

this patient while in hospital; and all of them with whom I spoke, asked me whether a probang had been used to explore the throat. I got quite ashamed of my remissness in research, and that shame and my own curiosity were strong temptations to make the trial. But the power which remained, of occasionally retaining food under the influence of medicines, rendered immediate action unnecessary; and, moreover, confirmed me in my original diagnosis of simple ulceration, and in resistance to the temptation. Thus was avoided the painful feeling which would have been left upon the mind had an instrument been passed, and death soon followed the operation. Let me not be understood as objecting unreservedly to the use of the probang or œsophageal tube; for where the dysphagia is spasmodic, and, possibly, in some cases where permanent stricture has followed a bruise or other cicatrix, and of course in every instance where starvation is imminent, the use of these means is a duty. But where morbid action, as indicated by pain, is still active, and life can yet be kept up by some portion of food being administered, I do not think we are justified in such forcible interference. And when we *are* called upon to rush in, let us tread in fear, remembering the neighbours by which our patient, the œsophagus, is surrounded. A false passage in the urethra is a bungle and an inconvenience; but here it goes into the very fountains of life.

A NEW METHOD FOR THE STUDY OF THE NERVOUS SYSTEM.

By AUGUSTUS WALLER, M.D., F.R.S.

THIS method of study is equally applicable to the anatomical distribution of the nerves, to the functions of the nervous system, and to the diseases of this system, during life and after death.

The process consists in the section of different parts of the nervous system, either of the nerves or of the spinal marrow, so as to interrupt their connexion with the central parts. After having kept the animal operated upon alive, for a period which may vary from one to three or four months, the changes which take place in the peripheric and central parts are determined by the assistance of the microscope.

We know that when the connexion of a spinal nerve with the spinal marrow is interrupted, its elementary parts become disorganised. These experiments have been made on the sciatic nerves of frogs and rabbits. In making the experiments, the preparation of these nerves for microscopic examination presents considerable practical difficulties, on account of the extreme facility with which the soft and pulpy substance, of which the intratubular part of the nerve is composed, loses its transparency and is disaggregated. These difficulties are such, that although an advanced state of disorganisation is easily recognised, it is not the same with merely a slight disorganisation, for the altera-

tion of nerves by their preparation, is often more considerable than that which arises from disorganisation in its early stages.

To avoid all possible chance of error, we must therefore choose a membrane which, while containing very minute nervous ramifications, is sufficiently transparent to be observed under the microscope without further preparation.

Although several membranes, such as the intradigital membrane of the frog, the bladder of the same animal, or that of the mouse, fulfil these conditions, none of them equal the elastic and eminently transparent tongue of the frog. It receives two pairs of nerves: the first, which can be regarded as corresponding to the hypoglossal, is perceived beneath the transparent fibres of the mylohyoid muscle, when the skin is removed from the hyoid region. The second—the glosso-pharyngeal branch of the vagus—is seen through the mucous membrane of the mouth beneath the tongue, when, after opening the jaws, the tongue is drawn from its usual position.

The fungiform papillæ of the tongue contain, as I have already shown, nerve-tubes terminating in free extremities, and so superficial, that they are very readily seen during the life of the animal by distending the tongue. One method of examining these nerves consists in removing a small portion, of about the size of a pin's head, and submitting it to the microscope. It is generally very easy to distinguish the nerve-tubes, and even to count them. But if they are obscured by the vessels or the epithelium, these are easily eliminated by using a drop of caustic potash, which dissolves all the other tissues, leaving the nerves intact.

This organ presents all the necessary conditions for the study of the alterations of the nerves after section, for here the tubes are already spread out without any manipulation, and adapted for microscopic inspection. It is sufficient, after section of the principal trunk at the neck, to remove daily a small piece of the tongue, to follow step by step the progress of disorganisation.

If we divide, for example, a glosso-pharyngeal nerve, leaving the other as a standard of comparison, we see, at the end of four or five days in summer, that the tubes are already altered, and that transverse lines are seen in the intratubular substance, indicating its loss of continuity. At the second period, that is to say, after about ten days in summer, we find that the nerve-tubes only contain round or oblong masses, of a more or less coagulated appearance, as if by the mixture of the two substances of which the intratubular matter is composed. At a third period, this matter is found converted into black granules, possessing chemical properties differing from the normal intratubular substance, inasmuch as they resist the action of acids and alkalis. Henceforth the change which takes place in the nerves only consists in the elimination of these black granules, which is done very slowly in the full-grown frog; for at the end of a year, or more, they are to be seen in great quantities in the interior of tubes otherwise empty.

It is easy to perceive in removing larger portions, that the same change takes place in the larger branches as far as the point of section. *By means of these alterations, we can most exactly determine the course and distribution of the whole nerve; for in submitting the entire tongue to the action of a weak alkaline solution, so as to dissolve the epithe-*

lium, the ramifications of the altered nerve are rendered plainly visible. We then see that sometimes one of the nerves encroaches on the region of the other; and that sometimes even a branch of the left glosso-pharyngeal nerve distributes itself into the right tubercle of the tongue, and *vice versa*.

We can also distinguish the numerous anastomoses which exist in these nerves on the median line, for normal fibres are constantly found mixed with disorganised ones. No doubt can exist upon the origin of each species of fibre, for each can be easily followed as far as the principal branch. Disorganised fibres are continually found by the side of normal ones, sometimes following the same course, sometimes separating and mixing with each other in all imaginable proportions. In no case is it seen that the proximity of altered fibres affects the structure of normal ones.

To ascertain how the nerve-fibres act in the trunk, I cut a glosso-pharyngeal nerve half through at the neck. In examining the papillæ of the same side, I perceived that they contained fibres entirely disorganised, and sometimes fibres of each kind, in different proportions. We see, therefore, evidently, that in the trunk of the nerve in question, the fibres do not always occupy the same place, but that, in their course, there is the same mixture as in a plexus. If we cut one glosso-pharyngeal nerve, and then the other, after an interval of any duration between the two sections, we find that each nerve goes through the various stages of disorganisation totally unaffected by, and independently of, the other.

The alterations which are thus produced in the nerve-tubes are so invariable, and so readily distinguished, that one can, by inverting the problem, pronounce, by microscopic inspection of the tongue, not only which are the divided nerves, but also determine, *cæteris paribus*, the exact period of the section.

CENTRAL PORTION. While these numerous and characteristic changes take place in the inferior end, the superior end, on the contrary, which is in connexion with the central parts, preserves its normal structure. In a frog, whose glosso-pharyngeal nerve has been divided, it is found at the end of two months; the inferior portion only presents tubes full of black granules, while those of the central part are unaltered. At the end of six months, and even of a year, I have seen the same difference, that is to say, that the central end is in the normal state, while the peripheric part is disorganized.

REPRODUCTION OF NERVES. Since the experiments of Fontana upon the production of nerve-tubes in the cicatrix which unites the two ends of a divided nerve, and notwithstanding the numerous observations made by Schwann, Steinruch, Müller, Günther, Schon, and others, it does not appear to me that the question of the reproduction of nerves has made any essential progress. Fontana has observed that the two ends are reunited by tubes of new formation; and his observations are indubitably correct. It is important to remember that all the discussions which have taken place respecting the reproduction and the regeneration of nerves, have been only with regard to the regeneration of the tubes in the cicatrix. All observers, influenced perhaps by what passes in other tissues, have confined themselves to the examination of the tubes in the cicatrix, disregarding those of the peripheric ends.

It is, however, in this part that we find the key to answer all the questions concerning the reproduction of the nervous substance, and the discussions upon the reunion of motor and sensitive fibres at one end of the cicatrix, with those of the same denomination at the other. My experiments have given me the result, *that the old fibres of a divided nerve never recover their original functions*; and that the reproduction of a nerve is not only made in the cicatrix itself, but as far as the terminal ramifications.

To be satisfied of this fundamental fact, the ramifications of the glosso-pharyngeal nerve must be examined about three or four months after section. Almost all the fungiform papillæ will be found, *if there is reunion*, to contain tubes in the third degree of alteration; there is only rarely to be seen a fibre of new formation, which it is impossible to confound with disorganised fibres, or with normal fibres from another source. The new fibres present the following characteristics: they are very pale and transparent, have no double outline; their diameter is very unequal, sometimes very minute, sometimes swollen or varicose, like the fibres of the spinal marrow; their size is about the fourth part of the nerve-tube of a full-grown frog. By means of these appearances they are readily distinguished from the normal and the old disorganised tubes; but if they are compared with the nerve-tubes of the fungiform papillæ of the young frog, when the tongue makes its first appearance after the tadpole state, it is seen that they are precisely alike. According as we ascend from the papillary nerve to the more voluminous branches, these new fibres become more and more abundant, presenting always the same characteristics, and occupying the same situation: that is to say, they are interposed between the old fibres, which still possess a tubular membrane containing black granules. In all my researches on this point, I have never seen a new fibre in the interior of an old tube.

Before reunion takes place, or any new fibres exist in the cicatrix, none are to be seen amongst the disorganised fibres. At the end of nine months, I have found new fibres in almost all the fungiform papillæ, always presenting the same characteristics as above described; and I have never seen regenerated fibres, either in the frog or dog, attain the size, the regular diameter, or the well-defined double outline of the old fibres.

The intermediate portion which unites the two divided ends, is composed of tubes whose diameter is only the fourth part of those of which the central portion is composed. In the mammifera, by reason of the hardness of the cicatrix which unites the two ends, and of the quantity of fibrous tissue which exists there, it is impossible to isolate the nervous fibres; but in the frog they are completely isolated from the surrounding tissues, and it is easy to separate the nerve so as to have all the newly-formed part with a portion of each end. Examined with the microscope, the upper portion is seen to be in a perfectly normal condition. A sudden contraction marks, to the naked eye, the termination of the central part. Under the microscope, the difference between the old and new tubes is not less marked; for while the old tubes measure about $\frac{1}{6,000}$ of an inch, the new ones are only the $\frac{1}{15,000}$. The new tubes do not shew any difference until they attain the lower end, where the distinction is more marked than at the superior end, the

disorganised fibres of the peripheric end being seen here to join the new tubes.

INFLUENCE OF AGE. In the preceding experiments, I have always used animals in a state of maturity. If, on the contrary, the experiments are made upon the young frog, we find a considerable difference in the period of disorganisation, and in its appearance. In summer, in a young animal weighing fourteen grains, I have, in three days, found disorganisation very evident in the papillæ; while, in a full-grown frog, a similar alteration requires five or six days to be effected. At the period of the second degree of disorganisation, we find already numerous granules, of various dimensions, mixed with transparent intratubular matter. At the third degree of alteration, we find that the granular matter is much more fine, and less opaque, than at maturity. At the end of twenty or thirty days, these granules are more or less removed. The regeneration of the nerves, which takes place very rapidly on the young animal, does not appear to meet with such difficulties as with the full-grown frog, and the restoration of the nervous influence is also much more complete.

The **INFLUENCE OF TEMPERATURE** is very considerable on the alteration of the nerves of the frog. In the months of May, June, and July, disorganisation of the first degree is to be seen at the end of four or five days; but in winter, for the same vital action to be accomplished, it requires from ten to twenty days. In this respect, these phenomena are perfectly in unison with all the other phenomena of nutrition in these cold-blooded animals, as M. Milne Edwards has shewn in his work upon the physical phenomena of life. The advantage which the nerve-tubes present to us, is very manifest by their offering visible and circumscribed characteristics; while experiments upon the greater or less activity of respiration, require special and technical knowledge rarely in the domain of the physiologist. The other vital phenomena, such as the cicatrisation of wounds, present also the same differences on the frog, according as they are made in summer or winter; but they afford us, still less than respiration, means of measurement and of exact appreciation.

EFFECTS OF ELECTRICITY ON THE DISORGANISATION OF THE NERVES. To ascertain if electricity could supply the want of the influence of the central organs, after division of a nerve, I cut the two sciatic nerves of a full-grown frog. The right leg was galvanised for several minutes nearly every day, by applying one of the poles of a rotatory apparatus to the intradigital membrane, while the other touched the upper part of the thigh. Fifteen days after section, the right sciatic nerve was uncovered and galvanised, without causing any muscular contraction. Twenty-five days after section, the nerves in the intradigital membrane were examined on each side, at the same time, in order to be able to compare them. The nerves on both sides were disorganised; the intratubular substance in each was converted into globular masses, mixed with black granules. There was not the slightest difference between the nerves of the two sides. It appeared, therefore, evident to me that neither galvanism, nor the artificial exercise of the limb which it causes, influenced, in any degree, the nutrition of the nerves.

EFFECTS OF SECTION OF THE SPINAL MARROW. Inspection of the

nerve-tubes, after crushing or dividing the spine, allows us to resolve several interesting questions. The vertebral column was uncovered, and its middle part crushed immediately below the brachial nerves, as was afterwards ascertained. Strong reflex actions were obtained by pinching the skin of the thighs. This animal was kept for six months, always exhibiting very lively movements when the skin was touched, except the day before its death. Twenty-four hours after death, the nerves of the skin of the thighs were carefully examined, the skin of the upper part of the body serving for a means of comparison. I could not find any difference between the nerve-tubes of the skin on the paralysed side, and those of the other. In making these experiments, we are enabled to limit exactly the extent of the paralysed part; for in irritating the skin at different heights, we find that, after section, or crushing the spine, there exists a very distinct region, or zone, round the body, generally about a line in breadth, where mechanical irritation neither produces pain nor reflex action. This neutral line is very constant, and is observed as soon as the animal recovers from the effects of the ether, and remains the same during life. After the section of the spinal marrow, immediately below the brachial nerves, the neutral line forms an almost circular zone. In limiting this line by puncture, we thus obtain the bounds of sensibility and reflex action. An attentive examination has not enabled me to perceive any disorganisation in the tubes of the parts above or below this neutral line; but if the spinal marrow is divided above the eighth vertebra, so as to obtuse sensibility and reflex action at the same time, a different effect is produced, and we find then an evident disorganisation of the nerves of the skin and the lower limbs.

The spinal marrow of a frog was completely destroyed at the level of the sixth and seventh vertebræ: a complete paralysis, without reflex action, was the result. At the same time, the right sciatic and brachial nerves of the same side were divided, and a portion removed. At the end of six months the limbs were in the same condition. The wound at the thigh was not yet cicatrised; that of the arm was completely so. The ends of the divided sciatic were separated by an interval of several lines; there existed no sign of regeneration of the part removed. The extremity of the upper end was red and tumid; the inferior extremity formed a slender cone, which contrasted by its paleness with the opaque whiteness of the rest of the nerve. The lower end of the divided sciatic was quite in the black granular state, which was the case with the most minute ramifications of the nerves of the leg and of the intradigital membrane. The muscular fibres of the same side, compared with those of the other leg, were more pale, with less distinct striæ, and finely granulated. The central arch, or part of the same nerve, contained disorganised tubes; in some, the intratubular substance was granulated; in others, it was only in the second degree; while in others it was transparent, and with a double outline. The sciatic nerve of the left side was still less disorganised than the two above mentioned parts. In almost all the tubes the tubular substance was only disjointed; the brachial nerve, at its upper part, was not altered; the lower part was in the same state as the lower part of the right sciatic. Other frogs were operated upon at the same time, in the same way, and have given similar results.

When the section is made immediately above the origin of the brachial, the nerves of the skin of the arm are all in the normal state.

The result of the foregoing facts is, that no system of nerve-fibres can be isolated by the section of the spinal marrow, and that reflex action may be regarded as indicating that all the nerves of a segment of the spinal marrow, isolated from the brain, are in a condition to resume their functions, if the influence of the will be reestablished. On the contrary, when the section is below the limit of the reflex power, we observe that disorganisation takes place with a rapidity, greater in proportion as the segment of the spinal marrow which remains is less. The existence in this case of the same state of disorganisation in all the nerves which proceed from the isolated portion of the spinal marrow, indicates the marked difference between this and a nerve. The experiments correspond in this respect with those of Van Dien, and incline us to attribute to the grey fibres the power of connecting the medullary nerve-tubes, the effect of which is to produce on all parts of the segment a state of equal polarity, the power of which is evident in the degree of alteration in the peripheric nerves.

The process of section of the spinal marrow, and the observation of the nerves, offer us a fruitful subject for research. By the formation of segments more or less extensive, we may probably be enlightened upon the existence of nervous centres, more or less limited to different points of the spinal marrow, similar to that discovered by the experiments of M. Flourens, which have limited in so distinct a manner the vital region.

SECTION OF THE ROOTS OF THE SPINAL NERVES. By means of the experiments of Müller, we have the true demonstration of Sir Charles Bell's discovery. The degeneration of the nerves furnishes us with additional proof, which is not without interest. If we cut the three posterior roots of the nerves of one of the extremities, the animal generally lives in winter for an indefinite period. In a frog, which had survived this operation six weeks, I found all the nerves of the skin on the right side at the second degree of alteration. At the same time, the animal presented the same symptoms as at the first day of the experiment, *i.e.* complete paralysis of sensation in the right leg, with the motor power so perfect, that I could not perceive, without very attentive observation, on which side the paralysis of sensation existed. The nerve-tubes in the muscles were all normal; and I could not see, in their ultimate ramifications, any appearance of disorganisation. The muscular nerves of the limbs are much more difficult to examine than the nervo-muscular branches of the tongue; but observation has, nevertheless, induced me not to admit the existence of nervous ramifications proceeding from the posterior roots in the muscles. In the branches of a higher order, it was easy to perceive disorganised fibres. Galvanism of the two sciatic nerves gave proof of an equal muscular action of the two sides.¹

¹ Since writing the above, I have had occasion to examine more fully the influence of ganglia on the nutrition of the fibres which traverse them, and find, that after division of the posterior root of a spinal nerve, the fibres extending from the ganglion to the peripherics never become disorganised. I shall communicate my researches on this point on a subsequent occasion.

Section of the anterior roots of the same part furnishes us with equally clear results. After this section, we observe, as Müller describes, entire paralysis of movement, with retention of sensibility; but, at the end of two or three days, sensibility becomes so obtuse, that it is difficult to discover. In this respect, the two roots present an important difference. The cause of this phenomenon is still unexplained. In examining the sciatic nerve, some days after section, a considerable diminution of muscular action is found, when compared with that of the opposite limb. Notwithstanding the almost entire loss of sensibility, we do not find that the ramifications in the skin are altered, while those in the muscles are in the second degree, and that the reticular ramifications of the nerves of the anterior part of the tongue, and especially in the tubercles of the tongue, are altered exactly in the same manner, and in the same degree, as the cuticular nerves.

Section of the two hypoglossal nerves is followed at the end of some days by death; this is more rare after the section of the glosso-pharyngeal. To divide both these last with safety, it is necessary to resort to the same means as for the former; that is to say, to wait until one nerve is cicatrised, and its functions partly re-established, before dividing the other. In this way, we can obtain complete disorganisation of the two hypoglossal nerves.

On an animal thus operated upon, I found all the muscular and superficial ramifications of the inferior surface of the tongue in a granular state. These results, which I had already obtained in 1849, in all their essential points, have been since repeated with similar results. In studying the functions of these nerves more precisely than formerly, by means of galvanism, these results are fully confirmed. When an undivided glosso-pharyngeal nerve is galvanised, on an etherised frog, a contraction is obtained, which is often limited to one side of the tongue. On a non-etherised frog, galvanism produces a general contraction of all the muscles of the lower jaw and of the chest, often a violent snapping, and even an effort resembling the action of vomiting. These contractions are derived from a reflex action; for, in dividing this nerve towards its upper end, the same phenomena are always obtained.

My observations, however, upon the alterations resulting from division of the anterior roots, are not so positive as those of the posterior pairs; on account of the difficulty of examining the ramifications of the nerves in these parts, and of the greater mortality of the animals operated upon.

ON SECTION OF NERVES AS A MEANS OF STUDYING THEIR ANATOMICAL DISTRIBUTION. If it were possible, by means of a chemical process, to distinguish the sensitive and motor nerves, so as to dye one set of them black throughout all their course, while the others retained their natural whiteness, there is no doubt it would be very important for anatomy; and these nerves, thus changed, would be immediately pursued throughout all the tissues of the economy. Let us apply section to the glosso-pharyngeal and to the hypoglossal nerves of the frog, and afterwards to the nerves of the superior animals; but, previously to so doing, it will be advisable to give a short account of the normal anatomy of the tongue in the frog, and in the mammifera.

OUTLINE OF THE NORMAL ANATOMY OF THE TONGUE OF THE FROG, AND OF THE MAMMIFERA. Without any previous preparation, by simple inspection with the naked eye, it is easy to perceive the great resemblance between the two kinds of papillæ of the frog's tongue, and those of the human tongue. This analogy is confirmed by a closer acquaintance with their structure. If a piece of a frog's tongue is allowed to macerate for one or two days in a saturated solution of arsenious acid, we see the epithelium become converted into a gelatinous matter, which leaves the membrane beneath exposed to view. The fungiform papilla is composed of a nerve terminating in free extremities, surrounded with blood-vessels and striated muscular fibres, which ramify like the branches of a tree. The finest branches of muscular fibre do not exceed the $\frac{1}{4,000}$ of an inch in diameter, and are united to the epithelial cells. Professor Kölliker, who has been the first to describe this structure of striated muscular fibre of the frog's tongue, represents it as terminating under the epithelium, beneath the *glands of the tongue*. Without remarking upon the inexactitude of applying the name of glands to these organs, of which they have neither the structure nor the functions, I will only observe, that the learned professor of Wurzburg is in error, when he states that the muscular fibres terminate between the papillæ. In the fungiform papillæ, nothing is more easy than to assure oneself of the contrary, after the removal of the layer of epithelium by means of arsenious acid. We then see that muscular fibres are distributed in opposite directions, at an angle of at least 190, so as to form a complete network around the nerves and blood-vessels, and which reach the summit of the papillæ. As soon as the muscular fibres enter the papillæ, they divide into branches, which, again subdividing two or three times, spread out into exceedingly fine fibres, at the sides of the papillæ, immediately in contact with the epithelium. The conical papillæ rarely contain muscular branches, but almost always elastic fibres, besides a spiral filament, which traverses the axis of the cone from the base to the summit. After they are thus deprived of their sheath of epithelium, it is almost impossible to distinguish them from the simple papillæ of man or other mammifera.

It is worthy of notice, that amongst all the reptiles I have examined, the nerves of the fungiform papillæ in the frog are the most developed, and the most numerous. In placing these reptiles according to their position in this respect, we find, first, the frog, then the toad, the uromastic, and lastly the salamander. In a full-grown toad, the nerves of the fungiform papillæ are not more developed than a half-grown frog. In the uromastic, the fungiform papillæ, with the exception of their less degree of development, present the same characteristics as those of the frog. The salamander, which is lowest in the scale, has upon the tongue globular bodies, which may be regarded as fungiform papillæ; but they contain neither nerves nor blood-vessels, and are not more advanced in their structure than those of the tadpole, three or four days after the appearance of the tongue. It is evident that the same gradation exists with regard to the mobility of the tongue in the above-mentioned animals. The nerve of taste is, therefore, developed in proportion with the degree of motor power.

The extremity of the club of the tongue of the chameleon has no

papillæ, but presents upon its surface a series of rectilinear elevations and depressions, in which I have not been able to discover any nerves.

In the forked tongues of serpents, no papillæ are to be seen, neither on the tongue nor on the vascular membrane of the gullet.

The best type for studying the forked tongue of reptiles, is that of the *acanthus dactylus scutulatus*. In this little lizard, this organ is admirably disposed for microscopic observation. It is to be regretted that its rarity should render it so difficult of access for the microscopist. No animal membrane which I have had occasion to observe, seems to offer, by its transparency, and the variety of organic tissues, nerves, blood-vessels, muscles, epithelium, etc., such a combination of advantages. The employment of ether, as with the frog, would doubtless permit of its examination during life.

The tongue of the mammifera presents very slight anatomical differences in the various animals. We find in all fungiform and compound conical papillæ, mixed with others of a simple nature, which are concealed beneath the epithelium. The greatest differences which exist are exterior, and are confined to the sheath which covers the summit of the conical papillæ, which is sometimes soft, as in the tongue of man, and sometimes hard and sharp, as in beasts of prey.

To study the nerves of the papillæ, and of the mucous membrane, I make use, as with the frog, of strong caustic potash, of which one or two drops dissolve the other tissues before the nerves, which are last attacked. Last winter, I macerated large fragments of sheep's tongue in pure water, in which was a cylinder of phosphorus. By this means, the nervous ramifications could be easily traced by the naked eye, as far as their entrance into the fungiform papillæ. Oxalic acid in solution, is one of the best agents in the study of the nerves. By its use, at the end of one or two weeks, the epithelium is converted into a pulpy mass, which detaches itself easily from the papillæ. The nerves retain their natural transparency. With a thin slice of the tongue of a sheep, and the employment of potash a little weakened, we see the muscular fibres reunited into bundles of four or eight, surrounded by a very delicate cellular sheath, ascending to the lower part of the mucous membrane, where, before entering into the chorion, they cease abruptly, giving place to a fibrous tissue, which spreads out into diverging filaments above the muscular termination. By the interlacing of these tendinous fibres in every direction, the chorion of the tongue is formed. In the piliform or conical papillæ, these fibres reach to the summits of the secondary papillæ, and interlace with each other. In the fungiform papillæ they take an oblique direction from opposite points, and traverse the chorion at the base of these papillæ. I have never been able to follow the muscular fibre into the interior of the fungiform papillæ. The fibrous tissue is the continuation of the sheath of the bundles of muscular fibre. Its filaments penetrate into the secondary papillæ.

The papillary nerves exhibit a great difference, according to the kind of papilla. In the fungiform papillæ, the nerve is very voluminous, and contains about twenty or thirty tubes, which are surrounded by the fibrous sheath passing from the base into the secondary papilla. To examine the termination of the nerves in the fungiform papillæ, one of these papillæ must be removed from a very fresh tongue, and

submitted to the action of the alkali, under the microscope. If the papilla is not too much obscured by the black pigment which is deposited generally in the centre of these papillæ, it is very easy to perceive numerous tubes with free extremities, spreading out towards the secondary papillæ, of which they reach the base, or half their height. Thin slices of the human tongue give us the same results as that of the sheep, except that the chorion is not so thick; but the fibro-elastic tissue is always found to succeed abruptly to the muscular tissue, of which the fibres ascend towards the surface in every direction, to attach themselves in the manner described.

The size, and in general the opacity, of the papillæ of the sheep's tongue, are obstacles to the examination of the nerves—difficulties still greater in that of the horse and the ruminantia. In animals of a smaller size, their minuteness presents difficulties in separating a fungiform papilla from the adjacent ones. The human tongue offers them to us under the most favourable circumstances; but the disorganisation of these nerves after death has induced me to examine them from the living tongue. This little operation, which I have frequently performed upon myself and several other persons, is done almost without pain, with very sharp scissors. The little globular head, thus obtained by the observer, and possessing still in some degree the vital power, contains arteries and veins, nerves, fibro-elastic tissue, blood still in motion, and epithelium, which covers the whole surface. By the addition of water, the papilla becomes sufficiently transparent to witness the movement of the blood in the capillaries, which is partly caused by the contraction of the vessels, and the external compression of the papilla, and also, probably, from absorption of the water into the interior of the vessels. This movement lasts sometimes two or three minutes, until the vessels are emptied, or the blood coagulates. The capillaries form more or less intimate loops at the summit of each secondary papilla. All the vessels communicate together at the base of the secondary papillæ, where they unite with the arterial and venous branches. It often happens that, without any preparation, the nerve-tubes are to be seen, going from the central parts of the papilla towards the summits of the secondary ones; but, in the greatest number of cases, the employment of alkali is necessary to show them clearly. We then find that these tubes terminate, precisely as in the frog, in free extremities, which are often considerably dilated; and, in the centre of this species of nervous spongiole, we find a black spot, corresponding to the axis cylinder.

The removal of the conical papillæ may be made in the same manner; but the vessels and nerves are much less distinct, on account of the long sheaths of epithelium which cover each secondary cone, forming a considerable prolongation, and being about two-thirds of the length of the cone. Each of these papillary processes is composed of layers of epithelium, very distinct at their point of insertion on the papilla, but near the apex the sheath becomes more hard, and even horny. In the normal state, this is covered with a thick crust of granular matter, which is easily detached after death, which accounts for its not being described by physiologists, who have only examined these papillæ after death.

If, instead of making the section, we place a ligature round a fungi-

form papilla, a rather sharp sensation of pain is felt, much greater than that felt by cutting. This soon ceases, and the only sensation which remains is that of having a foreign body on the tongue. At the end of the third day, I generally experienced a hot and diffuse pain; and a few hours afterwards the papilla was detached, and a little conical stump left, which at the end of a week seemed to have attained its usual size. In this experiment, no subjective sensation of taste is felt, as happens with the irritation of other special nerves. I have repeated this experiment upon people of different constitutions. One of the subjects was a young man of a lymphatic and scrofulous temperament, with very feeble circulation, upon whom the slightest wounds healed with great difficulty. The sensations he described exactly corresponded with the above-described, and the papilla separated at the fourth day. The separated papilla contains no blood-globules, only some portions of nerves are visible.

The examination of the papillæ of the dog, cat, rabbit, hare, rat, mouse, guinea-pig, pig, hedgehog, and squirrel, during life, under the influence of chloroform, or after death, has given me the same results as the human papillæ. The differences are limited to the structure of the *papillary processes*, which I will not describe here. In the last-mentioned animals, where the papillæ are very small, in removing a portion of the membrane by means of potash, a network of nerves is seen, which sends off ascending branches to the papillæ. In every instance, the same superiority in size of the nerves of the fungiform papillæ existed. In none of the mammifera have I been able to discover any striated muscular fibres in the papillæ. In the tongue of the rabbit, I have seen fibres, which resembled muscular fibres, penetrating into the papillæ; but I have never met with any striated fibres. I think it very possible that in the tongue of the giraffe or the ant-eater they might be present, as these animal possess similar elastic tongues to the frog.

With respect to the distribution of the nerves of the tongue of the mammifera, there remains to determine the exact distribution of the three nerves which enter it. For, although the discoveries of Sir C. Bell have thrown a great light upon the functions of each of these nerves, it is impossible by the usual means to be certain if the hypoglossal gives off fibres to the papillæ, and what is the exact distribution of the lingual and of the glosso-pharyngeal. By means of the section of these nerves, this question is at once decided.

The right lingual nerve of a dog was divided, and a portion removed the 10th Dec. 1850, and the animal died the 2nd Feb. 1851, in convulsions. After the section of the nerve, complete paralysis of sensation of the same side was observed; the tongue moved as usual, but in lapping he lost a great quantity of the liquid. At the end of three days, the tongue was lacerated on the side of the section by the teeth, and the surrounding vessels ingested. Eight days after section, a small portion of the tongue was removed from the right side and the left. The nervous network in the mucous membrane on the right side was quite disorganised, and in the granular state, while on the left the nerves were normal. After death, the tongue was found to measure, from the point to the root, $3\frac{1}{4}$ inches. The nervous ramifications in the mucous membrane, and in the fungiform papillæ, had almost entirely

disappeared over a portion measuring two inches from the tip of the tongue, where there only remained very feeble traces, containing a few very fine black granules. Beyond this limit, the nervous ramifications and the nerves of the papillæ were all in a normal condition, but were much less numerous in comparison with those of the anterior part; and at $2\frac{1}{2}$ inches backwards, the papillæ were either simple, or much less covered with secondary cones than those at the anterior part of the tongue. All the nerves in these papillæ were normal. On the median line, as in the frog, the intermixture of the fibres of the two lingual nerves was to be seen. On the left side, all the nerve-tubes of the mucous membrane and papillæ were normal, from the tip to the root. At $2\frac{1}{4}$ inches backwards from the tip, the two sides of the tongue were compared together, and presented no difference as to the number and appearance of the tubes. The divided ends of the nerve were recruited by a membrane of cellular appearance. The peripheric parts of the divided nerve were atrophied, in comparison with that of the left side, and the contents consisted of black granules. All the ramifications of this nerve which could be followed, were found in the same state. The central part was not examined. On the left side, the lingual nerve was normal.

Section of the right hypoglossal nerve was made on a dog, while under the influence of chloroform. For several hours after the operation, he gaped constantly. His tongue turned towards the left, and the animal had great difficulty in swallowing. Sometimes he bit his tongue, and cried with the pain; but it never became ulcerated. When the tongue was pinched, the right anterior part remained flaccid, and presented only a tremulous movement, caused, probably, by the muscular fibres coming from the other side. At the end of some days, deglutition was much more easy, although the right side remained paralysed. At the end of twenty days, there was nothing extraordinary to be remarked; the functions of the right side were nearly reestablished, but the right side was atrophied. At the twenty-fifth day, the dog appeared agitated, and walked round and round *en manège*. He continued this movement in spite of all obstacles which were placed in his way: a pan of water, for example, was placed in the circle, and he walked over it without altering his course. After continuing two days in this condition, he became more and more weak, and died in convulsions. Microscopic examination of the papillæ and mucous membrane of the left side shewed the nerves to be all in the normal state; but when the subcutaneous muscular layer was examined, the great alteration of all the tissues of the right side was very apparent. The smaller musculo-nervous ramifications, consisting of two, three, or four tubes, had almost disappeared, and were very difficult to follow; but the disorganised nerves in the larger branches were traced easily, by means of their black granules. The muscular fibres on the same side were also disorganised, almost all without striæ, and transparent, but finely granulated, and their size much less. The nuclei of these fibres were more elongated, and much less distinct, than on the other side. In some sections, considerable *non-muscular* nervous branches were found.

The cicatrix between the divided ends presented new fibres, of which traces were to be seen in the small branches, but none in the ultimate ramifications. The central end was normal. After the preparation

had been kept several days, decomposition had altered the muscular parts of the right side, while on the other side they were unaltered. Finally, the right side became putrefied, green, and very soft, while the other was red, and its microscopic structure almost unchanged. This experiment has been often repeated with the same results.

The difference in the phenomena of putrefaction, which is observed between the tissues disorganised by section of the nerves, appears to me to be an invariable result; and already, as a general rule, we may say, that at the end of some days after section of the lingual nerve, the sheath of the papilla is separated on the side of the section, and only on the anterior parts of the tongue which receive the branches of the lingual. After section of the hypoglossal, putrefaction begins sooner in the paralysed muscles. The theory of the phenomena of nutrition of the animal body seems likely to me to receive considerable light from these facts, and already we can perceive the close relation between the destruction of the tissues during life and after death.

To examine more correctly the state of the blood-vessels after section of the nerves, I caused the tongues of dogs and rabbits to be injected. One of these was the tongue of a young dog, of six or eight months, whose left hypoglossal and lingual nerves had been divided on the 10th August, 1850. The animal was killed the 10th October following. After the injection, the papillary sheaths detached themselves as usual, much more easily on the left side. The fungiform papillæ on this side were much atrophied and almost invisible, the conical papillæ were very little altered or atrophied. On the left side, the vessels in the fungiform papillæ were much less numerous, and were smaller than on the right side, where they formed a rich network of loops and knots, anastomosing frequently, while those on the left side formed only simple loops, communicating only at the base of the fungiform papillæ without any coils. It appeared to me, therefore, that after the loss of the sensitive and motor functions the current in the vessels was slower and more feeble, the result of which was to obliterate the numerous capillary coils and the anastomosing branches, leaving only a feeble current in the principal trunks. In the muscles, the vascular alterations were not less evident. On the paralysed side, the capillaries were much less abundant, with fewer coils, and usually smaller than on the other; the little arteries and veins were also more irregular. Thus, instead of finding the gradual diminution of diameter as on the healthy side, a large vessel was seen to be suddenly contracted to the size of a capillary. In the venous portion also, the capillaries terminated in a kind of sinus, instead of the gradually increasing branches, as in the normal state. In several parts, the capillaries and the afferent and efferent vessels appeared to have a foreign deposit in their internal parietes, probably of a fibrinous nature, which caused rugosities and obstructions internally. After injection, nerves could no longer be discerned in the papillæ, even on the healthy side; but at the peripheric end of the divided trunks, the tubes were generally in the black granular condition, even as far as the smallest ramifications. The two nerves were found to be in exactly the same degree of alteration at their peripheric ends; their central part was in the normal state.

PNEUMOGASTRIC AND SYMPATHETIC NERVES. The important functions of these nerves govern in a degree animal physiology. The examination of these appeared to me capable of receiving much light by means of the alterations consequent upon its section at various points. I was anxious to ascertain if these nerves, so different from all the others of the animal economy, would exhibit similar alterations, or if they would take place in the same manner, and also if they would occur as rapidly as in the other nerves. The following experiment replies to most of these questions.

The hypoglossal, lingual, pneumogastric, and sympathetic nerves of a young cat were divided September 28, 1850, under the influence of chloroform. The cervical sympathetic was divided between two ligatures tied on the vagus nerve and the carotid artery of the right side. The pupil instantly contracted considerably on the same side, the eye turned inwards, and the nictitant membrane covered a considerable portion of the eye. The animal was killed with prussic acid October 29, 1850.

On examination, the right pneumogastric was redder, more transparent, and less pearly than on the left side. Under the microscope the tubes were very indistinct, and those most distinct were filled with black granules; followed into the chest, they were found to be in the same state as at the neck, with the exception of a few normal tubes, which traversed the disorganised ones, evidently being derived from a source below the point of section. The branch of the pneumogastric, going towards the last cervical ganglion, was examined as far as the ganglion, and its filaments were found to be disorganised in the same manner as the rest of the trunk. The two other branches of the ganglion, which go off to the middle cervical ganglion and to the cervical nerves, appeared to be in the normal state.

The upper end of the sympathetic cord, that which was joined to the upper ganglion, was quite disorganised, presenting fusiform masses of black granules, amongst which were a few quite normal tubes. On the opposite side, the nerve which proceeded from the ganglion presented the usual structure of tubes of different diameters. The upper branch of the first ganglion was normal, as were the ganglion-globules. The peripheric parts of the lingual and hypoglossal nerves were in the condition of black granules. Their central parts were healthy.

We conclude from this experiment,—1. That the tubes of the sensitive nerves (lingual), motor (hypoglossal), mixed (vagus), and ganglionic (sympathetic), are all disorganised in the same manner and with the same rapidity. If we admit the existence of a nervous fluid, we must conclude that it does not influence, or, at least, influences in a very slight degree, the phenomena of absorption. 2. The unaltered condition of the ganglion-globules permits us to draw a very clear line of demarcation between these nervous elements and the nervous tubular matter. I have found the same effect take place with the spinal ganglions of the posterior roots; for when, after section, the nerves are altered, the ganglion-globules remain quite sound. 3. The disorganised state of the branch, between the pneumo-gastric and the last cervical ganglion, indicates very decidedly that the generally received opinion respecting the course of this nervous branch, is the correct one, and that it does not come from the ganglion. I was unable

to recognise any of its tubes on the other side of the ganglion amongst the branches between the cervical pairs and the middle cervical ganglion, all the tubes there being perfectly sound.

My researches upon other parts of the sympathetic have not produced any result, on account of the death of the animals. These have consisted in cutting the lumbar spinal marrow of dogs and rabbits, in the hope of being able to examine the branches of the sympathetic at the lower end, and which required the lapse of a month, or more, after section, to ascertain their condition. In the cat especially, it would be important to be able to examine the disorganisation of the nerves which enter into the Pacinian bodies. I propose to carry out these investigations without delay; the results I shall have the honour to communicate to the Academy.

In concluding, I must say, that three years' labour upon the section of nerves has convinced me that their examination by this means will exert great influence upon the progress of anatomy, in causing us to leave the field of hypothesis, and to decide without hesitation upon the source of each filament whose origin is doubtful. For physiology, it has already been the means of bringing numerous facts to light, and will no doubt furnish many more. It allows us to judge, without danger of being deceived, upon the source of the numerous branches of which a nerve is composed; and it is remarkable, that its indications become more clear and distinct in proportion as the part to be recognised is in less quantity; for when a nerve is reduced to the granular state, if fibres from another source join it, its fibres can be followed for a considerable distance one by one, which would be impossible in a collection of normal fibres, on account of the plexiform manner in which they twist round each other. To speak more exactly, it is easy to distinguish a sound nerve-tube, with double outlines, amongst a hundred or more disorganised ones. It is the *methode isolatrice* of Flourens carried to its highest degree, of which the section of the vagus nerve at the neck is sufficient for proof. Like the thread of Ariadne, it conducts us to the unravelment of all the different complicated anastomoses of the nerves of the head, and will demonstrate exactly the influence of the ganglions upon the nerves which traverse them, or lose themselves within them, as we have seen with the vagus nerve in the last cervical ganglion. Henceforth, the examination of no nerve will be complete, until it has been studied by sections made at different heights. This method, applied to the vagus nerve, will allow us, as I have done upon the two glosso-pharyngeals of the frog, to isolate completely all its fibres from those of the sympathetic. For section of these two nerves at different periods admits of keeping the animal alive, without injury to the distinctive characteristics of the disorganised tubes. It would be superfluous to describe the divers applications of this process to the other nerves of the body. It would be of great use to comparative anatomy, when applied to all invertebrate animals for the study of the nerves, and to distinguish the true nervous centres.

My experiments on the central parts of the nervous system have not yet given me any positive results. Three months after division of the lumbar spinal marrow of a frog, I could see no alteration of the tubular and globular matter; but, if we simply consider the reunion of

wounds of the spinal marrow on the frog, and the researches set forth in the celebrated pages of the *Recherches Experimentales sur le Système Nerveux*, we shall see the analogy which exists in the mammifera, between the reunion of these parts and that of the peripheric portions of the nervous system, both with respect to the period of reunion, and to the return of their functions, to be too great to allow of our rejecting the possibility of the same law being applicable to both.

The first application to pathology of section of nerves, will probably be the examination of the lingual papillæ in cases of paralysis of the lingual nerve, or of the upper part of the fifth pair. To avoid error, it will be sufficient, as in my experiments, to compare the diseased with the healthy side. The advantage which the physician will derive in such a case for diagnosis and treatment, is too immediate to admit of hesitation in performing this little operation. The application of the microscope to the study of the nerves, in cases of paralysis of other parts of the body, although not feasible during life, will be of use as a touchstone in obscure cases of diagnosis, and will give us a means, as in the foregoing experiments, to classify nervous diseases into—nervous diseases with and without alteration of structure. For the preservation of the portions removed, the precaution of keeping them at a temperature of 0° centigrade, which admits of their being kept for an indefinite period, is the most effectual.

The foregoing paper was addressed to the Academy of Sciences of Paris; and an extract from it was published in the *Comptes Rendus*, Dec. 1st, 1851. The observations and experiments which it contains were commenced in 1849, and form a continuation of a paper communicated by me to the Royal Society, on the section of the glossopharyngeal and hypoglossal nerves of the frog, inserted in the *Philosophical Transactions*, Part II, 1850, when I first employed the alterations consequent on the disorganisation of a divided nerve, as a means to trace its anatomical course and distribution. The section of the lingual and hypoglossal nerves in the mammifera, is but a continuation of the same mode of investigation.

In March 1850, when I went over the experiments on the frog with Dr. Sharpey, I demonstrated to him, at the same time, the effects of section of the lingual nerve in the dog, on the nerves of the papillæ fungiformes, and on the ramifications in the mucous membrane of the dorsum of the tongue. Shortly after, I repeated the same experiments before Mr. Quekett. In May 1850, I addressed an application to the Royal Society (Committee of Russell Fund), in which I described briefly some of my observations on the mammifera, and mentioned the importance of applying my new method of investigating the course and distribution of the nerves throughout the whole system.

In addition to my thanks to the two above mentioned gentlemen, who were kind enough to witness my experiments, and to express much interest in them, I take this opportunity of acknowledging the kindness of Professors Owen, Carpenter, and Wheatstone, who were all made acquainted with the nature of my researches. I am also much indebted to Mr. Hett, whose excellent injected preparations are so well known, for the care with which he injected various subjects for me, especially the tongues of some animals whose nerves had been divided, and had become disorganised.