excitor," viz. that we have no ground to doubt that the motor nerves which enter a ganglion "excite" its action, and bear to it a stimulus, precisely as the nerves connected with the spinal excitor roots do themselves. To the terms spinal, sensational, or cerebro-spinal, the objection is, that they imply either too much or too little. Distributed chiefly to the surfaces of skin, mucous membrane, or vessels, the designation surface-nerves might be an allowable Germanism, did it not exclude the filaments which we must assume to confer impressibility on parts, which have no free surface. The only physiological guide seems to consist in this impressibility, which is common to all the nerve-tubes of the posterior cerebro-spinal roots. They agree in that they all communicate an impression made at their periphery; affecting the chord when only spinal action follows; implicating the brain if sensation ensues. In all investigations concerning ganglionic action, the distinction between these cerebral and spinal components is purely inferential, and cannot be founded on anatomical demonstration. Wherever a contribution to a ganglion proceeds from a posterior spinal root, it contains both kinds of nerve-tube, and may be described as an *impressional* nerve.

A ganglion having to superintend molecular organic processes, its first element is that of the organic cell and nerve. Having to associate this organic activity in some instances with impressions made under various modifications on other tissues, the second element is, that it gives passage to an impressional nerve. Associated with the comparatively regular action of involuntary muscles, the third element is that of transmitting an involuntary motor nerve. All but the purely grey simple ganglion, therefore, may be considered as compound;—double, when two elements exist, as in the spinal ganglion; triple, when to the grey and to the impressional nerve, a motor one is added, as in the sympathetic ganglia.

A spinal ganglion, in furnishing organic excitement to parts, is controlled only by the action of the impressional nerves distributed to them, and by the general condition of the ganglionic system. Hence it need transmit its own particular nerves of impression only. But the organs supplied by a sympathetic ganglion must respond to stimulation, sometimes of one, sometimes of another discontinuous part. Hence, a sympathetic ganglion requires a supply from the general centre of origin common to the nerves of all these associated parts. Such a supply is obviously obtained most conveniently by a small contribution from the nerves distributed to each of these parts being sent to the ganglion. In accordance with these functional requirements, we find that spinal ganglia never receive contributions from any other nerve than that to which they especially belong; excepting always the grey filaments of communication which are common to all ganglia alike. They never give off any branches distinct from their grey filaments packed up in the nerve of distribution.* Whereas, a sympathetic ganglion receives contributions from any neighbouring nerve having a functional connection with parts over whose organic activity the ganglion presides ; and gives off branches for distribution in any direction.

A spinal ganglion is always placed on the roots of nerves. A sympathetic ganglion on the branches. A few ganglia, triple in their composition, and so far resembling the visceral ganglia in general, have certain peculiarities which entitle them to an intermediate place between the purely spinal ganglia and the visceral. They are placed neither on nerve-radicles like the former, nor on nerve-branches like the latter ; but always on a nerve-trunk, part only of the filaments of which they involve. Intermediate also in their physiological relations, being allied to the spinal in their more especial functional connection with the individual nerve-trunk on which they are placed ; yet resembling the sympathetic in possessing motor elements. The inferior ganglion of the vagus is a type of this class. As this has been termed " plexiform," we may distinguish the class by the same name, with the condition that, in proportion to the varying amount of their entrant nerves, all ganglia are plexiform. The inaccuracy is of less importance than the possible obscurity which might arise from adopting a more correct new name. Nor in this respect is there any inferiority to the received nomenclature of the other ganglia, since all compound ganglia are literally both spinal, as transmitting spinal nerves, and sympathetic, as maintaining organic sympathies with related parts. As a synonym for a plexiform or nerve-trunk ganglion, the term " fusiform" might be adopted, implying the ordinary form, without signifying anything as to structure or function. Thus, if a ganglion be placed on the roots of a nerve, give off no branches, and receive no contributions from any other nerve, either motor or impressional, than the one to which it belongs, it is a spinal ganglion. If a ganglion be found connected with any other portion of a nerve than its radicles, it will also be found to receive contributions from at least one motor nerve, and generally to give off direct branches of distribution, and is a sympathetic ganglion. If a mere nodule, entirely grey, and connected with other ganglia only by means of grey filaments, it is a simple ganglion—neither spinal nor sympathetic. Of the sympathetic ganglia, if one be an eminence containing grey cells in the course of a nerve-trunk, through which a portion of the nerve-tubes pass, it will be found to receive contributions from other nerves of different function, and is a fusiform sympathetic ganglion, or a nerve-trunk ganglion. The remaining ganglia may be called isolated sympathetic ganglia, or nerve-branch ganglia.

* The filaments described by some anatomists as proceeding from the Casserian ganglion itself, and others from the roots of the fifth nerve centrad to this ganglion, to the membranes of the brain, I have never been able to find.

Assuming the correctness of these distinctions, there can be no longer any difficulty in classing the ganglia. When two occur connected with the same nerve, as in the glosso-pharyngeal and vagus, one only can be spinal, since one only can be attached to the nerve-roots. The second can always be demonstrated to receive a motor contribution, and by this alone is proved to be a sympathetic ganglion. The threefold division of the ganglia is equally plain if founded on physiology. The simple, or as consisting of one element merely, the single ganglion has no direct relation with either impressions or movements; the spinal, or double ganglion, is connected with impressions, but not directly with muscular motion; the sympathetic, or triple ganglion, is connected both with impressions and with muscular action. A sympathetic ganglion usually receives filaments from various motor nerves. This is true of all the prævertebral ganglia. It is true also of several of the encephalic, (*e. g.* the lower ganglion of the vagus; the otic; the submaxillary.) One motor nerve may send filaments to more than one ganglion, (*e. g.* the facial nerve); but there is no proof that the same motor filament ever passes through two ganglia.

It is otherwise with respect to the impressional nerves. Every gangliated impressional nerve has already passed through its own spinal ganglion before its entrance into a sympathetic ganglion. But, moreover, the same impressional nerve may pass through a series of sympathetic ganglia; the glosso-pharyngeal and the vagus, for example, each send a contribution to the two fusiform ganglia on the *portio dura;* to the otic; submaxillary; and perhaps to Meckel's ganglia. Tracing the filament from the glosso-pharyngeal nerve to the submaxillary ganglion, it passes through, 1*st*, the spinal ganglion of the glosso-pharyngeal (*Ganglion jugulare*); 2*d*, the fusiform ganglion of the same (*G. Petrosum*); 3*d*, along with the *ramus auricularis* of the vagus, through the inferior fusiform ganglion of the *portio dura;* 4*th*, as a component part of the *chorda tympani*, through the submaxillary ganglion; through the medium of which it may extend its influence, if not its course, to the sublingual gland, thus constituting a direct medium of connection in functional activity between the several salivary glands, and gustation, so far as that depends on the glosso-pharyngeal. This will be more fully considered hereafter; but at present it serves to illustrate the physiological reason, or final cause, of the presumed difference of arrangement between the impressional and the motor nerves in relation to the ganglia. A muscle has a given duty to perform in obedience to the will, or to excitement of a particular surface. During its action, increased secretion may be desirable on its own related surface, but not on several distinct surfaces or on several distinct organs, at the same moment; unless when the associated action of a group of muscles is necessary, in which case, the nerves of impression must be implicated, and will discharge sufficiently any required association. Hence, a muscular nerve can directly influence only the one ganglion which presides over the organic activity of the surface which the muscle obeys. Were it not so, the contraction of a single muscle might excite secretion in several unallied parts, which would be an extravagance. An impression, on the contrary, requiring excitement of organic action in one part, usually needs it simultaneously in several (*e. g.* any part of the process of digestion); this is at once effected with small expenditure of structure, by causing the same impressional nerve to set to work simultaneously all the allied ganglionic centres.

With similar economy is a sympathetic ganglion subjected to the influence of several, or, occasionally, (as in the superior cervical ganglion,) of very many nerves, any of which can probably excite the action of the ganglionic cells, without, as already inferred with respect to the ophthalmic ganglion, affecting the state of the other nerve-tubes transmitted by the ganglion. This, which is an important law, is proved by the structure of a complicated ganglion, such as the superior cervical, as distinctly as it could be by the most accurate experimental investigation, were the question open to complete solution by such means. Unless the white tubes, which pass through the ganglion, do influence it, of what use would be their transmission? Unless all, whatever their functional endowment, influenced it alike, would there not be some difference discernible in their relative arrangement? and unless each nerve could act on the ganglion without exciting its fellow white nerves, would not strange confusion of action result? When gastric excitement, for example, through the medium of the *par vagum* acted on the superior cervical ganglion, stimulated the *nervi molles*, and distended the capillary system of the face, producing heat and flushing, if the excitement spread to the other nerve-tubes transmitted, we should have always, and of necessity, conjoined the muscular actions presided over by divisions of the facial, hypoglossal, spinal accessory, and upper cervical nerves, in addition to a conjoint excitement of the transmitted impressional nerves. The influence of the transmitted tubes on the ganglionic cells is deducible again from the double gangliation of several important nerves. Unless it can react on the grey cells, why is a motor tube so carefully excluded from a spinal ganglion which supplies parts, whose organic activity would be injured by direct and therefore constant connection with muscular movement, whilst it is always admitted into a sympathetic ganglion which governs organic processes constantly under the influence of muscular contraction? The lower ganglion on the vagus, on the glosso-pharyngeal, the various subsidiary ganglia on branches of the fifth exist, not because the ganglia on the roots of these respective nerves could not have furnished organic nerve force sufficient, but because a portion of the nerves only must have its supplied parts associated with muscular action, whilst the remaining and larger portion of the nerves is distributed to parts not constantly under the influence of muscular movement. For the same reason are the ganglia on the spinal nerves so accurately restricted to the posterior roots. The anterior motor roots avoid the spinal ganglion, not because their voluntary power would be checked by the mere circumstance of their passing through it, but because the uncertain, unequal, irregular action of a voluntary nerve would greatly interfere with the functions presided over by the ganglion. For the same reason, it may be, are spinal ganglia necessary at all, to constitute centres distinct from the chord, and sympathetic ganglia to constitute centres distinct from both. Since in man, as we found in the INVERTEBRATA, nervous centres are amalgamated or disjoined, according as the functions governed are connected or dissociated. But for this, the sympathetic, vagus, and glosso-pharyngeal would not need three separate, but similarly constituted ganglia lying side by side, nor would the eye require an especial ganglion, whilst the lacrymal gland does not.

In the circumstance of some white tubes passing through several ganglia, we see a confirmation of conclusions otherwise obtained. On the hypothesis of every ganglion being a source of motor force, these white tubes could not excite movement in the ultimate ganglion (D), without at the same time exciting contraction of muscles supplied by each of the other ganglia, (A, B, and C,) through which they had previously passed. If ganglia conduced to sensation, a part supplied by a sensational nerve could not have its sensibility affected singly. Its own would be conjoined with sensation in every organ supplied by the other related ganglia, (A, B, and C.) And if, under normal excitement, the grey cells of a ganglion excited the white-tubes transmitted, any one of the related ganglia (A, B, C, and D,) would be unable to act without occasioning the same sensations, and muscular actions; and the transmitted tubes re-acting on the cells in return, ganglion A could never act at all without implicating the rest. Experience teaches us that moderate excitement of one organ does not necessarily occasion either movement or sensation in another; although it frequently does occasion increased secretion. If, therefore, an impressional filament passes through A, B, C, and D, and then proceeds to its distribution, we conclude that it is in order to connect together the organic activity of processes superintended by A, B, C, as well as D, with the state of sentient surface ultimately supplied by the nerve-filament in question.

Hypothesis of the rationale of ganglionic action.—A simple ganglion appears to be merely a centre of multiplication for ganglionic nerves, by means of which one grey filament from the compound ganglion A, may carry excitement to ten or twenty grey filaments arising in the simple ganglion B. Herein no other than grey filaments are implicated as far as the simple ganglion is concerned. But in addition to this conduction of excitement along the grey nerve of intercommunication possessed by all ganglia, a double or spinal ganglion is stimulated by the white impressional nerve-tubes which pass through it. An impression on the skin stimulates the cutaneous nerve at its periphery. The excitement affects the entire length of the nerve, and where the white-tubes separate from each to inclose the grey cells of the ganglion, they impart the excitement to these cells. Thus excited, the grey nerves of the ganglion cause increased organic activity in the part to which they are distributed, which is always the same as that which the corresponding impressional nerve supplies. The result may show itself in mere attraction of blood to the capillaries, (rubefaction from friction), or in secretion, (sweating or vesication). From the same impression, the spinal chord being excited, involuntary muscular action may ensue; or, the influence extending to the brain, sensation and voluntary movement occur. In neither case will the muscular motion have any direct influence over the spinal ganglia. On them emotion appears to be the only additional agent which possesses this power of acting from within.

It is otherwise in a sympathetic ganglion. The mucous surface of an intestine cannot undergo irritation without the stimulus affecting the impressional nerve, the chord, and the spinal motor nerve. In the internal tegument, spinal excitors exceed the nerves of sensation; the reverse obtains in the skin. The motor re-action being uncontrolled by the will, is not a matter of chance but is constant. Hence, in a sympathetic ganglion the grey cells and nerves are submitted to a double excitement. Stimulated on the one hand by the impressional, on the other by the motor nerves, organic activity corresponds both to the impression made and to the movement which results. In this, as in every other arrangement of nervous mechanism, the final cause is twofold; perfect obedience to a normal stimulus; perfect protection from abnormal irritation. By the response of the sympathetic ganglion to the impressional nerve, defensive mucus is instantly poured out; by its further response to the motor nerve, the mucous channel becomes still more lubricated, whilst the cause of irritation is passed on. In this view the chord is made the key-stone of the arch in the action of every compound ganglion; and it generally is so, because increased ganglionic action in most instances responds to stimulation of some surface, and the grey are not surface-nerves. But they are probably the vascular nerves, as far as the capillaries are concerned; and through the medium of the blood, an impression may be made on them earlier and more powerfully than is commonly made on the impressional nerves through the medium of external stimuli. There appears no reason why peripheral stimulation of the grey nerve may not occasion change of action in the ganglionic cells, and in virtue of this change have its own influence over capillary and molecular actions affected; distinct from and independently of any excitement of spinal or cerebral nerve-tube.

We may illustrate this by referring to the frequent variation in the activity of a secreting gland. In the kidney, for example, when the presence of more blood than usual, or the existence in it of some diuretic, occasions increased urinary secretion, it may be that the stimulation affects only, first the secreting cells, then the grey nerve, which in turn causes increased afflux of blood and still more rapid molecular change. Or the grey nerve may be the first link in the chain; and secreting cell and capillary the second. In either case it is unnecessary to assume any implication of white tube, or any reflex action. Still in almost every instance with which we are familiar, the chord is co-operative with the ganglion; and in many the brain participates. When lithic acid is irritating the kidney, it checks secretion by deranging the grey nerve; it may cause cramp by deranging the spinal nerve; and pain in the loins by deranging the cerebral. A small dose of turpentine will do the same.

A second series of phenomena from the same cause, in higher intensity, may be renal irritation, spasmodic retraction of the testis, nausea and vomiting, and febrile disturbance. In this and in every analogous case, brain, chord, and ganglion, all work together. In fever commencing with the blood (true typhus), the derangement may affect in order, blood, grey-nerves, and ganglia, chord and brain, inducing their various reactions, which include every possible kind of derangement of which the system is susceptible.

In the nervous supply to a gland we find white tubes. In the large renal plexus, although grey nerves predominate, there is a quantity of white nerve. The kidney possessing no inherent contractility requires no muscular nerves. For the blood-vessels and excretory ducts a few may be required. And as the kidney, like other glands during normal action, conveys no sensation, although some nerves of sensation are needed in it, as in every other living structure, to give us timely notice of disorder, yet for this,—the exception not the rule,—added to the small requirement for motor nerves, the proportion of white tubes appears greater than would have been necessary. The urinary secretion is greatly under the influence of the condition of the blood, as to quantity and quality; and of the circulation, as to force and rapidity; yet when over-secretion in the kidney is consequent on a given state of some distant part, no general interference with the action of the heart or the condition of the blood existing, the command to the kidney can be conveyed only through the nerves. Imitation and fear influence the organic nerves of the kidney through ex-centric action of the nerves of sensation; cold to the skin, partly through sensation; chiefly through spinal action, affecting the secretion of the kidney through impressional nerves, the contraction of the urinary canals through motor nerves.

Ovarian irritation in hysteria occasions diuresis, partly by emotion, partly by spinal excitement, in a similar way. Now, if analogous sympathies occur without our consciousness of their operation, without sensation or emotion, we have no evidence of cerebral participation, and may reasonably infer that the effect is produced entirely through the medium of the chord and ganglia. The sympathy between the stomach and the kidney is a common illus tration. Reversing the order, and commencing in the kidney, irritation there can only re-act on distant parts through the intervention of a common centre. The chord and the brain are centres common to every part, and each admits of instant response to excitement. The ganglionic system is likewise a common centre of supply for the organic nerves, but is unfitted by its structure, and by the absence of direct relation to exposed surfaces, for producing sudden sympathetic actions of distant parts. A grey nerve has never been traced right through ganglion A, B, C to D, but if it joins A it ends there; another connects A with B, and so on. A grey nerve could not, therefore, convey excitement to D, without exciting in its course A, B, and C. It does this, and by so doing produces the general harmony in organic action met with in perfect health. But by doing this, it is unfitted for the production of sympathies. The ganglionic system is the engine, but the brain and chord are, one or both of them, the engineer. Either brain or spinal chord would, therefore, be more justly entitled the centre of the sympathetic system, than what we now term such; but by referring the various associated phenomena to different heads, according as ganglionic, spinal, or cerebral action predominates, we shall attempt to establish a natural arrangement of sympathies.

A secreting organ receives white nerve tubes, therefore, in order that it may be brought into such relation with chord and encephalon as will permit of sympathetic actions, normal or abnormal. For the purpose of governing the disposal of ganglionic energy, by the intimate connexion of the encephalic nerves, but more particularly of the spinal nerves, with all parts of the sympathetic, the brain and especially the chord seem peculiarly fitted. But still as the sensorium generally presides over the spinal motor tract, and yet the chord itself is an independent centre; so also the chord being the medium of quick communication between distant organs, presides over the consentaneous action of their ganglia, and yet the ganglia remain independent centres.

It is assumed throughout that the nervous force travels, in the sense in which similar language would be applied to the electrical force, *down the nerves*, whether the stimulus which calls it forth proceed from without, as in sensation, or from within, as in emotion. But this part of the hypothesis is not essential to the rest, and its refutation would nullify none of the other statements concerning ganglionic action. If it be preferred, therefore, to consider the impressional nerves as acting in all cases centripetally; the motor nerves centrifugally; the only difference in the explanation will consist in assuming that the excitor nerves stimulate the ganglia by acting in one direction; the motor and emotional nerves by acting in a reverse direction. According to this view the afferent nerves would excite the ganglionic nerves in a reflex; the efferent in a direct manner. It would be a necessary inference also, either that emotion acts only through motor nerves, which will not explain all the phenomena; or else that special nerves exist for conducting the emotional influence.

Relation of the Ganglia to Emotion.—Have we any reason for assuming that emotion influences secretion and nutrition through the medium of any special nerves; or does it not rather act through some or all of the nerves ascertained to possess other endowments? The state of excitement, or of marked depression, to which the term emotion is conventionally restricted, is merely a different degree of one, or more generally of several at once, of our common feelings of mental pleasure or pain. It is no one peculiar condition of mind; but a condition which may accompany any other. Feeling is essential to emotion; but we must not confound the state of mental consciousness which we so designate, and sensation. Sensation occurs with emotion, only when it excites our feeling; without it, when the sensation merely excites the intellect. Intellectual operations coincide with emotion when they arouse the feelings; but the highest efforts of pure intellect are compatible with freedom from emotion. Sensation can exercise itself apart from any act of volition, of intellect, or of feeling and emotion. Feeling can be exercised without volition, intellect, or sensation, but not without emotion, however low may be the degree. Volition can be exercised without reasoning, feeling and emotion, or sensation—although this rarely happens. Pure intellect can exercise itself without volition, sensation, or feeling and emotion. Emotion is never presented without feeling. Feeling is never presented without emotion. The centre for the one is probably the centre for the other. Accepting the ascertained power of functional independence as our guide for admitting separation of centre, we infer that the encephalon comprises a distinct centre for pure intellect; another for sensation; another for volition; and a fourth for feeling and emotion conjointly. Admitting association in the discharge of function to be a proof of such a structural arrangement existing between the different centres as shall permit, though not necessitate, consentaneous action—we must expect all the centres to be anatomically connected. Consciousness resides equally in all. To mark out an especial organ for consciousness appears absurd. We are conscious of willing, of thinking, of feeling and emotion, and of sensation. Of these assumed separate centres, each can rouse one alone, several, or all of the others to co-operate with itself. Now emotion when intense always does this. As the emotional centre must therefore possess such an anatomical relation to the other centres as to impart its influence to each and all of them, it may thus affect each and every variety of nerve-tube originating in the several centres. So far we find no ground for admitting the existence of special nerves for conducting emotion. Emotion will heighten or obtund sensation ; increase or diminish muscular power ; promote, check, or chemically alter secretions. Hence, if there be any special nerves of emotion, not only must some of these accompany all other nerves, but they must have the precise relation in their distribution which each kind of the other nerves possess. Again, although different emotions are manifested in a very different manner, many of the same muscles are excited in each ; in joy, grief, and rage, for example. Hence all the muscles of expression, *i. e.* almost every voluntary muscle in the body, would require a complete supply of emotional nerves, not only for emotion of one kind, but of every kind, originating therefore in every cerebral organ subject to emotion ; and as every cerebral organ may become emotionally excited, the source of supply must be excessive. It is far preferable to assume that a *centrum commune* exists in the encephalon, through the medium of which every centre may influence the same nerve-tubes ; where a sensation, a feeling, or an idea, may excite the non-psychical part of the nervous system, with or without the conjoint operation of the centre of volition on the same part.

Considering the centre of the feelings, and the centre of emotion, to be one and the same ; bearing in mind the variety of mental conditions which enter into what we are accustomed to view as a single emotion, and the number even of the names under which we enumerate these various complex mental states, we shall hesitate in assigning to any comparatively small portion of the encephalic mass the office of centre of emotion.

By assuming the existence of a *centrum commune*, or common point at which the mental acts produce their first obvious effects on the body, we explain away the main argument for placing a distinct centre of emotion lower down than the *corpora striata ;* viz. in some cases of extravasation into the lateral ventricle, muscular movements may be excited by emotion, notwithstanding all power of effecting these by an effort of volition is destroyed. In explaining this, we are reduced to two alternatives. (1.) The seat of emotion must be placed below that of volition. (2.) There must be some other channel besides that of the volitional centre, through which emotion may affect the origin of the motor nerve-tubes.

Recollecting that all the volitional fibres are crossed; that the sensational ones are part crossed, part straight; that certain fibres of the motor tract also are straight, and that these cannot be volitional; we have only to assume that emotion can affect every kind of nerve-tube, as its centre can influence every other encephalic centre, and we shall have a full explanation not only of the fact above noted, but by analogy of several others heretofore inexplicable. Emotion may still affect the direct fibres, both sensational and motor, on the palsied side, although by an extravasated clot the crossed fibres are disabled. Sensation is scarcely ever quite obliterated in hemiplegia, because each half of the body has sensational fibres from each side of the brain. If the crossed fibres are compressed, the straight ones are not. In palsy, a patient is occasionally enabled to hold an object when looking at it, but not otherwise. Here the special sensation of sight reacts through the assumed *centrum commune*, precisely as a spinal excitor reacts on its corresponding motor nerve. We may thus account for the ordinary reaction of sensational upon motor nerves constantly taking place, though without our notice, and also for the simpler instances of what has been termed the reflex function of the brain. In many of the less simple examples adduced, to the merely physical, always similar reaction of mere sensation has been superadded the psychical, ever changeable, influence of the mind, roused to action by the sensation. The instantaneousness of result is not greater than in many acts allowed to be volitional. Perhaps the rare instances of complete cerebral palsy, without any disease of the chord, in which excito-motory phenomena cannot be artificially elicited, may be due to the controlling influence of the sensational centre upon the motor tract in preventing spinal action.*

What relation has the cerebellum to this *centrum commune?* (See Figs. 29, 30, and 31.)

Assuming that the influence of emotion extends to all the ne-

* On the questions alluded to above, see a review of Noble on the Brain, in the British and Foreign Medical Review for 1846; Todd and Bowman's Physiological Anatomy, Vol. i. pp. 346 to 360; Dr Laycock's writings; a correspondence in the Lancet for 1845, between Mr G. Combe and Drs Reid and Laycock; Dr Marshall Hall in his "Diseases of the Nervous System," § 984; and in the Lancet for May 15th 1847. More especially the various works of Dr Carpenter by the complete development of whose views we may confidently expect the subject will be cleared up.

cephalic nerves, we have to ascertain its mode of action. It can madden with excitement or kill by shock. All emotion, therefore, acts either as a stimulant or as a sedative, and it acts from within. If we can imitate its effects on distant and separate organs, by applying stimulants and sedatives from without, we gain as fair an argument as the circumstances permit, that both kinds of agency can affect similar nerves.

In the experiments of Le Gallois and of Wilson Philip, on artificially irritating various portions of the brain, and of the spinal chord after removing the brain, the action of the heart became accelerated. After tying the abdominal aorta in a frog, and thus cutting off the influence of the heart, on irritating the chord, the capillary circulation in the web of the foot underwent changes. Hence the same kind of stimulus may affect the same distant part through the medium of encephalic and of spinal nerves. The capillaries may be affected by irritating either the cerebral or the spinal nerves, but no experiments are recorded by which it is clearly established that they can be excited through the medium of the grey organic nerves alone, all assistance from the brain and chord being suspended. We may infer this, however, since it is proved that shock may so operate; and if the organic nerve responds to a sedative, it would doubtless do the same to a stimulant if we understood how to test it.

Instant death from a blow on the head or on the back is enough to prove that shock can act through either cerebral or spinal nerves. But if cases of accidental injury be unsatisfactory, the experiments of Dr Wilson Philip and of Brachet on warm-blooded animals, of Mr Clift on fishes, and of Dr Marshall Hall on batrachians, confirm the conclusion that shock from without,—and emotion is oftentimes but shock from within,—can act through cerebral, spinal, or ganglionic nerves. Through cerebral nerves combined with the other two; through spinal, disconnected from the cerebral, but combined with ganglionic; through the ganglionic nerves uncombined. From their structural relation to each other, the three kinds of nerve can only be isolated from above downwards. We cannot separate the chord from the ganglia in testing the action of spinal nerves, though we can cut off the ganglia from the chord in testing the grey nerves. We cannot separate the encephalon from either chord or ganglia in testing the cerebral nerves, though we can remove the influence of the brain in examining the spinal centre.

In Dr Wilson Philip's 17th experiment, the cervical part of the chord and lower half of the brain were first removed. Spirits of wine, tincture of opium, and tobacco, affected the action of the heart quite as much when now applied " only to that part of the brain which lies between the eyes of the frog, and precisely in the same way as when they were applied to the entire brain or spinal marrow." The chord and the origin of all the nerves connected directly or through the medium of the sympathetic with the heart were destroyed. Through what medium was the influence transmitted to the heart? If there be no fallacy in the matter, there would appear some ground for admitting that grey sympathetic fibres might join the lower part of the brain anterior to the point of section, and that the stimulus might act through them; an important fact, if it were so. It is more likely that the strong liquids were imbibed and reaching the heart as rapidly as (from Mr Blake's inquiries,) we know it can, there stimulated the lining membrane of the cardiac cavities, which the investigations of Dr Charles Henry and of Mr Ransome have proved to be very susceptible to such an influence.

The most interesting and the neatest experiment is one of Dr Marshall Hall's, (*loc. cit.* § 24.) "Both the cerebrum and the spinal marrow," he writes, "may be entirely removed in a frog, by small portions at distinct intervals, without destroying the circulation in the web: this function, then, depends on (?), and can be impressed by the ganglionic system *only*. There is neither cerebral nor spinal function left; there is neither cerebral nor power of reflex excited motion. If we now crush one foot, an extraordinary effect is produced: the circulation in the other is instantly and completely arrested! This effect can only have been produced through the ganglionic portion of the nervous system; and I think this is the only published experiment of the kind."

If we deduce the mode of action of emotion from its analogy to that of other agencies which are open to experimental investigation, we shall arrive at the following conclusions: (1.) The excentric conduction of emotional influence cannot be restricted to the motor nerves, as that would not explain all the phenomena. (2.) As we have no data to justify our admitting a distinct and special class of nerves for the conduction of emotion only; and as, emotion being able to affect every point supplied with nerves of any kind, such an apparatus would need to be co-extensive with all the rest of the nervous system; the arrangement would be extravagant and appears superfluous. (3.) Emotion being essentially a condition of mind can only in the first instance affect nerve-tubes originating in the brain; but in virtue of what, for the sake of avoiding repetition, I may term the law of synergetic action, these cerebral nerve-tubes will affect secondarily all the grey nerve-cells through which they pass, thus imparting the emotional influence to the chord, and then to the ganglia. (4.) In similar mode, the nerve-tubes arising in the grey cells of the chord, having had their origins excited by the transmitted cerebral nerve-tubes, impart *their* excitement also to the ganglia through which they pass.

(5.) In this way, directly or indirectly; primarily or secondarily, as regards our conception of the sequence; but considering the celerity of nervous action, instantly it may seem as regards the result; emotion can affect each and every nerve-filament in the body. (6.) So much being granted, the *occasional* conduction of influence in a centrifugal direction of sensational, spinal-excitor, and ganglionic grey nerve must follow.

We thus comprehend how it is that pleasurable emotions will assist, unpleasant ones derange, every function in the economy. We have confirmed what daily experience teaches, that to temperance and exercise we must add *good spirits*, to preserve health in its perfection. We see the philosophy of happiness, and the science of religion.

Various ganglia.—Amongst the ganglia of man enumerated by different anatomists, two have been named which subsequent examinations have failed to verify. The ganglion described by Cloquet as existing on the naso-palatine nerves in the anterior palatine canal, is in reality nothing more than the conjunction of the two nerves where they become enclosed in the same sheath. A ganglion stated by Huber to be placed on the spinal accessory and the posterior root of the first cervical nerve, where the two cross each other at a right angle, is merely a connection of the nerve-sheaths by means of fine areolar tissue. The ganglion of Ribes, on the communicating branch of the anterior cerebral arteries, I have never been fortunate enough to see. Its minute relations are not ascertained, but it is considered as the cephalic analogue of the *ganglion impar.* The spinal ganglia as a rule are never absent. Sometimes the first cervical nerve possesses no posterior root, and in that case it possesses no ganglion. In some amphibia the two highest cervical nerves always consist of the anterior non-gangliated portions only. The fusiform ganglia on important nerves and the more isolated sympathetic ganglia of the head are constantly present. Their function being the accurate association of certain intimately related sensori-motor parts, their deficiency would entail disorder of action. But the less especial sympathetic ganglia being rather for the augmented supply of organic nerves to parts widely related, than for special and exact association, vary considerably. All the small ganglia interspersed amongst the plexuses of the sympathetic in the carotid canal, in the neck between the carotid arteries, and in the thorax and abdomen; the nodules on the vertebral branch of the inferior cervical ganglion; the middle cervical ganglion, and the two or three higher prævertebral ganglia in the chest, are subject to variation. When deficient, their place is sometimes manifestly, perhaps always in fact, filled up by extra-development of a neighbouring ganglion. Thus, when the middle cervical ganglion does not exist, the spinal contributions belonging to it are sent to one or other of the two sympathetic ganglia of the neck.

Relation of the grey nerve to the encephalic and spinal centres.— It is difficult to determine whether the grey cells of a ganglion be directly connected with those of the brain and chord by means of grey filaments. It is quite certain that no purely grey nerve passes by itself from any ganglion to either of these centres; but as grey filaments are met with abundantly in many nerves of communication, we have to pursue these to their destination to decide the question. A "*ramus communicans*" between a sympathetic ganglion to a given cerebro-spinal nerve, where only one exists, will serve as the most intelligible type of the nature of the connection under consideration. If two exist, as frequently happens, one alone may possess the grey filaments. A perfect communicating nerve consists of both white and grey fibres. All the white tubes may be traced proceeding towards the chord, passing in distinct fasciculi into the anterior and posterior divisions of the spinal nerve-trunk. The grey filaments are not diffused amongst the white tubes, but keep together, appearing when compressed as a flat band. When they have reached the nerve-trunk, all the white tubes direct themselves centrad and become lost amongst those of the two sets of spinal nerve-roots. The grey filaments comport themselves differently. Immediately on reaching the nerve-trunk, they separate into two distinct and diverging bundles. One fasciculus passes peripherad along with the nerve for distribution. The other proceeds centrad into the intervertebral ganglion, amongst the cells of which the grey filaments are lost. The division into these two fasciculi never takes place whilst the grey filaments are yet in the *ramus communicans;* it occurs as soon as this joins the spinal trunk, and therefore at a very variable distance from the chord. This is well exemplified by the communicating branches from the first thoracic ganglion in most mammals. A short thick branch joins the largest brachial nerve at some distance external to the intervertebral foramen, whilst the junction with the higher brachial nerves which is effected by that branch of the ganglion which is enclosed in the canal with the vertebral artery, is much nearer to the chord. Although the grey fasciculus of the *ramus communicans* splits into its centric and peripheric divisions as soon as it reaches the nerve, yet as the junction with an extra-cranial nerve never takes place until after anterior and posterior portions of the cerebro-spinal trunk have become intermixed, we cannot ascertain at this point the actual relation of the ganglionic to the sensational and motor fibres in nerves of distribution.

So far as I have been able to ascertain, the whole of the grey filaments which direct themselves towards the chord, pass into the spinal ganglion, and there terminate. I have never satisfied myself that I could distinguish a single ganglionic filament in either the anterior, or the posterior roots of the spinal nerves. For examination, I have used principally the long roots of the *cauda equina* in some young small animal, as the rat, mole, kitten, rabbit, and puppy. Cylindrical nerve-tubes, which vary greatly in size, are seen to cross each other in wavy bands in each root; but the smallest in calibre is clearly distinguishable from the ganglionic filament. Nor have I ever found grey filaments at the origin of any motor cerebral nerve; nor in the cis-ganglionic roots of the trigeminus, the glosso-pharyngeal, and the vagus.

Viewing the sympathetic as the source, the obvious direction of its communicating branches to the cranial nerves indicates generally that the sympathetic seeks the nerves, and not the centre in which they originate. In man the projection of the jaws being less than in any other animal possessing a neck, the cephalic portion of the sympathetic is more nearly vertical, and has no greater direction forwards than might be due to the tortuousness of the canal in the base of the skull, through which it has to pass. Still, even in man, whilst the parts are undisturbed, no twig from the carotic plexus is seen to direct itself in such wise as to reach in the shortest manner the roots of any cerebral nerve. The filaments to the tympanic plexus certainly proceed backwards; but these are undoubtedly for the purpose of distribution. The filaments which join the sixth nerve, sweep forwards and upwards, never directly backwards, as if for the purpose of arriving at the cerebral origin of the nerve. It is true that at the point of junction these communicating nerves often form an obtuse angle behind, as if the final direction of the filaments was towards the brain; whilst another communication will present an obtuse angle forwards, as if its direction was towards the distributed portion of nerve. But this arrangement may be accounted for by considering the former communication to comprise chiefly the nerve-tubes from the brain to the sympathetic; the latter to convey principally the filaments from the sympathetic to the nerve.

It is only in reference to motor nerves that the question can be raised; since certain grey filaments invariably join every ganglion; and as the sympathetic never, I believe, effects its junction with a spinal ganglion by entering at its centric end, or in company with the roots of the impressional nerve on which it lies; and never enters its ganglionic substance, excepting at the part where its nerves are emerging for distribution, whenever the sympathetic is placed anteriorly to the spinal ganglion, certain grey filaments to that ganglion must pass in a backward and centric direction. This is the case with the prævertebral ganglia in general; their communications with the spinal nerves all seem to seek the origin of those nerves. Knowing the necessity for arriving at the spinal ganglion, this does not prove that the grey filaments proceed so far centrically as to enter the roots.

A similar remark will apply to the encephalic nerves of common sensation, all of which receive ganglionic twigs which proceed from the sympathetic towards their origins. Thus the upward and backward direction of the large grey division of the superior cervical ganglion, which passes towards the eighth pair of nerves, is sufficiently explained by its having to reach the ganglia on both glosso-pharyngeal and vagus, and also to furnish a grey contribution to each of the petrous nerves given off close to the jugular fossa. The slightly backward direction of some, but not of all, the twigs sent to the fifth nerve by the carotic plexus may likewise be owing solely to the relative position of the Gasserian ganglion at the entrance of the sympathetic into the cranium. The sympathetic crops out of the base of the skull, just under the anterior and inner margin of the ganglion of the fifth nerve, and pursuing its original course forwards and upwards for a short distance, must necessarily direct backwards any contribution for the ganglion. Still, even in man, these retrograde communications are few and small in comparison with the filaments which direct themselves forwards to join the distributed portion of nerve. A grey filament is never found to connect itself with a sensational nerve-root, although it may pass this in close proximity, pass also the ganglion through which the root is transmitted, and then be reflected into the ganglion. This however would merely prove, that if the sympathetic filament be destined to enter the nerve-root, it must first pass through the spinal ganglion. Hence we are reduced to appeal to the non-gangliated nerves for solution of the question. Now, if a purely motor nerve, in any case, conveyed grey filaments to its own centre, it would be most convenient for the sympathetic to furnish the supply as near to the origin of the nerve as its own position would permit. But if on the other hand the supply were for distribution only, we should expect the communication to take place at any part centrad to the distributed portion of nerve; to be directed *from* the brain, unless some peculiar convenience of transmission prompted otherwise; and to vary according to the relative position of parts in different animals.

In man, although the junction of the sympathetic with purely motor nerves favours the conclusion that the grey nerves do not pass towards the brain, yet it takes place sufficiently near to the origin of the nerves to be inconclusive. There is never, however, any contribution sent to the motor root of the fifth whilst within the cranium although the sympathetic lies in such close contiguity. But in animals without a neck, where there is less necessity for protecting the sympathetic during movement of the neck and face, by packing it up in the neurilem of a stronger nerve, any communication that can be distinctly made out between the sympathetic and the motor nerves of the eye, takes place within the orbit. And the long ascending branch from the first thoracic ganglion, which accompanies the vertebral artery in mammalia, might readily connect itself with the radicles of the spinal nerves, if any grey filaments were really destined to the chord. But it never does so; its communications are always made with the compound nerve external to the ganglion.

Hence, if I might depend entirely upon my own observations on this point, I should conclude that there are no grey filaments from the encephalic or the spinal nerve cells direct to the ganglionic cells, but the ganglia are only indirectly connected with either brain or chord by means of the transmitted white tubes. We may at least infer that if they exist, any such grey filaments of communication must be extremely few in number, and to be made out only with difficulty, since of the physiologists who have paid most attention to this question, and who answer it in the affirmative, Remak states that he has occasionally succeeded in detecting organic filaments in the roots of the spinal nerves. Mayer has done the same, and Bidder and Volkmann rate the proportion in which they are present in the root of a spinal nerve of a frog, whether motor or sensitive, as scarcely two per cent.

Connection of the Sympathetic with the Encephalic Nerves.

In *Fishes*, the sympathetic chain is but slightly developed, and its cerebral connections, so far as they have been demonstrated, are less extensive than in higher animals. Cuvier supposed it to be devoid of ganglia, an oversight corrected by Weber, who detected these enlargements on the sympathetic in *silurus glanis* and *lucius perca.* Their existence, however, when the sympathetic joins the spinal nerves, is not constant. Carus was the first to describe the connection with the vagus and fifth nerve in *gadus lóta*, (burbot). He also states distinctly that he found small ganglia where the sympathetic connected itself with the intervertebral nerves. In the skate, Swan could not discover any cerebral connections of the sympathetic, unless its communications with visceral branches of the *par vagum* might be so considered. He describes, however, a small ganglion connected with the fifth nerve, underneath the skin of the lower jaw, near each angle of the mouth, which he considers may be homologous to the submaxillary ganglion. In the cod, there is a distinct connection between the sympathetic and the fifth, glosso-pharyngeal and vagus; no connection with the sixth; but within the orbit, a prolongation from the sympathetic, where it lies beneath the fifth, joins the third nerve, (fig. 23.) In the cat-fish, (*silurus glanis,*) Weber found the sympathetic to be connected only with the vagus; but a nerve proceeded from this towards the fifth, and Weber had no doubt that in reality the sympathetic was joined to both fifth and eighth nerves. Cuvier supposed that the sympathetic joined the sixth nerve in the cod. This is not supported by subsequent observations; but Owen finds such a connection does exist in the carp and lump fish.

In *Amphibia*, the sympathetic has been chiefly examined in the frog, snake, and turtle. Carus and Otto could not discover a sympathetic nerve in serpents. Weber likewise failed to find any trace of it in the serpent, probably because the species dissected were too small. He found it in lizards, but was unable to make out its relations. His description of the sympathetic in the frog is very minute and accurate. The arrangement in different species is the same. Weber appears to consider the ganglion on the vagus as the encephalic extremity of the sympathetic, and describes branches proceeding from it as communications from the sympathetic. In this way he makes the sympathetic to communicate with the ganglion on the vagus by one nerve, and with the ganglion (?) on the fifth by two. Of the latter, one had previously been described erroneously by Carus as joining the sixth nerve. In the turtle, the sympathetic has an intra-cranial connection with the facial nerve and with the second division of the fifth; an extra-cranial connection with the facial, glosso-pharyngeal, vagus and hypo-glossal nerves, (Swan); and, according to Cuvier, it possesses very distinct ganglia where it unites itself to the spinal nerves by double filaments on each side of the spinal column. In the snake, (*boa constrictor*), Swan finds a distinct superior cervical ganglion, of the connections of which he gives an extremely beautiful representation in his eighteenth plate. It communicates largely with the glosso-pharyngeal; to a smaller extent with the vagus, facial, and hypo-glossal. It sends forward a long branch through a canal at the base of the skull, which joins the second division of the fifth in two places. At each point of junction there is a small ganglion, from which filaments are supplied to mouth, palate, and nostrils.

In *Birds*, the sympathetic, the glosso-pharyngeal, vagus, hypoglossal, facial, and second division of the fifth have been found to intercommunicate in all the species which have been examined. The facial is most closely connected with the sympathetic; the hypoglossal with the vagus. The connection between the sympathetic and the glosso-pharyngeal is so intimate, that their ganglia often appear to have coalesced. This is the case in the pelican, in which Swan figures a long nerve from the ganglion homologous to the superior cervical and petrosal combined, passing forward into the orbit, where it supplies Harder's gland, and becomes connected by separate filaments with the branch of the third nerve passing to the inferior oblique muscle of the eye, and with the ophthalmic division of the fifth nerve. The second division of the fifth receives a contribution from the sympathetic, and afterwards gives off the lacrymal nerves. In the goose, the sympathetic, the glosso-pharyngeal, and the vagus are intimately connected together. Weber figures a distinct ganglion on the glosso-pharyngeal, another on the sympathetic, but none on the vagus. Swan figures the superior cervical ganglion apparently amalgamated with that of the glosso-pharyngeal in one instance, separated from it in another.* Bazin draws these two ganglia as distinct in the eagle; and in the ostrich, he represents a distinct enlargement on the vagus, another on the glosso-pharyngeal, and another on the sympathetic lower down in the neck, after it has emerged from the canal of the vertebral artery. In birds generally, Weber remarks the superior cervical ganglion is peculiar in the circumstance, that it receives no communicating branches from the spinal nerves, its continuation in the canal of the vertebral artery being joined by its ganglia with each root of the cervical nerves. He failed to discover the intra-cranial connection of the sympathetic with the sixth nerve asserted by Cuvier. Owen states, however, that through the aperture of exit for the vagus, sympathetic filaments pass in to join both fifth and sixth nerves.

In *Mammalia*, the superior cervical ganglion always exists as a distinct ganglion. It is variable in shape, but always elongated from above to below. It is relatively larger than in the three lower classes. It sends off towards the encephalon communicating filaments to the fifth nerve, glosso-pharyngeal, and vagus; to the sixth, *portio dura* of the seventh, spinal accessory, and hypoglossal nerves. Occasionally it has been found connected with the trunk of the third and of the fourth nerves.

It needs but a small share of practical experience with the difficulty of accurately dissecting the minute relations of the sympathetic at the base of the skull to induce us to receive with jealousy any but positive evidence concerning them. It is so easy *not* to find a given connecting filament, that its non-detection, except after repeated observation by different anatomists, is scarcely a satisfactory proof of its non-existence. Still from the sketch which has been furnished from the dissections of the highest authorities on the subject, we may glean some important inferences. (1.) As there is no distinct sympathetic nerve in the head of the skate, either ganglionic action is not essential to the functions of the encephalon; or otherwise, the function of the sympathetic may be occasionally discharged by some other gangliated nerves. That the latter is the legitimate conclusion is presumable from the alternation in point of development between the trigeminus and the

* See his 23d plate, figs. 1 and 2.

vagus on the one hand, and the sympathetic on the other. (2.) If a cerebral ganglion can thus replace a sympathetic one, acting vicariously, there can be no essential difference in the mode of action of different ganglia. (3.) As the connection of the sympathetic with the purely motor nerves is very uncertain in its existence, and variable as to the nerves to which it relates, it cannot confer on the motor nerves anything essential to their especial function. (4.) As in every single instance where the sympathetic has been found at the base of the skull, it has been ascertained to connect itself to all the sensational nerves, such a connection does appear to be indispensable.

Destination of the grey filaments which join motor nerves.—The much noticed connection between the sixth cerebral nerve and the sympathetic has probably been overrated in importance. It cannot be essential to either nerve, or its existence would be universal and uniform, under similar circumstances of requirement. Weber was in error in denying its existence in the calf and the sheep. It is present, although to a much less marked extent than in the dog and cat. In these, again, it is less considerable than in man. The true reason may lie very near the surface. Where the antero-posterior axis of the skull is the longest, the sixth has to pass forwarder, before by descending towards the sphenoid, it comes into proximity with the sympathetic. But where the long axis is vertical, as in man, the sixth is the nearest nerve to the sympathetic, on the emergence of the latter from the *foramen lacerum.* In every animal, either directly, or mediately after twining round the sixth nerve, the greatest number of sympathetic filaments proceed to the divisions of the fifth nerve. Still there are some connecting filaments proper to the sixth nerve; others have been traced to the third, and more rarely to the fourth nerve, both in man and in the higher mammalia; and from the direction of these connections, it is presumable that they are intended at least in part for distribution.

In fishes, the sympathetic furnishes distinct filaments to the orbit which can be seen to enter secreting structures, or else appear to be lost in the meshes of the pellucid areolar tissue. They cannot be traced into the orbital muscles. Hence, it would seem that grey sympathetic filaments are wanted for the other soft textures in the orbit, but not for the ocular muscles. In man also, the muscular nerves of the eyeball give off extremely minute filaments, which are apparently lost in the surrounding areolar tissue. As these motor nerves are usually unmixed with sensational fibres,* the filaments referred to are probably ganglionic; motor, from their distribution, they cannot be. Every gland having a special

* A common exception is when the fifth and sixth have previously communicated within the skull.

relation to some other part, has usually an especial ganglionic supply for the purpose of maintaining that relation. The adipose and areolar tissue undergo change of nutritive action in response to the system at large, and to the local activity of contiguous parts; but they have no particular functional relationship to any special processes occasionally or periodically called into play. Hence they need no especial ganglia, but are supplied by the sympathetic sufficiently to bring them in unison with the existing condition of the system at large.

As regards the orbit then, minute anatomy has shown that the areolar tissue occasionally receives filaments from muscular nerves; but has not by the microscope demonstrated the character of these filaments. Comparative anatomy proves that the sympathetic sometimes does, and sometimes does not furnish grey fibres to the ocular motor nerves; and that in the latter case, it invariably sends grey filaments directly to the areolar tissue in the vicinity of the muscles which the motor nerves supply (*e. g.* various fishes). As we cannot doubt but that the orbital muscles are just as energetic in their nutrition and muscular action (? the same thing), where they have not received filaments from the sympathetic, as where they have, the supply is probably not destined for the muscles, even when it is enclosed in the sheath of the motor nerves. The white motor nerve-tube may possibly stimulate the grey unisolated filament as the two pass together in close proximity, and thus secretion in the cells of the surrounding areolar tissue may proceed *pari passu* with the action of the muscle; or, the grey filament may merely join the stronger nerve-tube for convenience of packing and transmission. The blood-vessels and the glands in the orbit being furnished with organic nerves in another way, the supply is not likely to be for them. The adipose and areolar tissues alone remain. Both are secreting structures; and both, as shown in other parts of the body, are influenced greatly by the system in general.

It is difficult to adduce pathological proof that the nerves can directly modify the secretion in the fat, and in the areolar tissues. In the local œdema around an inflamed part, we cannot ascertain how much of the increased exhalation in the areolar tissue is due to the mere physical obstruction of over-distended blood-vessels, and how much to disordered innervation. In the dropsy of anæmia, how much to mere transudation of too thin blood, and how much to an impairment of those nervous reactions which, in the higher animals, seem to be essential to vigorous health. In the œdema of cancer, and of *morbus Brightii*, how much to a morbid condition of blood irritating the organic and other nervous centres, and how much to general dyscrasy. Hence, in these cases, the rationale being purely conjectural the most obvious is the most received. The mechanical influence of gravitation in producing swelled legs where the system is greatly enfeebled; of pulmonic, cardiac, or hepatic obstruction, in causing their various forms of serous effusion, is reasonably referred solely to the physical condition of the blood-vessels and their contents, irrespective of nervous agency. But when the hemiplegic side in a case of palsy becomes œdematous, and the œdema is accurately limited by the mesial line, what gives the limit? Granting an alteration in the state of the capillaries of the palsied side, the vessels can only be sufficiently affected through the medium of the nerves. The vessels do not end abruptly at the median plane; the nerves do. In severe hemicrania, the eyelids on the affected side will sometimes become œdematous, whilst those on the other side remain unaffected. The over free application of nitrate of silver to a single point of the uvula will often occasion instant œdema of the whole. Strong applications in gonorrhœa will sometimes have a similar effect on the prepuce. The œdematous wheals of severe urticaria, and the puffy swellings almost instantly occasioned by the sting of an insect, are other instances of effusion into areolar tissue, hardly to be explained without admitting the direct influence of the nervous system over the natural secretion. Mere mechanical exudation from over-distension of vessels is not sufficient. The eyelids contain more blood in conjunctivitis, the uvula in tonsillitis, the prepuce in chordee, the skin in measles, without any such œdema; and it occurs, too instantaneously, to be so explained.

As regards adipose tissue, it is not to be supposed that any action of the nerves can cause the deposition of fat from blood not fitted by its chemical composition to lay it down. But nervous irritation is well known to check this, whatever the condition of the blood, to an extent beyond what its obvious interference with the state of digestion, circulation, and respiration, and muscular action will account for. Probably, however, of all the soft tissues, fat is least under the direct influence of the nervous system.

Until we know how the organic nerves terminate, and their mode of action on the parts under their influence, it is no real objection that the grey filaments assumed to preside over secretion, in adipose and areolar tissues, appear few in proportion to the extent of the textures they supply.

Destination of the grey filaments which join sensational nerves.—All reasoning on this question must be inferential; nothing has been demonstrated. Even if we could satisfactorily trace the precise relations of the grey filaments in the peripheral terminations of impressional nerves, which has not yet been accomplished, we could not possibly ascertain whether a given grey filament had its origin in the spinal, or in the sympathetic ganglion, which are both so intimately related to the nerve trunk. Having no reason to suppose, as already remarked, that one ganglion acts differently to another, we infer that the sympathetic has no occasion to furnish grey nerves to the same points of structure already supplied by a gangliated impressional nerve. All purposes of general harmony will be sufficiently fulfilled by the nerve-tubes which connect the cells of the sympathetic with those of the spinal ganglion. If so, the peripheral contribution, which the sympathetic supplies to every impressional nerve, will not be distributed to the same parts as the terminations of the impressional nerve. We have, therefore, to inquire in each instance what organic processes in the part are functionally associated with the action of the impressional nerves, and what are not. The former will be superintended by the spinal ganglia, the latter by the sympathetic. Many such processes being at the same time connected with impressions and with muscular movement, are presided over by the sympathetic ganglia especially appropriated to them. The addition of the motor element makes the distinction.

Classification of the Ganglia.

A. Simple ganglia; always offsets from compound sympathetic ganglia; uncertain in their seat. Single, containing the ganglionic element only.

B. Compound Ganglia.
   1. Spinal.
   2. Sympathetic.
      a. Fusiform ganglia.
      b. Distinct ganglia.

1. Spinal ganglia; always formed on the roots of impressional nerves; neither giving nor receiving distinct nerves except at their peripheral margin; never connected with a motor nerve. Double, consisting of the ganglionic and of the impressional nerve elements.
   1. All the intervertebral ganglia.
   2. The Casserian ganglion.
   3. The superior ganglion of the vagus.
   4. The superior ganglion of the glosso-pharyngeal.

2. Sympathetic ganglia; never found on the roots of cerebro-spinal nerves. Triple, consisting of the ganglionic, of the impressional nerve, and of the non-volitional motor nerve elements.

a. Fusiform ganglia; always found imbedded in the course of a nerve-chord.

Constant.
   1. The inferior ganglion on the glosso-pharyngeal.
   2. The inferior ganglion on the vagus.
   3. The superior ganglion on the *portio dura.*
   4. The inferior ganglion on the *portio dura.*
   5. The ganglion on the inferior maxillary nerve.

Inconstant.
   1. A fusiform ganglion on the *ramus auricularis* of the vagus.
   2. One on the *chorda tympani.*
   3. One on the Vidian (?)

b. Distinct ganglia, placed on nerve-branches, never on the roots or main trunks, receiving and furnishing nerves in any direction.
   1. Ribes's ganglion (?)

2. Carotidean ganglion.
3. Ophthalmic.
4. Otic.
5. Spheno-palatine.
6. Submaxillary.
7. All the prævertebral ganglia.

Holmes Chapel, Cheshire,
May 28th 1847.

Description of the Plates I., II., and III. to Essay on the Ophthalmic Ganglion. Vol. lxvi. p. 312.

All the figures are represented as seen under a magnifying power of 300 linear diameters.

PLATE I.

Fig. 1. Various appearances of nerve-tubes in grey part of spinal chord of sheep.

a. Two views of the same nerve-tube. In one the compression was increased so as to displace vesicles which previously concealed the portions of tube proceeding from the sides of the bulbous dilatation.

b. Isolated translucent varicose tubes.

c. A single nerve-tube forcibly compressed and rubbed; showing the difference between the appearance thus occasioned and that presented by the varicose nerve-tubes.

Fig. 2. From brain of chub.

a. Nerve-tube with its dilatation imbedded in grey cells.

b. The same, the cells having been displaced; showing that the apparent termination of *a* in a bulb was fictitious.

Fig. 3. A caudate vesicle from brain of common eel.

Fig. 4. From spinal chord of eel.

a. Varicose nerve-tubes.

b. A single varicose tube forcibly squeezed.

Fig. 5. From optic lobes of brain of water-hen.

Fig. 6. From *corpus striatum* of rabbit.

a. Ring-like arrangement of tubes and vesicles.

b. Irregular junction of tubes and vesicles.

PLATE II.

Fig. 7. Vesicles and tubes from vagus ganglion of rabbit, isolated accidentally on object-glass.

Fig. 8. Other objects singled out in the greyer part of the ganglion.

Fig. 9. Vesicles and tubes from centre of cæliac ganglion of rabbit.

Fig. 10. From Casserian ganglion of rabbit.

Fig. 11. From a spinal ganglion of rabbit.

Fig. 12. From another spinal ganglion.

Fig. 13. Do. accidentally isolated.

PLATE III.

Fig. 14. Various appearances of objects from grey portion of the pituitary body of rabbit.

Fig. 15. Do. from cæliac ganglion of fœtal kitten.

Fig. 16. From a ganglion of the sympathetic lying on psoas muscle of rabbit.

Fig. 17. Objects seen in sympathetic ganglia of a human fœtus at the fifth month.

PLATE IV.—*Diagrams made from Nature.*

Fig. 18. Sympathetic ganglion in the cat, corresponding to the infe-

rior cervical of the left side. Shows the different distances from the chord at which the *rami communicantes* are connected with the cerebro-spinal nerves; the difference in the size of these rami, and in the proportion of grey and white fibres which enter into their composition.

C. 3, 4, 5, 6, 7. Five lowest cervical nerves with their posterior gangliated roots.

D. 1, 2, 3. Three highest dorsal nerves.

a. Middle cervical ganglion and descending chord of sympathetic.

b. Large ganglion lying in front of the head of the first rib, and receiving communications from the first and second intercostal nerves, and from the five inferior cervical nerves. The *ramus communicans* to the lowest cervical nerve being the shortest, thickest, and by far the greyest.

c. A lash of almost entirely grey fibres which expand in a fan-like manner as they approach the cardiac plexus.

d. Bundle of axillary nerves turned up.

e. Ganglionic branch which accompanies the vertebral artery in its canal, is connected by filaments to each of the cerebro-spinal nerves in its vicinity, and is said to supply filaments to every branch of the artery.

f. The first dorsal ganglion of the sympathetic after the large one *b*.

Fig. 19. The angle where the *ramus communicans* is joined to the seventh cervical nerve, magnified fifty times. There is no attempt at accuracy of representation as regards the dimensions of the nerve-fibres, or their relative number. The diagram is intended to illustrate the difference in the course of the grey fibres on arriving at the nerve; one bundle directing itself towards the spinal chord (C. centrad); the other diverging and accompanying the white nerve-tubes towards their destination (P. peripherad). Only two larger nerve-tubes are represented in the *ramus communicans*. This is merely for the sake of clearness. In reality, there exist many such, although the ganglionic fibres greatly preponderate.

Fig. 20. Ophthalmic ganglion in the ox. Showing the great share which the third nerve has in its formation; also, that the branch furnished by the fifth really does proceed from the Casserian ganglion, and that it cannot consist of grey filaments merely given off from the ophthalmic ganglion to accompany the nasal nerve to its distribution.

C. G. Casserian ganglion.

2, 3, 5. Second, third, and fifth cerebral nerves.

a. Ophthalmic ganglion.

b. Sensational root of do. dividing into

c. Ganglionic branch; and

d. Non-ganglionic ciliary branch.

e. Ganglionic ciliary nerves.

f. A wandering branch of that part of the third nerve which supplied the *rectus superior*.

g. A slender nerve lost about the inner canthus. The two last (*f* and *g*) for short distance from the ophthalmic ganglion were enclosed in the same neurilem, and appeared to be traceable across the surface of the ganglion into the most anterior branch of *c*.

Plate V.

Fig. 21. Connection of the sympathetic with the cerebral nerves in the young puppy-dog. Showing that the general direction of the communications, taking the sympathetic as their chief origin, is from behind forwards.

3, 4, 5, 6. Third, fourth, fifth, and sixth cerebral nerves. A communicating branch passes between the ophthalmic division of the fifth and the sixth.

8. Eighth nerve.
Sp. A. Spinal accessory.
V. G. Vagus ganglion.
S. C. G. Superior cervical ganglion of the sympathetic; all its communications external to the skull destroyed.
V. Inferior vidian nerve receiving the superior vidian.
Fig. 22. Another dissection in the dog.
5. Fifth nerve—ophthalmic division.
C. G. Casserian ganglion.
6. Sixth nerve with its communication from the fifth.
S. Sympathetic sending a large grey contribution beneath the ganglion of the fifth to join its three great divisions just at their origins; and also, largely connected with the sixth.
Fig. 23. Connection of the sympathetic with the fifth and third nerves in the cod-fish. Showing that the sympathetic comes very forward before effecting its junction, and implying that it supplies filaments to the third nerve for distribution only.
3. Third nerve.
5. A large root of the fifth turned up.
S. Sympathetic nerve.
C. G. Casserian ganglion, with a large supply of sympathetic filaments entering the origin of the nerves which proceed from it.
C. A. Ciliary artery.
C. N. Ciliary nerves.
S. C. Sympathetic ciliary nerve-trunk, proceeding from the ganglionic mass beneath the ganglion of the fifth; becoming connected to the third nerve within the orbit; intermingling with the filaments of the third nerve to form the ciliary nerves, but not forming an ophthalmic ganglion.

Plate VI.

Fig. 24. Diagram of the spinal nerves of the cod-fish, taken from upper part of dorsal chord, where the body of the fish is largest, and where the difference in size between dorsal and ventral nerves consequently is most considerable. The arches of the vertebræ are supposed to be removed, and the upper aspect of the *medulla spinalis* exposed.
D. D. D. D. Four dorsal nerves, destined to ascend vertically towards the dorsal fins. Each is composed of a non-gangliated fasciculus from the posterior root (2), and of a motor root (also non-gangliated,) which descends from the anterior root of the nerve next above it (1.) Hence each dorsal nerve derives its posterior root from a lower segment of chord than that which furnishes its anterior root.
V. V. V. V. Four ventral nerves, very large, passing beneath the muscles and gaining the inner surface of the walls of the abdomen. Each consists of an anterior root, and of a gangliated posterior root, which arise from the chord on the same transverse level.
L. Lateral nerve composed of both gangliated and non-gangliated portions of the fifth nerve, and to a small extent of nerve-fibres from the vagus. It crosses the dorsal nerves at right angles, communicating with each. No ganglion exists at the point of conjunction. The nerves to the dorsal fins (*locomotive gills?*) are thus made up of fifth and eighth, (compound, sensational and motor; gangliated and non-gangliated;) and of spinal fibres from both roots, but neither of them gangliated.
1. 1. Anterior roots (cut off) of dorsal nerves.
2. 2. Posterior roots of the same, diverging from the other fibres of the posterior roots before (*i. e.* spinad,) these enter the intervertebral ganglion.

3. A compound ventral nerve, the antero-dorsal nerve (1*) cut short to display the splitting of the posterior roots through which it passes, and the ganglion which, before displacement, it covers and conceals.

4. The next ventral nerve, with a portion of its posterior roots removed, in order to expose the anterior root, giving off before its conjunction the antero-dorsal branch.

5. Another ventral nerve in its natural state.

6. A ventral nerve cut short at the point where the anterior root enters the same sheath with the posterior, (*i. e.* distad to the ganglion.)

Plate VII.

Fig. 25. Displays the decussation of the anterior portion of the two sensational columns in the *pons varolii* of the sheep.

Plate VIII.

Fig. 26. Displays the oblique direction of the decussating sensational fibres on leaving the *pons varolii* on the left side in the dog. Also, a more complex arrangement of parts on the anterior aspect of the *medulla oblongata* than is usually described.

Plate IX.

Fig. 27. Displays the non-decussation of the posterior portion of the sensational columns in the dog. Also the complex arrangement of parts on the posterior aspect of the *medulla oblongata*, especially with reference to the cerebellum.

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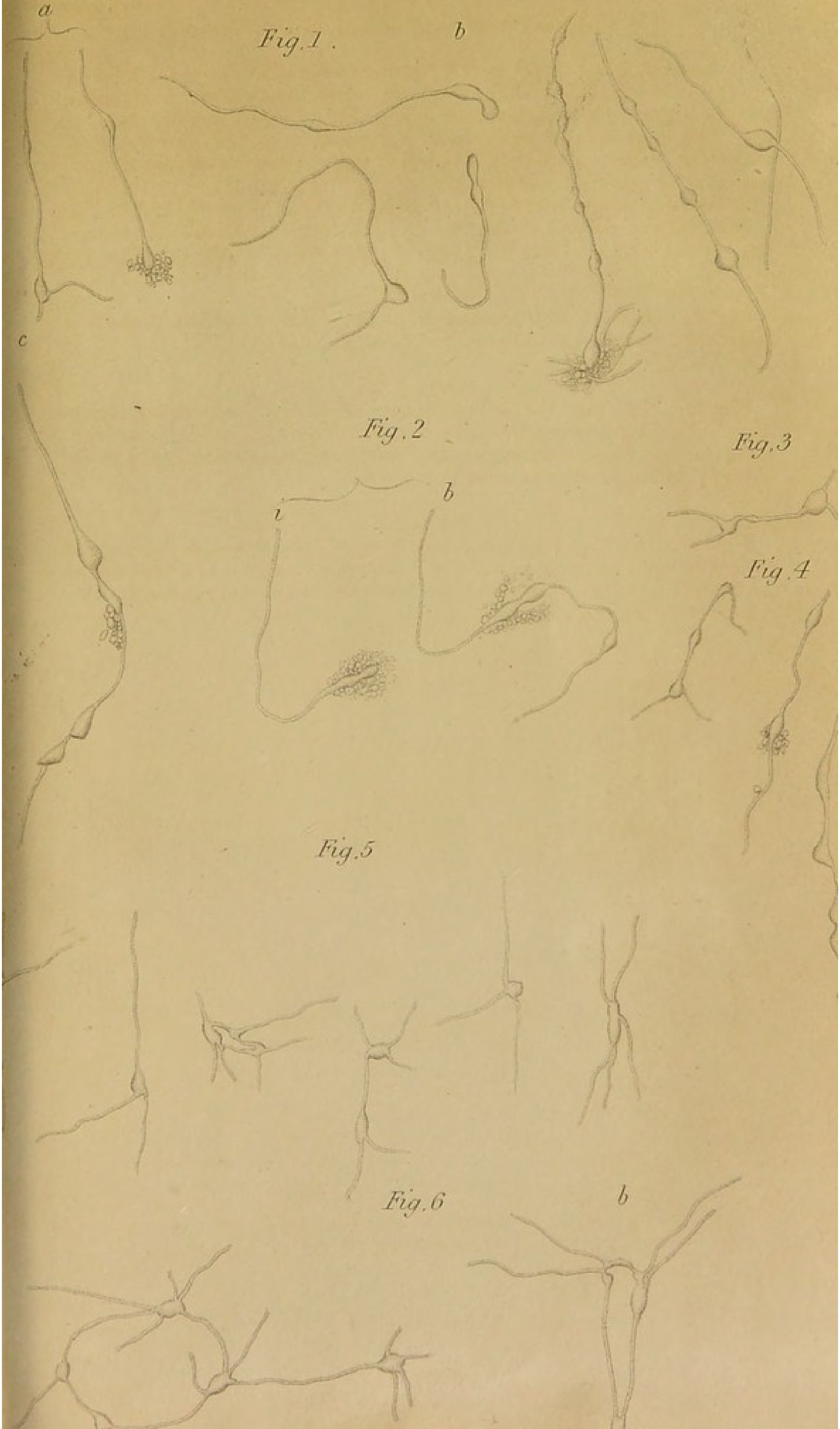
Fig. 1.
a
b
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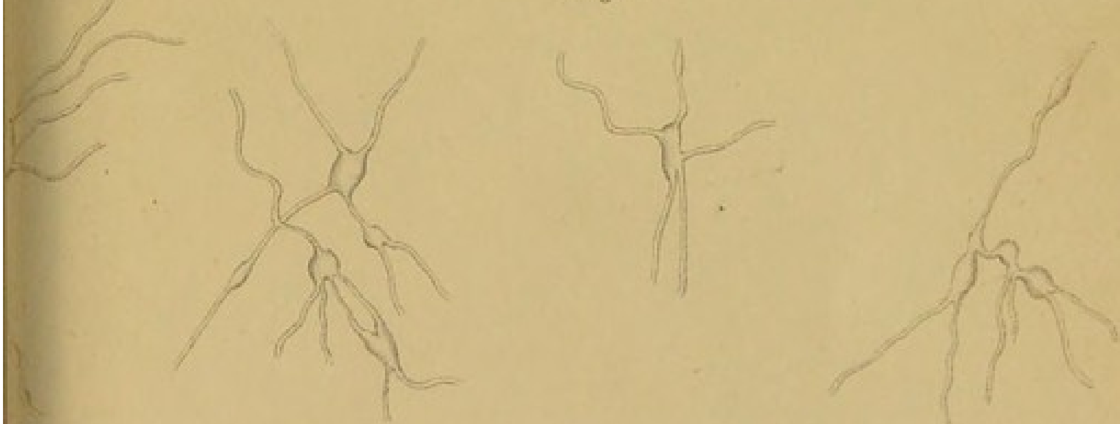
b

Fig. 7

Fig. 8



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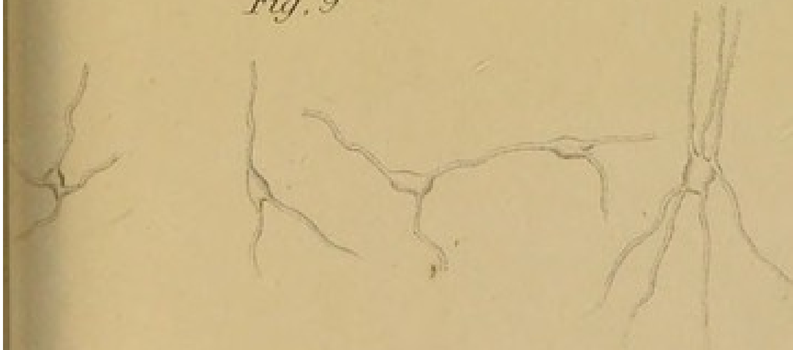

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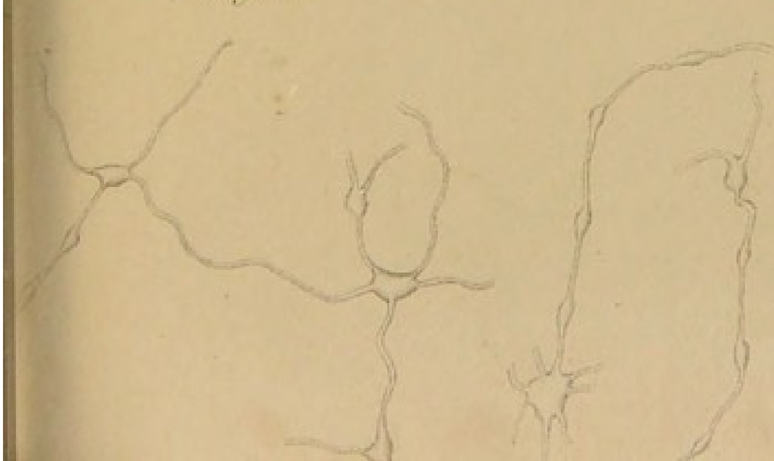

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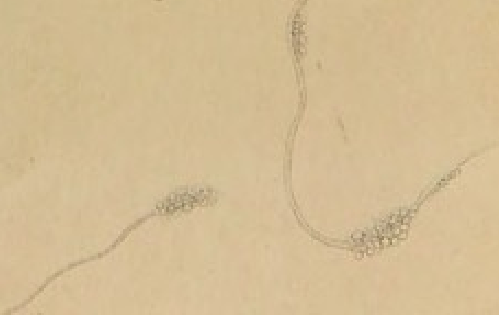

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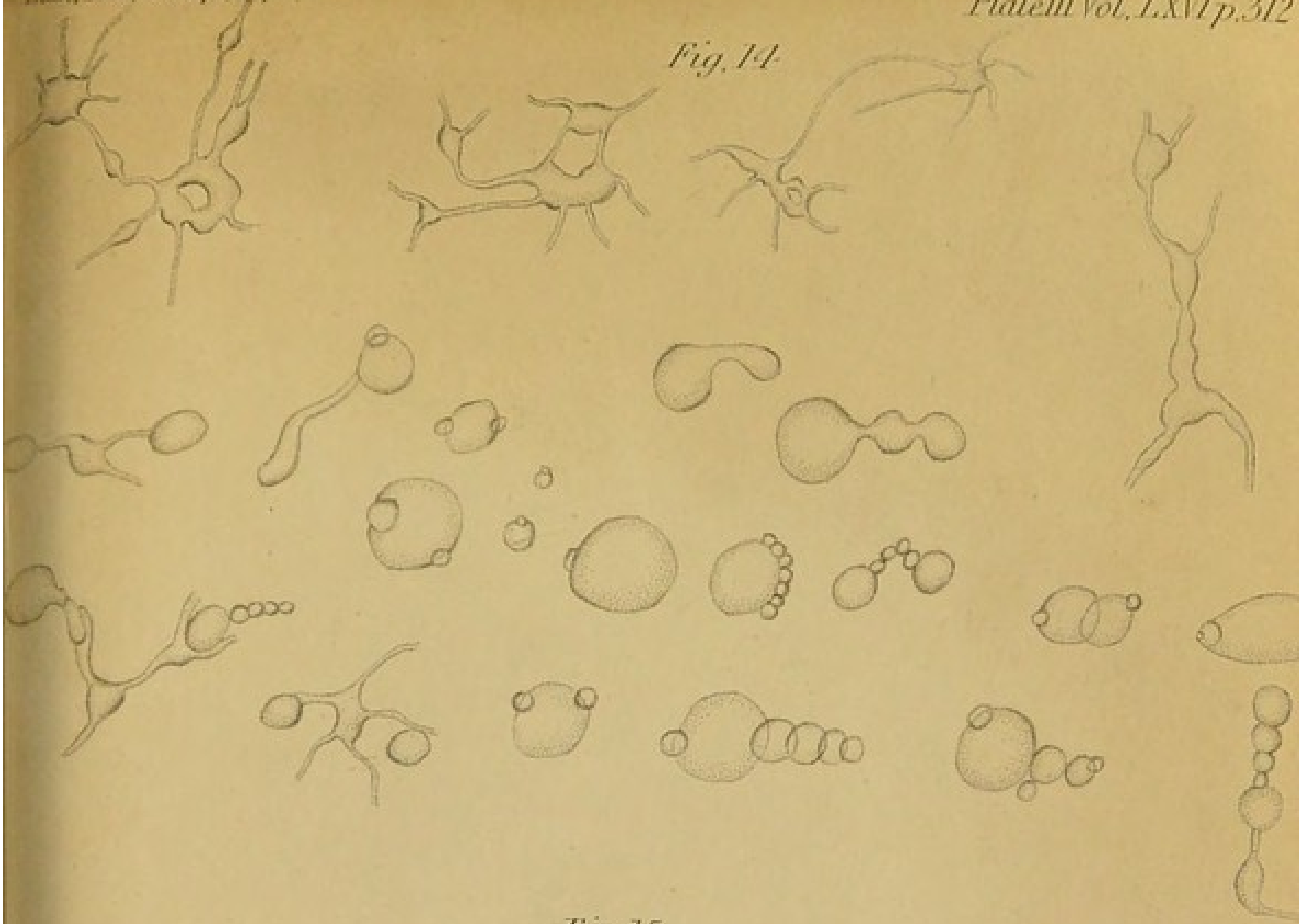
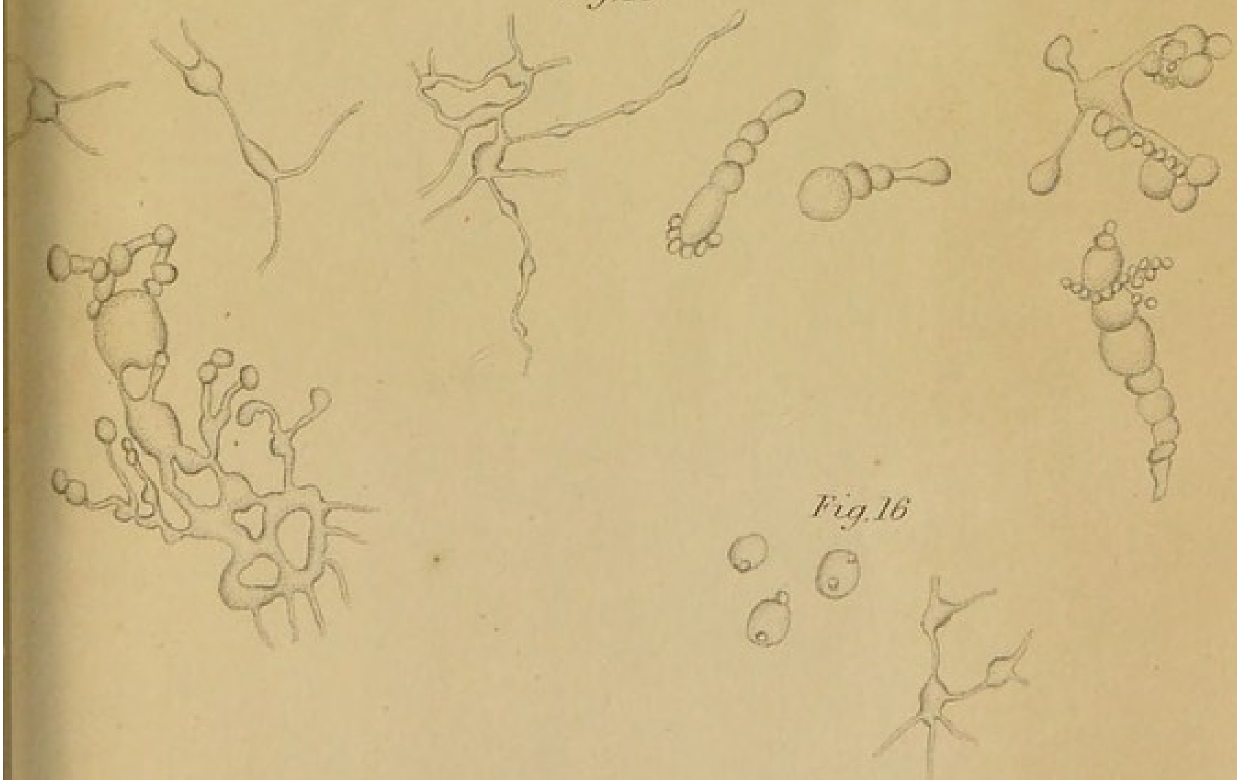


Fig. 15

Fig. 16



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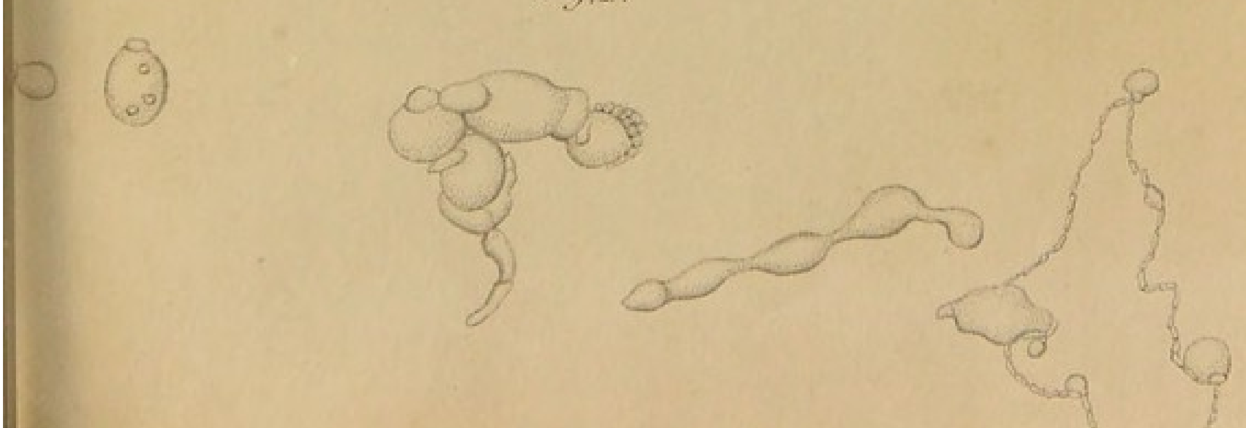

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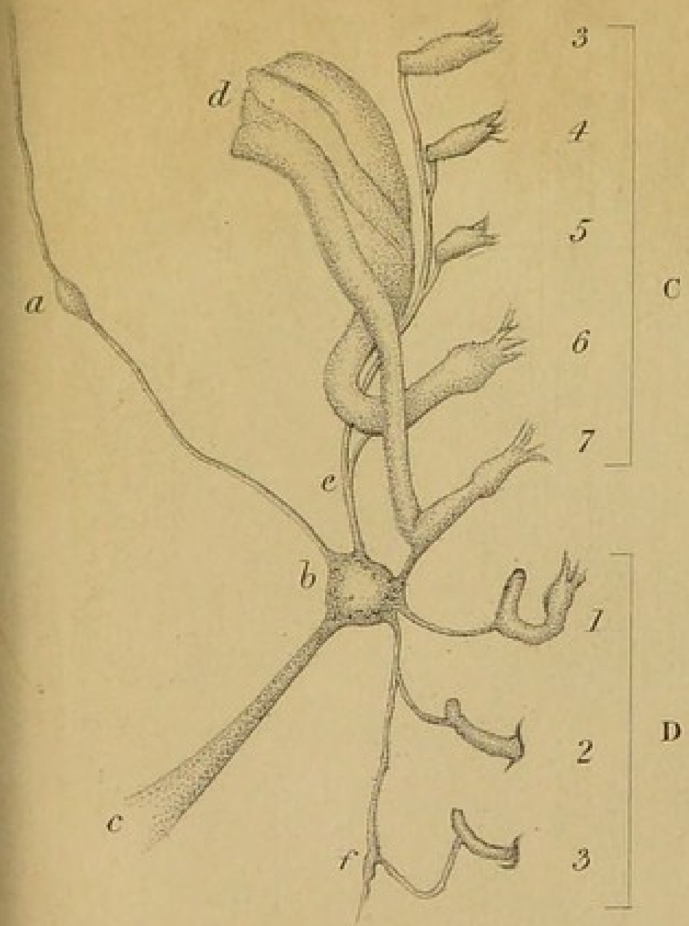

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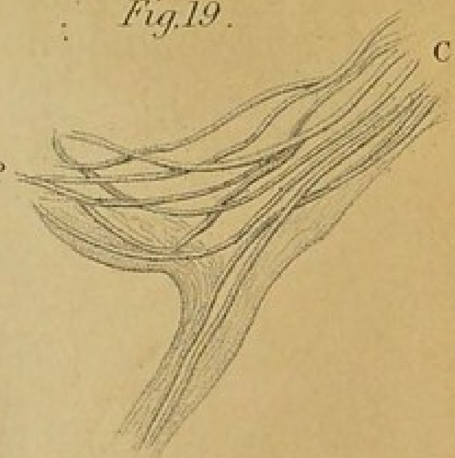

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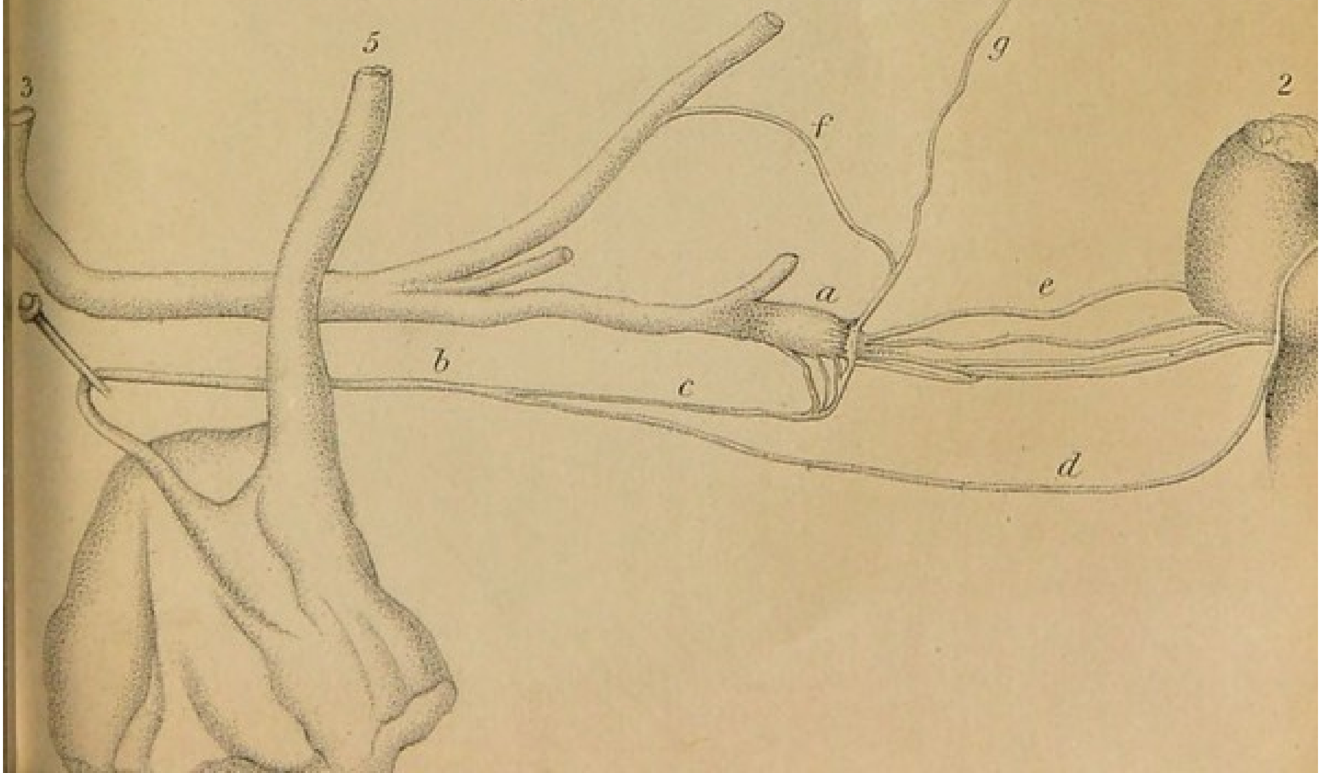

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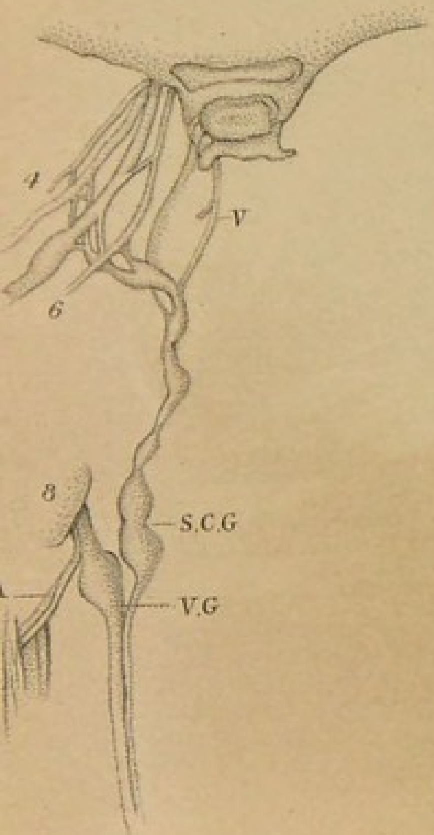

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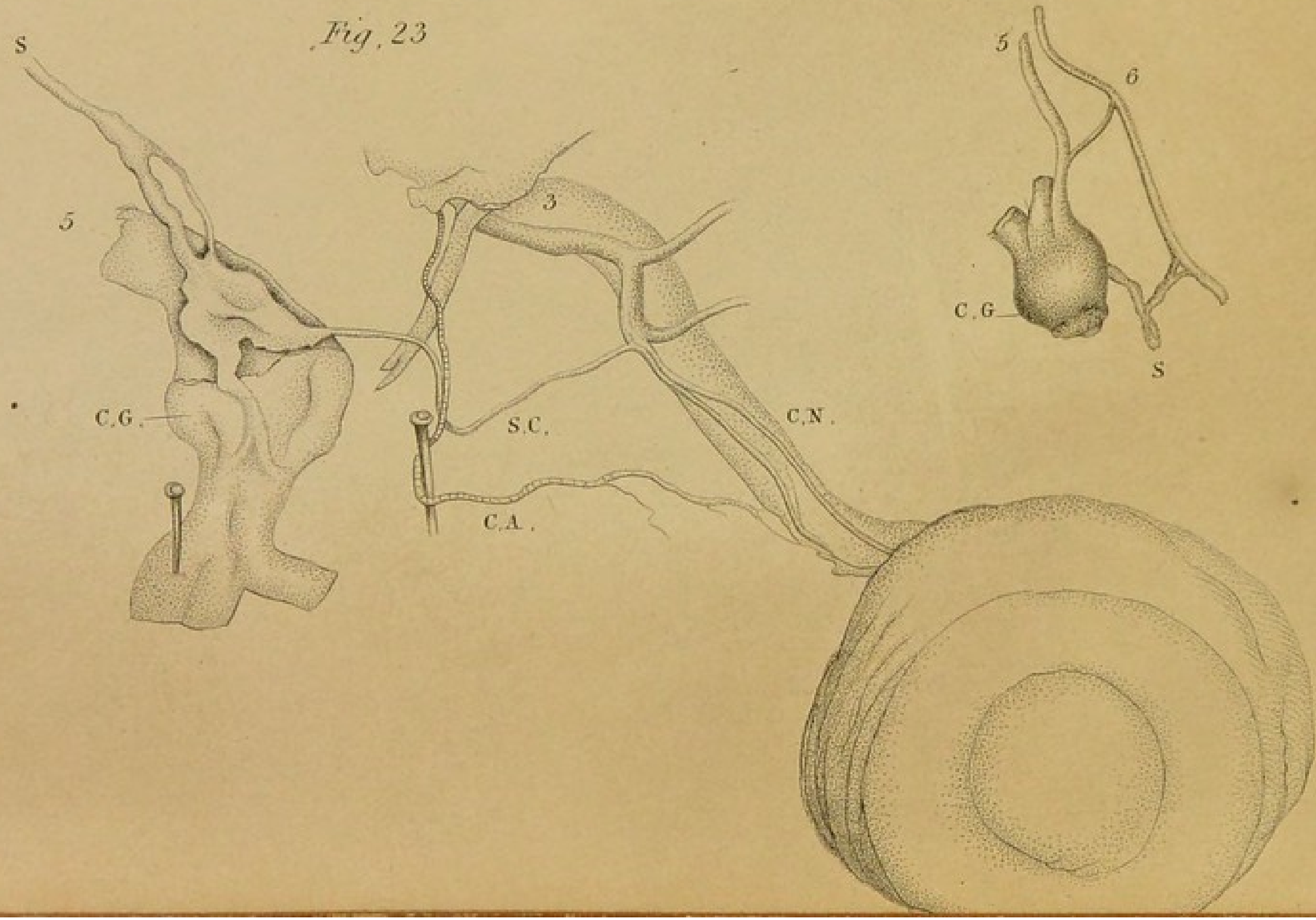

Fig. 22

PLATE VI.

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Fig. 24

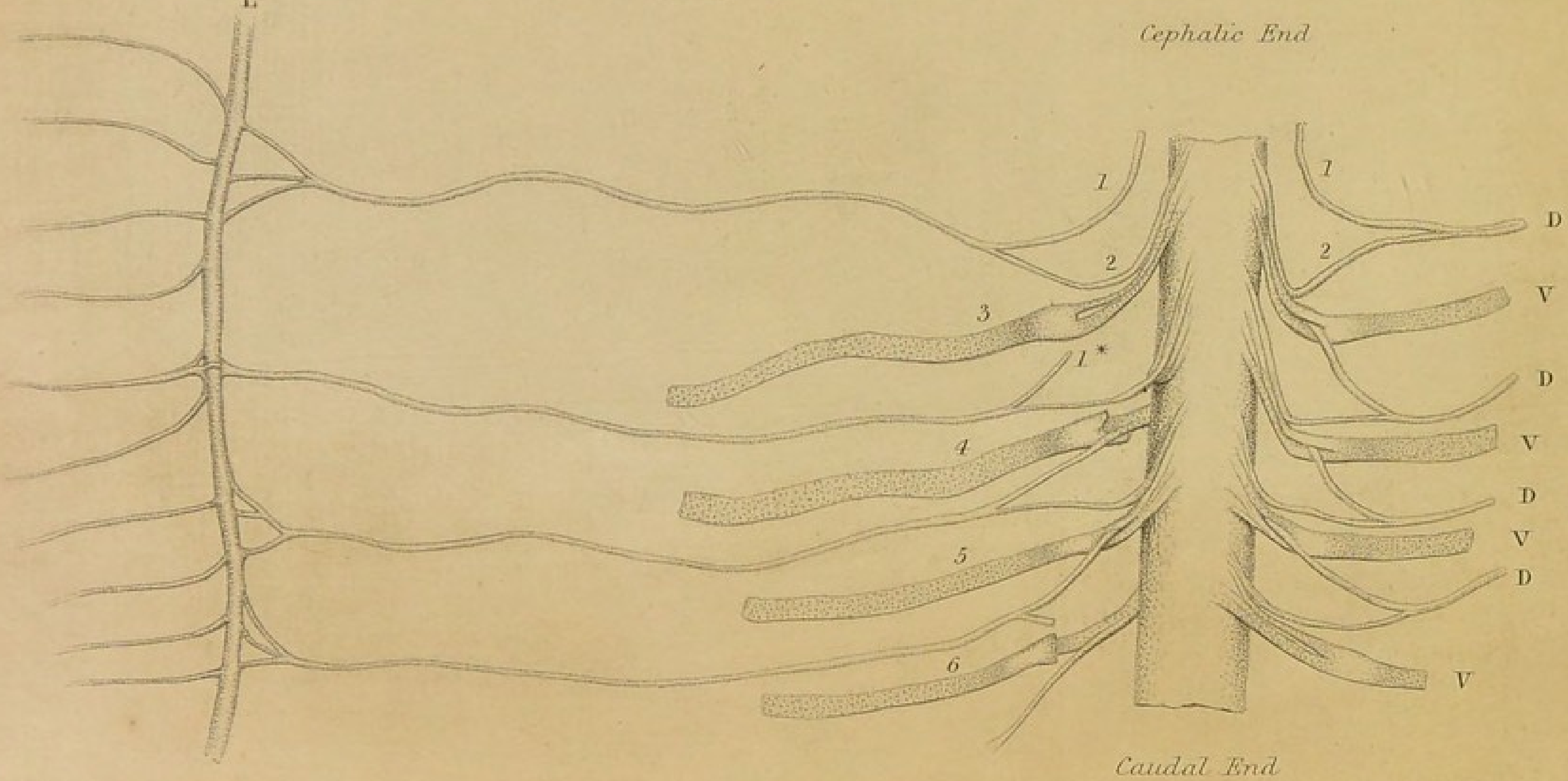

Fig. 25.

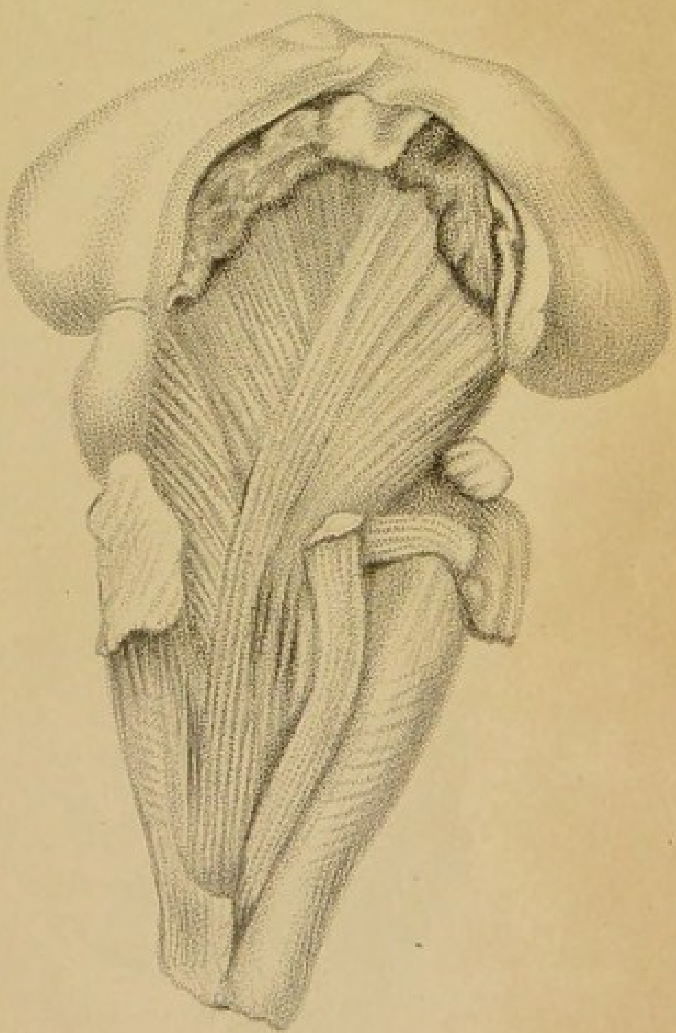

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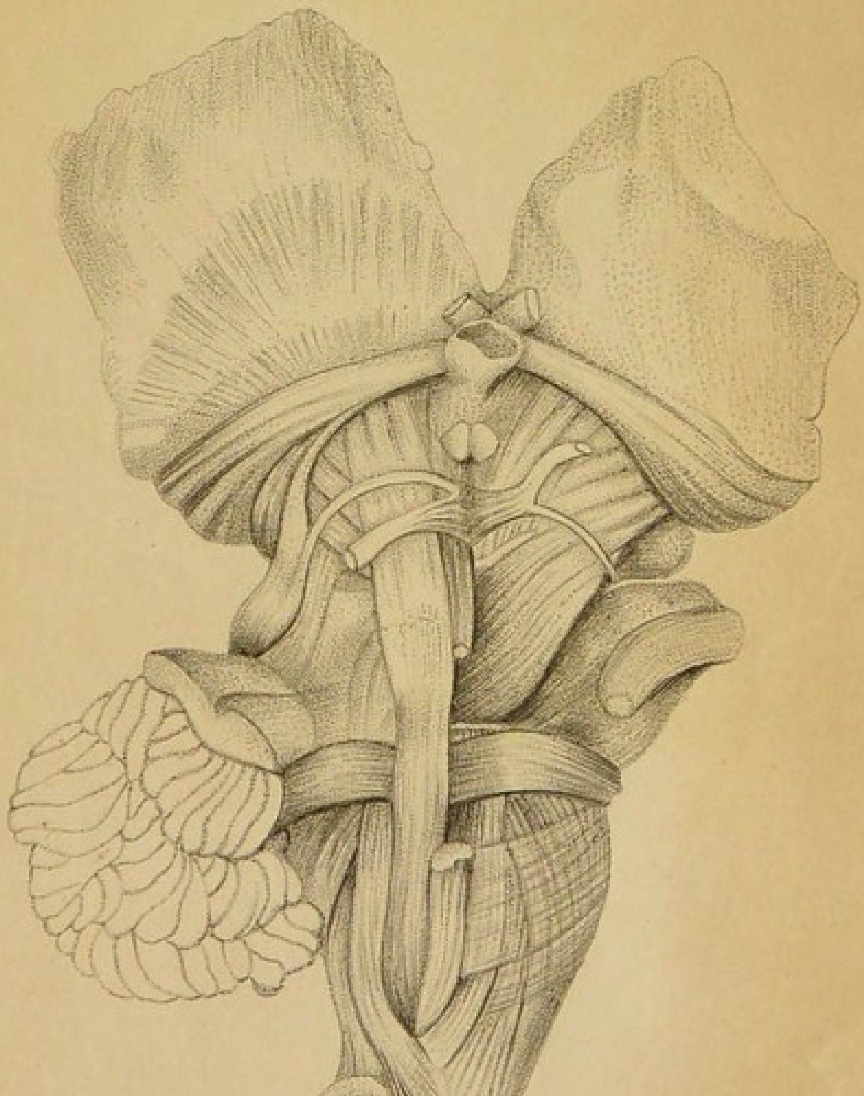
Fig. 26



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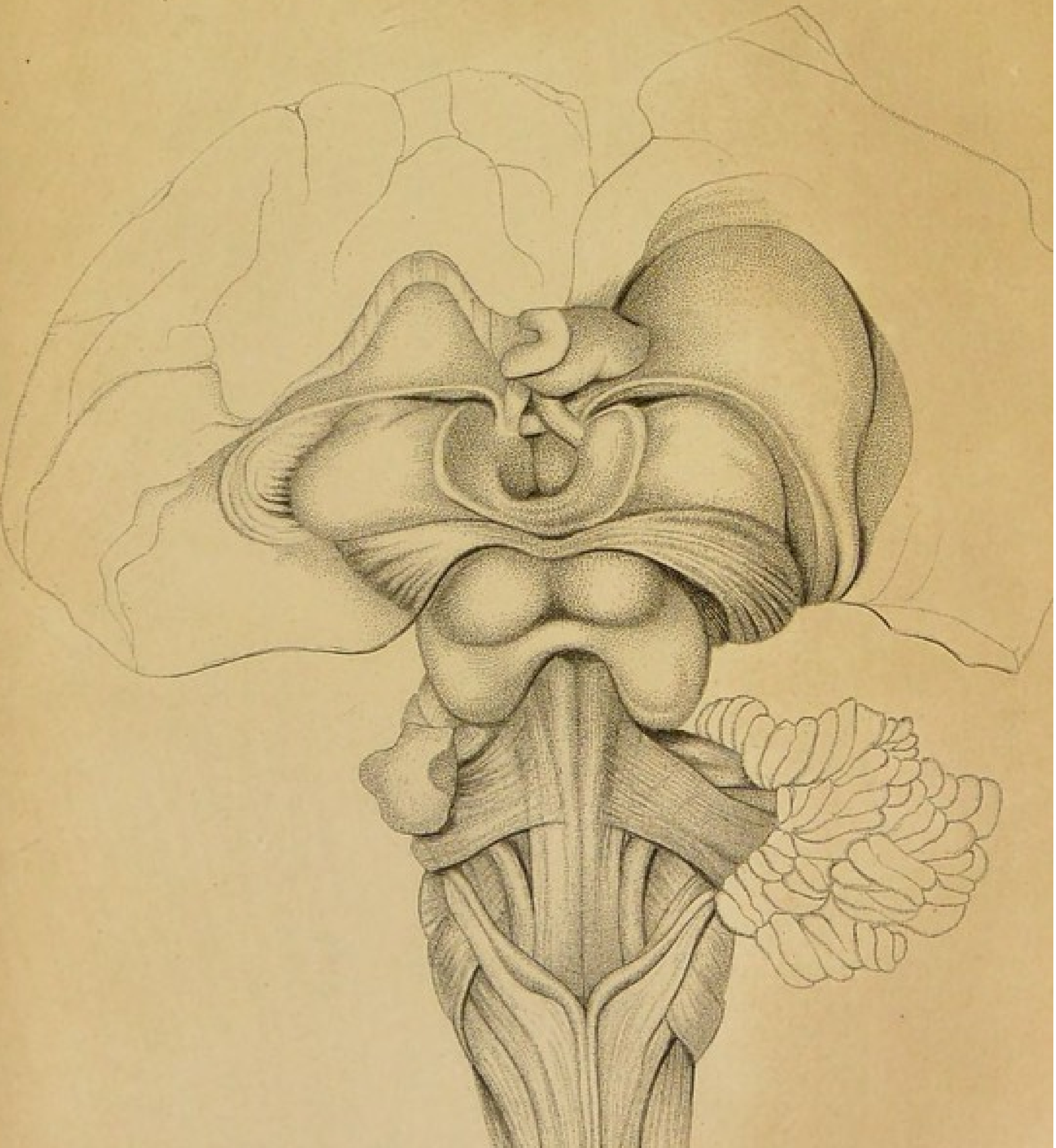

Fig. 27