XXVI. *On the Reflex Function of the Medulla Oblongata and Medulla Spinalis.* *By* MARSHALL HALL, *M.D., F.R.S. L. & E., &c. &c.*

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1. *Introduction.*

THE higher departments of every science are doubtless its general principles and its laws. These have a claim to our consideration beyond that of insulated facts or mere details. Impressed with this truth, I have hitherto devoted my attention chiefly to the laws and principles of physiology. In a former memoir*, I gave the outline of one of the most general of the laws of this science,—that of the inverse ratio of the respiration and of the irritability. In the present memoir, I propose to give an account of a principle of action in the animal economy, which has not hitherto, I think, been distinguished with sufficient precision from the other vital and animal functions.

The principle to which I have adverted is connected, in a peculiar manner, with the medulla oblongata and the medulla spinalis. There is still much discrepancy of opinion amongst physiologists, in regard to the properties and functions of these parts of the nervous system. LEGALLOIS concluded, from his interesting series of experiments, that the spinal marrow, as a whole, and in distinct portions, is the exclusive source of sensation and voluntary motion. He observes†, "La vie du tronc dépend de la moëlle épinière, et celle de chaque partie dépend spécialement de la portion de cette moëlle dont elle reçoit ses nerfs. De plus, il est facile de démontrer que cette prérogative de la moëlle épinière, d'être la source du sentiment et de tous les mouvemens volontaires du tronc, lui appartient exclusivement à tout autre organe." The Reporters of the Institute adopt the conclusions of LEGALLOIS: "M. LEGALLOIS," they observe‡, "a démontré que la section de la moëlle épinière sur les

* Philosophical Transactions for 1832.

† Œuvres de LEGALLOIS, Paris 1824, tome i. p. 62.

‡ Ibid. p. 251.

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premières ou sur les dernières vertèbres cervicales, n'arrête que les mouvemens inspiratoires, et qu'elle laisse subsister dans tout le corps le sentiment et les mouvemens volontaires. Cette distinction est capitale: personne ne l'avait faite avant lui*." M. CRUVEILHIER, on the other hand, denounces this view of the functions of the spinal marrow as one of the errors of modern physiology. He observes†, "L'indépendence des diverses parties de la moëlle les unes des autres, l'indépendence de la moëlle du cerveau, assez généralement admise dans ces derniers temps, me parait une grave erreur physiologique fondée sur d'ingénieuses expériences. L'opinion des anciens, qui regardaient la moëlle comme un gros cordon nerveux destiné à répondre lui seul à tous les nerfs de l'économie, pour transmettre en définitive au cerveau les impressions, ou pour en recevoir les impulsions volontaires ou organiques, cette opinion est bien plus en harmonie avec les faits, avec la grande loi anatomique de la continuité du système nerveux."

It will not be difficult to prove that the conclusions of LEGALLOIS and the Reporters of the Institute, are not legitimate deductions from the facts before them. But M. CRUVEILHIER altogether overlooks these facts, which are amongst the most interesting in physiology, and adopts an opinion which, however true, is far too exclusive.

On the more recent occasion of a report upon the admirable work of M. FLOURENS, the Perpetual Secretary of the Institute states his opinion on this point in a manner far more problematical. "L'auteur," he observes, "conclut que la sensation et la contraction n'appartiennent plus à la moëlle épinière qu'aux nerfs; et cette conclusion est certaine pour les animaux entiers. Ce serait une grande question de savoir si elle l'est également pour les animaux qui ont perdu leur encéphale, et qui, dans certaines classes, paraissent loin de perdre sur-le-champ leurs fonctions animales‡."

* More recently, M. MAGENDIE, M. LALLEMAND, and M. OLLIVIER have repeated the same opinion: Anatomie des Systèmes Nerveux, par A. DESMOULINS, Paris 1825, p. 561, &c.; Observations Pathologiques propres à éclairer la Physiologie, ed. 2, Paris 1825, pp. 88, 96, &c.; Traité de la Moëlle Épinière, ed. 2, Paris 1827, p. 17, &c. The subject is unnoticed by M. SERRES: Anatomie Comparée du Cerveau, Paris 1824. The physiologists of our own country have adopted the same views: Philip on the Vital Functions, ed. 3, p. 120; MAYO's admirable Outlines of Human Physiology, ed. 3, p. 227–231, &c.

† Anatomie Pathologique, Fasc. III.

‡ Du Système Nerveux, par P. FLOURENS, Paris 1824, p. 70.

It was a singular mistake to imagine that the same conclusion could be just in reference to the entire animal, which was incorrect in reference to the animal deprived of its encephalon. The facts are these: in the entire animal, sensation and voluntary motion, functions of the cerebrum, combine with the functions of the medulla oblongata and medulla spinalis, and may therefore render it difficult or impossible to determine those which are peculiar to each; if, in an animal deprived of the brain, the spinal marrow, or the nerves supplying the muscles, be stimulated, those muscles, whether voluntary or respiratory, are equally thrown into contraction, and, it may be added, equally in the complete and in the mutilated animal; and, in the case of the nerves, equally in limbs connected with and detached from the spinal marrow.

The operation of all these various causes of muscular contraction may be designated *centric*, as taking place *at*, or at least in a direction *from*, central parts of the nervous system. But there is another function the phenomena of which are of a totally different order and obey totally different laws, being excited by causes in a situation which is *eccentric* in the nervous system, that is, distant from the nervous centres. This mode of action has not, I think, been hitherto distinctly understood by physiologists. It is involved in the question which Baron Cuvier considers as so full of interest, and is that treated of in the following pages.

Many of the phenomena of this principle of action, as they occur in the limbs, have certainly been observed. But, in the first place, this function is by no means confined to the limbs: for, whilst it imparts to each muscle its appropriate tone, and to each system of muscles its appropriate equilibrium or balance, it performs the still more important office of presiding over the orifices and terminations of each of the internal canals in the animal economy, giving to them their due form and action; and, in the second place, in the instances in which the phenomena of this function have been noticed, they have been confounded, as I have stated, with those of sensation and volition; or, if they have been distinguished from these, they have been too indefinitely denominated instinctive, or automatic. I have been compelled, therefore, to adopt some new designation for them, and I shall now give the reasons for my choice of that which is given in the title of this paper.

This property is characterized by being *excited* in its action, and *reflex* in its

course: in every instance in which it is exerted, an impression made upon the extremities of certain nerves is conveyed to the medulla oblongata or the medulla spinalis, and is reflected along other nerves to parts adjacent to, or remote from, that which has received the impression.

It is by this reflex character that the function to which I have alluded is to be distinguished from every other. There are, in the animal economy, four modes of muscular action, of muscular contraction. The *first* is that designated *voluntary*: volition, originating in the cerebrum, and spontaneous in its acts, extends its influence along the spinal marrow and the motor nerves, in a *direct line*, to the voluntary muscles. The *second* is that of the *respiration*: like volition, the motive influence in respiration passes in a *direct line* from one point of the nervous system to certain muscles; but as voluntary motion seems to originate in the cerebrum, so the respiratory motions originate in the medulla oblongata: like the voluntary motions, the motions of respiration are spontaneous; they continue, at least, after the eighth pair of nerves has been divided. The *third* kind of muscular action in the animal economy is that termed *involuntary*: it depends upon the principle of irritability, and requires the *immediate* application of a stimulus to the nervo-muscular fibre itself. These three kinds of muscular motion are well known to physiologists; and I believe they are all which have been hitherto pointed out. There is, however, a *fourth*, which subsists, in part, after the voluntary and respiratory motions have ceased, by the removal of the cerebrum and medulla oblongata, and which is attached to the medulla spinalis, ceasing itself when this is removed, and leaving the irritability undiminished. In this kind of muscular motion, the motive influence does not originate in any central part of the nervous system, but at a distance from that centre: it is neither spontaneous in its action, nor direct in its course; it is, on the contrary, *excited* by the application of appropriate stimuli, which are not, however, applied immediately to the muscular or nervo-muscular fibre, but to certain membranous parts, whence the impression is carried to the medulla, *reflected*, and reconducted to the part impressed, or conducted to a part remote from it, in which muscular contraction is effected.

The first three modes of muscular action are known only by actual movements or muscular contractions. But the reflex function exists as a continuous muscular action, as a power presiding over organs not actually in a state of

motion, preserving in some, as the glottis, an open *, in others, as the sphincters, a closed form, and in the limbs, a due degree of equilibrium, or balanced muscular action,—a function, not, I think, hitherto recognised by physiologists.

The three kinds of muscular motion hitherto known may be distinguished in another way. The muscles of voluntary motion and of respiration may be excited by stimulating the nerves which supply them, in any part of their course, whether at their source, as a part of the medulla oblongata or medulla spinalis, or exterior to the spinal canal: the muscles of involuntary motion are chiefly excited by the actual contact of stimuli. In the case of the reflex function alone, the muscles are excited by a stimulus acting mediately and indirectly in a curved and reflex course, along superficial sub-cutaneous or sub-mucous nerves proceeding to the medulla, and muscular nerves proceeding from the medulla. The first three of these causes of muscular motion may act on detached limbs or muscles. The last requires the connexion with the medulla to be preserved entire.

All the kinds of muscular motion may be unduly excited. But the reflex function is peculiar in being excitable into modes of action not previously subsisting in the animal economy, as in the cases of sneezing, coughing, vomiting, &c. The reflex function also admits of being permanently diminished or augmented, and of taking on some other morbid forms, of which I shall treat hereafter.

I shall thus have occasion to speak of the reflex function as the source of equilibrium in the muscular system; as excitable into various actions, which, however familiar, are not constant; and as assuming morbid forms.

Before I proceed to the detail of the experiments upon which this disquisition rests, it may be well to point out several instances in illustration of the various sources and modes of muscular action which have been enumerated. None can be more familiar than the act of swallowing. Yet how complicated is this act! The apprehension of the food by the teeth, the tongue, &c., is voluntary, and cannot, therefore, take place in an animal from which the cerebrum is removed †. The transition of the food over the glottis and along the middle and lower parts of the pharynx depends upon the reflex function: it can take

* See Legallois, Op. cit. p. 176—178.

† Du Système Nerveux, par M. Flourens, Paris 1824, p. 90.

place in animals from which the cerebrum has been removed *, or the ninth pair of nerves divided †; but it requires the connexion with the medulla oblongata to be preserved entire ‡; and the actual contact of some substance which may act as a stimulus §: it is attended by the accurate closure of the glottis, and by the contraction of the pharynx. The completion of the act of deglutition is dependent upon the stimulus immediately impressed upon the muscular fibres of the œsophagus, and is the result of excited irritability.

The example which I have given is one of excited reflex function. The condition of the glottis during respiration, and that of the pharynx and of the sphincters at all times, except during the acts of deglutition, or of excretion, afford equally interesting and familiar examples of the permanent influence of that function. Whilst the nervous connexion between the larynx and the medulla oblongata is preserved entire,—in the rabbit (*Lepus cuniculus*), for example,—the glottis is preserved open, being slightly dilated during each act of inspiration; but if the superior laryngeal nerves be divided, the aperture immediately becomes so much diminished, that a state of excessive dyspnœa is induced. The sphincter ani, on the other hand, remains closed in the decapitated turtle (*Chelonia mydas*), if the lower part of the medulla spinalis be left in its canal; but it becomes immediately relaxed and open, if this part of the nervous system be withdrawn. The action of this muscle depends upon the medulla spinalis, and not upon the brain only.

However plain these observations may have made the fact, that there is a function of the nervous and muscular system distinct from sensation, from the voluntary and respiratory motions, and from irritability, it is right, in every such inquiry as the present, that the statements and reasonings should be made with the experiment, as it were, actually before us. It has already been remarked, that the voluntary and respiratory motions are spontaneous acts, not necessarily re-

* Du Système Nerveux, par M. Flourens, Paris 1824, p. 90.

† The Nervous System, by Charles Bell, F.R.S. 4to ed. 1830. Appendix, p. cxviii.

‡ De l'Usage de l'Epiglotte, par M. Magendie, Paris 1813, pp. 6, 23, &c.

§ This is the reason of our inability to perform the act of swallowing two or three times in rapid succession, without taking something into the mouth, or allowing time for the secretion of a portion of saliva. The reflex function must be excited into action by the contact of a stimulus. The act of swallowing cannot, therefore, be renewed unless some substance, as saliva, be carried into contact with the pharynx. See further, p. 661.

quiring the agency of a stimulus. If, then, an animal can be placed in such circumstances that such motions will certainly not take place, the power of moving remaining, it may be concluded that volition and the motive influence of respiration are annihilated. Now this is effected by removing the cerebrum and the medulla oblongata. These facts are fully proved by the experiments of LEGALLOIS and M. FLOURENS, and by several which I proceed to detail, for the sake of the opportunity afforded by doing so, of stating the argument most clearly.

I divided the spinal marrow of a very lively snake (*Coluber natrix*), between the second and third vertebræ. The movements of the animal were, immediately before, extremely vigorous and unintermitted. From the moment of the division of the spinal marrow, it lay perfectly tranquil and motionless, with the exception of occasional gaspings and slight movements of the head.

It became quite obvious that this state of quiescence would continue indefinitely, were the animal secured from all external impressions.

Being now stimulated, the body began to move with great activity, and continued to do so for a considerable time, each change of position or situation bringing some fresh part of the surface of the animal into contact with the table or other objects, and renewing the application of stimulus.

At length the animal became again quiescent; and being carefully protected from all external impressions, it moved no more, but died in the precise position and form which it had last assumed.

It requires a little manœuvre to perform this experiment successfully: the motions of the animal must be watched, and slowly and cautiously arrested by opposing some soft substance, as a glove or cotton wool; they are by this means gradually lulled into quiescence. If at this moment the figure last assumed be sketched upon paper, and the animal be left, protected from external impressions, it will be found to retain the same identical form when all vitality has ceased.

The slightest touch with a hard substance, the slightest stimulus, will, on the other hand, renew the movements of the animal in an active form. But that this phenomenon does not depend upon sensation, is further fully proved by the facts, that the position last assumed, and the stimuli applied, may be such as would be attended by extreme or continued pain, if the sensibility were undestroyed: in one case the animal remained partially suspended over the acute

edge of the table; in others the infliction of punctures, and the application of a lighted taper, did not prevent the animal, still possessed of active powers of motion, from passing into a state of complete and permanent quiescence.

The same observations were made upon various other animals—the turtle, the viper (*Vipera Berus*), the toad (*Bufo vulgaris*), the frog (*Rana temporaria*), the eft (*Triton cristatus*), &c. It may therefore be stated as a general fact, that if an animal be deprived of the cerebrum and medulla oblongata, and placed under an inverted bell-glass, or otherwise protected from external stimuli, it will not move, however easily it may be excited to motion by external impressions.

I must now solicit the attention of the Society to three important points: it is obvious,

1st, That sensation can act, in inducing muscular motion, only through the medium of volition;

2ndly, That, in the experiments which have been described, volition,—the *will*, and not the *power*, to move, was annihilated;

3rdly, That, in such cases,—volition being destroyed and the agency of sensation excluded,—the influence of external impressions, which might be supposed to induce pain, must have been exerted upon some property of the nervous system different from sensibility.

The absence of spontaneous motions in decapitated animals, proves the privation of volition; and the privation of volition removes all evidence of sensibility in excited motions, and indeed positively excludes its influence. Sensation, volition, and motion, may be viewed as three links of the chain, in the case in which motion is induced by pain. If the second link be destroyed, the *connexion* between the first and third is dissolved. The proof, in fine, that the excited motions which belong to the reflex function are independent of sensation, is precisely of the same character as that by which the motions due to irritability are distinguished from the same principle.

We are hence led to the conclusion that the excited motions of decapitated animals are dependent upon a principle different from sensation and volition; and we are further led to the inquiry—What is the nature of that principle—what the cause of those motions, which remain after sensation and volition are destroyed?

But before I enter upon this question, it is important to show still more distinctly than I have done, the distinction between the movements arising from the reflex function of the medulla oblongata and medulla spinalis, and those arising from irritability itself. If the glottis of an animal be touched, there is an immediate contraction. If the heart be touched, the same phenomenon is observed. What is the difference between the excited movements of these two organs? If the brain be removed, the same events still take place. If the medulla oblongata be removed, the contractions of the stimulated larynx suddenly cease, whilst those of the heart continue as before. The difference consists, then, in the presence of the medulla oblongata, which is essential to the contractions of the larynx, but of which those of the heart are entirely independent. The influence of the stimulus upon the heart is immediate. That of a stimulus applied to the larynx must pass to the medulla oblongata, and be reflected upon the part moved.

It is interesting to compare the excited movements of the glottis and the submaxillary textures, of the sphincter ani and the tail, and of the heart, in these several parts of the recently killed turtle, placed together upon the same table. All continue vigorous for a considerable time, until the medulla oblongata or the medulla spinalis be withdrawn, when the movements of that portion of the respiratory apparatus which is attached to the head, or of the sphincter and tail, cease in an instant.

The reflex function of the medulla is most permanent and apparent to observation in those animals in which the respiration is lowest. The cold-blooded animals, the hybernating animal, and the very young of the warm-blooded, are therefore the subjects in which this function can be best studied. It may be retained, or restored, however, in the adult warm-blooded animal, by retaining the respiration, or by renewing the respiration artificially,—a fact, which constitutes another characteristic of the reflex function, and distinguishes it from irritability, and which is, in my opinion, one of the most remarkable in physiology, and highly worthy of further investigation. These remarks will readily suggest the proper choice of animals, and mode of experiment, for the display of the reflex function. I now proceed to the detail of the various experiments which I have made upon this subject, and shall then deduce the conclusions which appear to flow from them.

II. *Experiments.*

The phenomena of the reflex function, like those of the irritability, are, as I have just stated, more observable in the lower orders of animals, in the very young of the higher orders, and in the state of hybernation. It will be found, however, that the full-grown mammalia are not less distinctly endued with this property of the nervous system, whilst the functions of respiration and circulation are continued.

The first experiment which I made was upon the turtle.

This animal was decapitated in the manner usual with cooks, by means of a knife, which divided the second or third vertebra.

The head being placed upon the table for observation, it was first remarked that the mouth opened and shut, and that the submaxillary integuments descended and ascended, alternately, from time to time, replacing the acts of respiration. I now touched the eye or eyelid with a probe. It was immediately closed: the other eye closed simultaneously. I then touched the nostril with the probe. The mouth was immediately opened widely, and the submaxillary membranes descended. This effect was especially induced on touching the nasal fringes situated just within the anterior part of the maxilla. I passed the probe up the trachea and touched the larynx. This was immediately followed by a forcible convulsive contraction of the muscles annexed to it. Having made and repeated these observations, I gently withdrew the medulla and brain. All the phenomena ceased from that moment. The eye, the nostril, the larynx were stimulated, but no movement followed.

The next observations were made upon the other parts of the animal. The limbs, the tail, were stimulated by a pointed instrument or a lighted taper. They were immediately moved with rapidity. The sphincter was perfectly circular and closed; it was contracted still more forcibly on the application of a stimulus. The limbs and the tail possessed a certain degree of firmness or tone, recoiled on being drawn from their position, and moved with energy on the application of the stimulus. On withdrawing the spinal marrow gently out of its canal, all these phenomena ceased. The limbs were no longer obedient to stimuli, and became perfectly flaccid, having lost all their resilience. The sphincter lost its circular form and its contracted state, becoming lax, flaccid, and shapeless. The tail was flaccid, and unmoved on the application of stimuli.

This experiment affords evidence of many important facts in physiology. It proves that the presence of the medulla oblongata and spinalis is necessary to the contractile function of the eyelids, the sub-maxillary textures, the larynx, the sphincters, the limbs, the tail, on the application of stimuli to the cutaneous surfaces or mucous membranes. It proves the reflex character of this property of the medulla oblongata and spinalis, and the dependence of these motions upon the reflex function. It proves that the tone of the limbs, and the contractile property of the sphincter, depend upon the same reflex function of the medulla spinalis,—effects not hitherto suspected by physiologists.

I must now state that the phenomena which have been detailed subsist in distinct portions of the divided nervous system. If, after severing the head of the turtle, the lower extremities and the tail be separated together, in the manner usual with cooks, the phenomena which I have described are still observed in the distinct and separate portions of the animal. The head, the anterior extremities, and the tail present the movements which have been described, when severally stimulated. The posterior extremities alone were observed to be flaccid and unimpressible by stimuli; and these were found, on examination, to have been separated from their connexion with the spinal marrow.

An interesting experiment demonstrates the powerful influence of the reflex function over the sphincter ani in the turtle. If, after the removal of the tail and the posterior extremities, with the rectum, and of course with a portion of the spinal marrow, water be forced into the intestine, by means of READ'S syringe, both the cloaca and the bladder are fully distended before any part of the fluid escapes through the sphincter, which it then does on the use of much force only, and by jerks. The event is very different on withdrawing the spinal marrow: the sphincter being now relaxed, the water flows through it at once in an easy continuous stream, with the application of little force, and without inducing any distension, even of the cloaca.

I was first struck with the phenomena of the reflex function of the spinal marrow in the separated tail of an eft. On being excited by the point of a needle passed lightly over its surface, it contracted and moved as if it still formed a part of an entire animal.

On another occasion, having removed the head of a frog, I divided the spine between the third and fourth vertebræ, and separated the upper portion of the

animal from the lower. There were then the head, the anterior extremities, and the posterior extremities, with their corresponding portions of medulla, as three distinct parts of an animal. Each preserved the reflex function. On touching an eye, it was retracted, and the eyelids closed, whilst similar phenomena were observed simultaneously in the other eye. On removing the medulla, these phenomena ceased. On pinching the toe of one of the anterior extremities, the limb and the opposite limb equally moved. On removing the spinal marrow, this phenomenon also ceased. Precisely similar effects were observed in regard to the posterior extremities.

Similar phenomena are also observed in the snake. If the head be removed, and a pointed instrument or a lighted taper be brought into contact with any part of the surface, it is instantly moved. The motion consists in a flexion of the entire part, and in a concentric movement of the integuments towards the point irritated; so that the muscles situated along the spine, and certain muscles analogous to the panniculus carnosus, are excited to contraction. The extremity of the tail is most impressible. The function which presides over these movements subsisted in every part of the animal separated from the rest, but instantly ceased on removing the spinal marrow.

On touching a point immediately within the teeth of the upper jaw, the larynx was suddenly drawn downwards and closed. These movements could also be excited by touching the nostrils. They ceased on removing the medulla oblongata.

Similar phenomena are seen also in the very young of the mammalia. A rabbit, one day old, was immediately deprived of all voluntary or respiratory motion, with the exception of gaspings, by dividing the spinal marrow near the occiput. Yet the head and the limbs moved, on stimulating the ears or the feet. These movements ceased in a quarter of an hour, but were renewed by artificial respiration. The phenomena were precisely similar after decapitation, hæmorrhage being prevented and artificial respiration maintained. All ceased on removing the medulla oblongata and spinalis.

One of the most remarkable of the phenomena attached to the reflex function in animals, is that presented by those muscles of the hedgehog (*Erinaceus europæus*) by means of which that animal assumes, in certain circumstances, the form and firmness of a ball. The reflex function seems especially to con-

nect the roots of the spines with the muscles. If the animal be examined under the influence of hybernation, the reflex function continues for some hours after the brain is removed; the panniculus carnosus, the limbs, the tail, the larynx, the sphincter ani, remain excitable, and retain a degree of tone. These phenomena cease on removing the medulla spinalis.

The phenomena of the reflex function seen in the panniculus carnosus, and in other muscles of the hedgehog, are also particularly displayed in the very young animal, in which the peculiar movements of this creature are excitable for a considerable time after decapitation, or the division of the spinal marrow, and long after the cessation of the voluntary and respiratory motions, when it is in a languid and dying state.

In the case of the decapitated young hedgehog, after all gasping has ceased, motions of the larynx are still excited on irritating the nostrils, or on irritating the medulla itself; just as the peculiar motions of the trunk are excited on irritating the limbs, tail, or spines,—or the spinal marrow.

Nor are we without evidence that the same principles obtain in the human subject. The condition of the infant born without cerebrum or cerebellum, and breathing from the influence of the medulla oblongata alone, is precisely that of the reflex function, with the addition of respiration. Such a case has been witnessed and described by Mr. LAWRENCE *. "The child moved briskly at first, but remained quiet afterwards, except when the tumour was pressed, which occasioned general convulsions. It breathed naturally, and was not observed to be deficient in warmth, until its powers declined. I regret that, from a fear of alarming the mother, no attempt was made to see whether it would take the breast: a little food was given it by the hand. It voided urine twice in the first day, and once a day afterwards: it had three dark-coloured evacuations. The medulla spinalis was continued for about an inch above the foramen magnum, swelling out into a small bulb, which formed the soft tumour on the basis of the skull. All the nerves, from the fifth to the ninth, were connected to this." This brief detail is full of interest. The respiration was natural, the medulla oblongata being entire. Swallowing was effected when food was brought into contact with the pharynx; the sphincters performed their functions; the limbs were moved when the skin was first impressed by the

* Medico-Chirurgical Transactions, vol. v. page 166.

atmospheric air. There was no indication of sensation—the child remained quiet after the first brisk movements; and no event is mentioned which could establish the existence of voluntary motion,—the acts of swallowing, and of the expulsion of the urine and fæces, with the functions of the larynx and of the sphincters, belonging distinctly to the reflex function.

M. Lallemand has briefly described a case of anencephalous fœtus*. "J'ai vu, il y a quatre ans, à l'Hôtel-Dieu, un fœtus anencéphale, à terme, ou à peu près, qui vécut trois jours. Pendant tout ce temps il poussa des cris assez forts, exerça des mouvemens de succion toutes les fois qu'il sentit quelque chose entre ses lèvres; mais on fut obligé de le nourrir avec du lait et de l'eau sucrée, parce qu'aucune nourrice ne voulait lui donner le sein. Il exécutait des mouvemens assez étendus des membres thoraciques et abdominaux. Quand on plaçait un corps étranger dans ses mains, il fléchissait les doigts comme pour le saisir; mais en général tous ses mouvemens avaient moins d'énergie que ceux d'un fœtus de même âge.

"Le cerveau et le cervelet manquaient entièrement: il ne restait à la base du crâne que la moëlle allongée et la protubérance annulaire, avec l'origine des nerfs pneumo-gastrique, trifacial et optique. Le tout était recouvert par les débris des os du crâne, des méninges et de la peau."

A similar case is detailed by M. Ollivier†, who remarks—"J'observai l'enfant anencéphale deux heures après sa naissance. Les yeux étaient constamment fermés; il poussait des cris fréquens qu'on calmait facilement en introduisant le petit doigt dans sa bouche: il exerçait alors des mouvemens de succion répétés; il agitait ses membres avec assez de force, et serrait entre ses doigts les corps qu'on plaçait dans ses mains.

"Je le revis au bout de trois heures. Les pieds et les mains étaient devenus violets et froids; la respiration ne s'opérait plus à des intervalles aussi rapprochés; les mouvemens de la moëlle épinière, que j'avais remarqués d'abord, continuaient toujours d'avoir lieu, et suivaient chacune des grandes et longues inspirations qu'il faisait. Les cris étaient moins forts et moins fréquens: on lui donna à diverses reprises de petites cuillerées de vin vieux sucré.

"Insensiblement le refroidissement des extrémités gagna le reste des mem-

* Observations Pathologiques, p. 86.

† Traité de la Moëlle Épinière, ed. 2, Paris 1827, p. 155.

bres et le tronc; la respiration s'opérait à de plus longs intervalles: elle devint convulsive. Cet état persista pendant six ou huit heures; ses cris devinrent plus faibles et plus éloignés, de même que les mouvemens de la respiration, qui étaient accompagnée de convulsions générales, et il mourut dans un véritable état d'asphyxie, après avoir poussé un cri analogue à celui qui résulte du hoquet."

M. OLLIVIER adds, (p. 161)—"Il n'existait pas ici un seul rudiment de l'encéphale et des prolongemens de la moëlle alongée; la moëlle épinière seule était restée intacte, et cependant cet infant exerçait des succions répétées, et serrait avec assez de force entre ses doigts les corps qu'on plaçait dans sa main; ces mouvemens étaient loin d'être automatiques comme ceux qui agitaient les membres inférieurs."

These cases, in connexion with the preceding one, are full of interest. The peculiar cries, which resemble, in their rationale, the croup-like convulsion from dentition; the closed state of the eyelids; the action of suction excited by the contact of the finger; the closure of the fingers excited by objects placed in the palm of the hand, and the movements of the inferior extremities, in this acephalous infant, are phenomena of the reflex function of the most deeply interesting character.

The following facts are extracted from a letter addressed by Mr. SWEATMAN to Sir CHARLES BELL, and published in the "Nervous System"*:—"After the membranes had given way, and the liquor amnii had escaped, the midwife on examining found another membranous bag presenting, which she naturally supposed belonged to a second child, and therefore did not interfere. During the passage of this bag under the os-pubis, it suddenly burst, and the whole of the brain escaped from the opening very much smashed, and hanging together only by its membranes. The child breathed with perfect freedom and cried strongly, rolling its eyes about in a wild, staring manner. It moved its lower extremities freely, and that not from spasm, but obviously in obedience to external impressions. There was no motion whatever of the upper extremities.

"In this state it remained for about three hours, when all motion in the extremities ceased, the eyes became fixed, and the breathing gradually slower, till it ceased altogether, just seven hours after the birth of the child. During

* Appendix, p. cxxxvi.

this time neither urine nor meconium passed, nor had there been any hæmorrhage from the vessels of the brain.

"On examination the occipital bone and the posterior part of several of the cervical vertebræ were found wanting, and their place had been occupied by fluid, surrounded by a membranous bag; an instance of spina bifida of the neck. The spinal marrow was perfect.

"A somewhat similar case occurred to me about three years ago, when I had occasion from peculiar circumstances to remove the brain of a child through the anterior fontanelle. In that instance, about ten minutes elapsed before its birth, yet it drew a deep inspiration, and would have cried had it not been prevented; and the motions of the lower extremities continued about half an hour, although the whole of the brain had been removed, and a blunt instrument repeatedly thrust down the foramen magnum *."

It is distinctly proved, by this series of observations, that the reflex function exists in the medulla independently of the brain; in the medulla oblongata independently of the medulla spinalis; and in the spinal marrow of the anterior extremities, of the posterior extremities, and of the tail, independently of that of each other of these parts, respectively.

There is a still more interesting and satisfactory mode of performing the experiment: it is to divide the spinal marrow between the nerves of the superior and inferior extremities. We have then two modes of animal life: the first being the assemblage of the voluntary and respiratory powers with those of the reflex function and irritability; the second, the two latter powers only: the first are those which obtain in the perfect animal, the second those which animate the fœtus. The phenomena are precisely what might have been anticipated. If the spinal marrow be now destroyed, the irritability alone remains, —all the other phenomena having ceased.

The spinal marrow of a frog was divided between the anterior and posterior extremities. It was immediately observed that the head and the anterior extremities alone were moved spontaneously and with design, the respiration being performed as before. But the posterior extremities were not paralyzed: they were drawn upwards, and remained perfectly motionless, indeed, unless stimulated; by the application by any stimulus, they were moved with

* See a similar case by Mr. HAMMOND, in the Medico-Chirurgical Transactions, vol. xii. p. 308.

energy, but once only, and in a manner perfectly peculiar. The stimulus was not felt by the animal, because the head and anterior extremities remained motionless at the time it was applied. Nothing could be more obvious, and indeed striking, than the difference between the phenomena of the functions of sensation and volition observed in the anterior part of the animal, and those of the reflex function in the posterior: in the former there were spontaneous movements with obvious design; in the latter, the mere effect of stimulus.

The same experiment was made upon the toad; but for some reason, probably anatomical, it does not succeed so uniformly in this animal as in the frog.

The experiment was repeated upon a guinea-pig. The effect was an immediate and total paralysis of sensation and voluntary motion in the posterior extremities: there was no expression of pain when they were pinched, nor was there the slightest indication of a power of spontaneous motion: they were dragged along when the animal moved. But they were not unimpressible by stimuli, nor destitute of the power of moving when stimulated: on the contrary, when pinched, they displayed a sort of repeated, hurried motion, altogether peculiar. The power of the sphincters was evidently preserved. In a word, the reflex function remained entire.

In all these experiments the upper part of the animal presented the phenomena of sensation and of spontaneous movements; in the lower, there was total paralysis of these powers; yet the reflex function, the excitability, the firmness of the limbs, and the irritability remained. It now remains to be stated, that the reflex function admits of *exaltation* and of *diminution.*

If a frog be made to swallow a watery solution of strychnine or of opium, or if such a solution of strychnine or opium be applied to the skin, the animal soon becomes affected with symptoms perfectly similar to those of tetanus. The surface becomes highly susceptible to the impression of stimuli, and the muscles of the limbs become affected with continued spasmodic action. The affection is obviously one of augmented reflex function of the medulla. It accordingly ceases instantly on destroying the nervous masses.

A frog made tetanic by opium was decapitated, and divided just below the third vertebra. The eyes were retracted, and no movement could be detected on irritating the eyelids or skin. Both the anterior and posterior extremities remained susceptible, and tetanic, as before: the limbs were moved in the same

spasmodic manner by the same slight impressions. All was changed on removing the brain and spinal marrow. The eyes were no longer retracted. The muscles of the limbs were immoveable under the action of stimuli, and perfectly flaccid, having lost their exalted tone.

Precisely similar phenomena were observed when the frog was made tetanic by opium or strychnine and divided into three portions, the head, the anterior and the posterior extremities; and in the eft made tetanic and divided into the head, anterior and posterior extremities, and tail. Each part remained tetanic, impressible by the slightest touch, and spasmodically contracted on any application of stimulus. The tetanus in each is instantaneously terminated by destroying the corresponding portion of spinal marrow, the head, the limb, or the tail, instantly manifesting a perfectly relaxed and flaccid condition of the muscles. The irritability remains unimpaired.

These facts complete the proof that the phenomena which I have referred to the reflex function, do not depend either upon sensation and volition, or upon irritability. It is plain that the spasmodic actions in tetanus are not voluntary actions, and they obey the same laws as the movements observed in an animal, or parts of an animal, not tetanic, under the influence of stimuli. It is equally plain that phenomena which depended upon excited irritability would not cease whilst that irritability remained unimpaired*.

The phenomena of tetanus, in its effects upon the limbs, enable us to conceive more distinctly than we should otherwise do, the effect of the reflex function in its natural state, in maintaining the due degree of balance and antagonism of the muscles and firmness of the limbs.

If a few drops of dilute hydrocyanic acid be placed upon the tongue of a frog, a state of things the reverse of that just described as the effect of opium or strychnine is induced: the contractions which depend on the reflex function are observed to become less and less energetic and excitable, and at length cease altogether.

* Having observed these facts in connexion with the reflex function, it became a question whether the rigidity of the muscles immediately consequent to death depends upon the same principle. Two rabbits were killed; in one the spinal marrow was destroyed, in the other it was left entire. Both, however, became equally rigid. So that the spasm of death is a mere effect of irritability, and not of the reflex function of the spinal narrow.

Having thus detailed the phenomena of the reflex function, as they are observed in their ordinary and augmented and diminished degrees of force, I shall briefly enumerate some of those *excited* motions observed in various parts of the animal frame, which are obviously referrible to the same function.

The most healthy condition of the reflex function is that, the result of which is the due state of balance between antagonist muscles. But certain excited states of this function can scarcely be viewed as otherwise than healthy: such are—winking when an object touches the eyelid, the singular effect of dashing cold water on the face, and the singular effect of tickling* upon the respiration, sneezing from irritation of the nostrils, cough from that of the larynx, vomiting from that of the pharynx, strangury from irritation of the rectum, and tenesmus from that of the bladder, &c.

The excited reflex function is observed on touching the eye, the nasal fringes, or the larynx, in the separated head of the turtle; and on touching the sphincter, the tail, or the limbs, of the separated lower portion of that animal; in the frog, the lower extremities are sometimes moved with violence even, on the application of a stimulus, after the division of the spinal marrow. All the systems of muscles, therefore, obviously partake of this remarkable action.

It is plain, from the preceding observations, that the reflex function may be viewed as subsisting in its natural state, in its state of general excess or failure, and in its state of momentary and partial excitement.

III. *Pathology.*

There still remains an interesting part of this inquiry. What relation does the reflex function bear to the art of physic? It will soon be seen that it throws a ray of light over some obscure points in medicine. Indeed the study of the reflex function appears to me to reveal and explain a totally new order of facts in pathology, and to lead to a new division of the diseases of the nervous system, coinciding with the different modes of operation of their causes, into those of *centric* and those of *eccentric* origin.

One of the most interesting of medical subjects, in relation to the reflex

* I can readily imagine that tickling may have been carried to such an extent as to interrupt the respiration and prove fatal by asphyxia, as in a recent instance said to have occurred on the Continent.

function, is that of dentition. Dentition is a sort of natural experiment upon this function. The general convulsion, the strabismus, the spasm of the fingers and toes, the croup-like affection of the respiration, the repeated vomitings, the tenesmus, the strangury, the involuntary discharge of urine and of the fæces, from its operation, denote the influence of irritation of the maxillary nerves, through the medium of the medulla, upon the muscles of voluntary and respiratory motion, of the eye, the larynx, the sphincters, &c., in the human subject, and indicate so many arcs of the reflex function. However these *facts* may have been known, their true *rationale* has not been discovered. In all such cases the remedy is, to relieve the part in which the cause is operating. In the present instance the maxillary nerves and vessels are to be relieved by free scarification; the lancet should be used freely, daily, or still more frequently.

The young of other animals, and especially of the feline and canine species, are exceedingly subject to similar effects from dentition, which are not unfrequently fatal. The fatal event is frequently owing to interrupted respiration. In one instance, the asphyxia was averted, in a very young puppy, by artificial respiration, effected by alternate compression and relaxation of the parietes of the thorax.

The reflex function is far more excitable in the very young animal. The second dentition rarely, therefore, induces such affections as the first.

With the effects of dentition in infants, some affections of the adult may be compared, as chorea, some forms of epilepsy, and some forms of asthma. The diseases to which these designations have been given vary exceedingly in different instances; inasmuch as some cases are of centric and others of eccentric origin. One characteristic distinguishes the latter form of the disease,—it usually combines more affections of the reflex function than one. Such a form of epilepsy, for example, combines hickup, or even vomiting, with the epileptic attack. The usual source of those forms of disease is in the intestinal canal, the stomach being irritated by improper diet or the bowels by morbid contents. This division of the subject leads to an important distinction of these cases into those which admit comparatively more easily, and more difficultly, of cure.

Epilepsy is plainly of two kinds: the first has a centric origin in the medulla itself; the second is an affection of the reflex function, the exciting cause being eccentric, and acting chiefly upon the nerves of the stomach or intes-

tines, which consequently form the first part of the reflex arc. The fact of the frequent occurrence of a fit of epilepsy in coitu is very interesting in reference to the reflex function: it distinctly connects these two events; and it affords another instance of an influence exerted, through the medium of this function, between distant parts of the spinal marrow. There is but a step, as it were, from the normal affection of the nervous, muscular, and respiratory systems, in that circumstance, to an attack of epilepsy itself.

The disease termed asthma claims rather more than an incidental notice in this place. True asthma, viz. that form of this disease which occurs in youth, and assumes a distinctly spasmodic form and course, like so many other morbid conditions of the reflex function, frequently arises from gastric or intestinal irritation. It is also frequently excited by the contact of certain powders, as that of ipecacuanha, with the larynx, just as sneezing is induced by similar impressions upon the nostrils. It appears to consist in an action excited, through the reflex function, in the larger bronchia. The influence of the smoke of the stramonium in relieving the attack of asthma is another argument in favour of its being an affection of the reflex function. Indeed, a comparison of the various causes, the mode of attack, the course, and the effects of remedies, in this singular morbid affection, alike denote its relation to this peculiar function.

With the effects of dentition, those of gastric or enteric irritation, in their multiplied forms, may be compared.

Tenesmus and strangury are affections of other arcs of the reflex function.

One circumstance in the pathology of the reflex function is very remarkable. Several forms of the morbid affections of this function occur during the first sleep. This is the case with the croup-like affection arising from dentition, with spasmodic asthma, and with a peculiar painful affection of the rectum, not hitherto described.

Tetanus and hydrophobia appear equally to result from injuries inflicted upon the extremities of certain nerves, by means of which the morbid influence is conveyed to the medulla, whence it is reflected through the motor nerves to the muscular system. As free lancing of the gums in dentition, so the early division of the wounded nerve or amputation in tetanus, has, at once, checked the morbid affection. Is it possible that hydrophobia might be arrested by a

similar procedure? The subject is of intense interest, and deserving of the fullest attention.

Certain poisons, as the strychnine, induce excess in the reflex function; other poisons, as the hydrocyanic acid, destroy it altogether. In both cases the muscular irritability remains perfect and undiminished. It is probably through the medium of the same functions that many other poisons act upon the animal economy.

In a frog, recently killed by strychnine, the irritability of the muscular fibre remained unimpaired,—a proof that the tetanus of strychnine is an exalted condition of the reflex function, and that the consequence is the exhaustion of that function, and not of the irritability. Another frog, destroyed by the hydrocyanic acid, presented similar phenomena of unimpaired irritability on the application of galvanism. In either case, if the animal be placed in water through which a slight galvanic spark is passed, the limbs are immediately and forcibly extended.

The study of the reflex function will doubtless throw an important light upon toxicology, as well as some parts of pathology, and of the causes and treatment of diseases,—subjects which, as they are more immediately connected with medicine, I purpose forthwith to pursue elsewhere.

Diseases of the nervous system, then, may be divided into those which have their origin at the nervous centres, and those which originate at a distance from those centres; and especially in some part of the nervous arc, the function of which has formed the subject of this paper,—into those of *centric* and into those of *eccentric* origin. It is highly probable that the diseases of the latter class are more numerous than they may at first be supposed to be. Chorea, hysteria, tremor, and convulsion have, doubtless, sometimes a centric, sometimes an eccentric origin. In the latter case, the nervous centres may become morbidly affected in the course of the disease, and the appearances after death may mislead the medical inquirer as to the original cause and seat of the disease. But the whole of this investigation must be reserved for the Transactions of another Society. I shall add but one fact more of a medical character in this place.

Legallois appears to have experienced great difficulty in explaining the occurrence of paralysis from disease of the cerebrum, impressed, as he was

that the spinal marrow constituted the source of voluntary motion. He observes, "Quand bien même on n'apercevrait aucun moyen de les concilier, il n'en demeurerait pas moins vrai, d'une part, qu'une affection bornée uniquement au cerveau peut ôter le sentiment et le mouvement volontaire à la moitié du corps, et de l'autre, que le sentiment et le mouvement volontaire peuvent subsister et être entretenus dans un animal décapité. Quelque opposés que ces faits paraissent être, il faut se souvenir que deux faits bien constatés ne peuvent jamais s'exclure l'un l'autre, et que la contradiction qu'on croit y remarquer tient à ce qu'il y a entre eux quelque intermédiaire, quelque point de contact qui nous échappe *." The facts which have been detailed in this paper enable us readily to remove this difficulty, and to account for the paralysis induced by disease of the cerebrum, on one hand, and for the movements of an anencephalous fœtus in utero, or of a decapitated animal, on the other. The paralysis consists in the loss of voluntary motion; the movements of the anencephalous fœtus result from the agency of the reflex function of the medulla spinalis. LEGALLOIS' error was that of mistaking the phenomena of the reflex function for sensation and voluntary motion; and his difficulty naturally arose out of this error. There is no real discrepancy between the two orders of facts to which LEGALLOIS refers.

The same facts enable us to understand how a perfect action of the sphincters is compatible with paralysis of the limbs from disease of the cerebrum, and even of the higher parts of the medulla spinalis; whilst paralysis of the sphincters is usually conjoined with paralysis of the limbs, arising from disease of the lower part of the spinal marrow. The first intercepts the principle of voluntary motion; the second affects the very seat of the reflex function which presides over the action of the sphincters.

IV. *Inferences.*

I shall now briefly enumerate the inferences which flow from the preceding facts and experiments.

Physiologists have hitherto enumerated only *three* sources or principles of muscular action,—volition, the motive influence of respiration, and irritability.

There is, however, a *fourth* source of muscular motion distinct from any of

* Op. cit. p. 21.

these, though not hitherto distinguished, to which I have ventured to give the designation of *the reflex*.

Volition and the motive influence of respiration are direct in their course, and spontaneous in their action; the former proceeding from the cerebrum, the latter from the medulla oblongata*.

The movements of irritability are the result of the immediate application of a stimulus to the nervo-muscular fibre itself.

The reflex function is different from any of these:

It remains attached to the medulla spinalis, when the cerebrum and the medulla oblongata are removed: it is not direct like volition, or the motive power of respiration.

Its seat is the medulla generally: it ceases when the medulla is removed, leaving the irritability entire: it is not excited immediately, like the movements of irritability, but mediately, in a reflex course, through the medulla, from the part stimulated to the part moved.

In a state of health, the reflex function presides over the orifices and terminations of the internal canals, such as the glottis and the sphincters, preserving the former open, the latter closed; and it maintains the due tone of each muscle, and the due equilibrium of each system of muscles.

When excited, it gives origin to the movements observed in deglutition, or vomiting, sneezing, tenesmus, &c. The fingers passed into the pharynx of a dog, through an incision made between the thyroid cartilage and the os

* M. Flourens seems clearly to have determined that sensation and volition are seated in the cerebrum. Legallois (Œuvres, p. 17,) and he have ascertained that one office of the cerebellum is to regulate the voluntary motions. Legallois and Sir Charles Bell have shown that the medulla oblongata[a] is the source of the respiratory motions. It is now, for the first time, I believe, shown that a peculiar function of the medulla, superadded to its functions as a mere nervous chord, is that of imparting a state of equilibrium to the muscular system, independently of the influence of the organs which originate and regulate the voluntary and respiratory motions. These several functions are separated, and, in a certain degree, isolated, by removing the cerebrum, the cerebellum, and the medulla oblongata in succession; the last stage of the experiment leaves the reflex function alone,—a function which supplies the deficiency left by the investigations of Legallois, M. Flourens, and Sir Charles Bell, and constitutes the complement of the functions of the nervous system.

[a] This discovery of Legallois is amongst the most brilliant in physiology, and obviously presents the nucleus of that, still more splendid, of the system of the respiratory nerves by Sir Charles Bell. Œuvres, pp. 63, &c. The Nervous System, pp. 222, cxxv. &c.

hyoides, excites the act of deglutition*; passed over the root of the tongue or the fauces, it excites the associated actions of the muscles of the larynx and of expiration†, which constitute the act of vomiting.

When morbidly augmented, it constitutes certain forms of disease, as tetanus, hydrophobia, certain forms of tremor, paralysis agitans, chorea, stammering, &c.; when diminished, it induces those forms of tremor observed when the vital powers are enfeebled.

When otherwise morbid, it occasions other forms of disease, as the convulsion, the croup-like respiration, the affection of the sphincters, observed in dentition, the various effects of intestinal irritation, &c.

The effects of the excited reflex function are sometimes observed in a part *near* that irritated, as in the eyelids in winking, in the glottis on inhaling a drop of water or particle of food, in the sphincter ani in dysentery, &c.; sometimes in parts *remote*, as in the irritation of teething when this induces strabismus, convulsion, the croup-like respiration, relaxed sphincters, &c.

However some of the facts detailed in this paper may have been previously known,—and many were so known‡,—they have never been accurately distinguished from sensation and volition, and associated with a peculiar reflex function of the medulla oblongata and medulla spinalis, influencing other organs besides the limbs, and constituting the principle of tone and of a particular series of actions. It has long been known, for example, that the limbs of a decapitated animal moved on being stimulated; but the phenomenon was confounded with sensation and voluntary motion. It has long been known that carbonic acid could not be inhaled through the larynx; but it has not been shown that this phenomenon depends upon the presiding agency of the medulla oblongata; nor has it been distinctly demonstrated that the functions of the sphincter ani, by which the intestinal excretions are retained for a time, is constantly dependent upon a similar agency of the lower part of the medulla spinalis. In like manner, the facts relative to the irritability were altogether known before Glisson and Haller finally separated this principle of motion

* De l'Usage de l'Epiglotte, p. 3.

† See a Memoir by the author on the Mechanism of the Act of Vomiting, in the Journal of the Royal Institution, 1828, Part I., (April to June,) p. 388.

‡ Compare Whytt, Legallois, Mayo, &c.

from sensation and volition, with which, like the reflex function, it had previously been confounded.

An interesting parallel might, indeed, be instituted between the principle of the reflex function and that of the irritability, in regard to their history and degree of importance: their history is the same; for both had been confounded with sensation and voluntary motion*: their importance is precisely the same; for each presides over its own distinct order of functions.

Legallois plainly mistook the reflex function of the medulla for the principle of sensation and voluntary motion; and no physiologist has distinguished its agency, in the function of the larynx and of the sphincters, from the influence of the brain, or from irritability. The view of M. Cruveilhier, that the medulla spinalis is a mere nervous chord, is at variance with all the facts and experiments detailed in the course of this paper.

It is obviously from the mistake which has been pointed out, that Legallois experienced the difficulty expressed in the following words: "Comment se fait-il qu'après la décapitation, les seuls mouvemens inspiratoires soient anéantis et que les autres subsistent? C'est là, à mon sens, un des grands mystères des puissances nerveuses, mystère qui sera dévoilé tôt ou tard, et dont la découverte jettera la plus vive lumière sur le méchanisme des fonctions de cette merveilleuse puissance†." It was impossible to explain this difficulty whilst the movements of the excited reflex function were confounded with those of voluntary motion; but when this distinction is duly made, nothing is more easy. Decapitation removes, in fact, the sources both of voluntary and of respiratory motion; both these kinds of motion consequently cease: but a class of motions still remains, viz. those of the reflex function, attached to the remaining portion of medulla. Thus is the veil raised from this apparent 'mystery'.

As Legallois has confounded the reflex function with the sensibility and voluntary motions, M. Brachet‡ has confounded it with the functions of the ganglionic system, or the sympathetic. The latter physiologist concludes, that whatever function remains after the division of the spinal marrow, in the organs below that division, must be referrible to the influence of the ganglionic system. In this manner he attempts to prove that some parts of the act and function

* Compare Whytt and Legallois.

† Œuvres, pp. 63, 64.

‡ Du Système Nerveux Ganglionaire, p. 246, &c.

of generation, in both sexes, besides the secretions, depend upon this influence; whereas it is certain that they depend upon the lower portion of the medulla spinalis and belong to the reflex function. It is obvious, that, whilst the secretions may depend on the ganglionic system, the act of excretion, and especially the action of the ejaculatory muscles, is an excited act of the reflex function, which has been fully proved to subsist in every portion of the divided medulla spinalis. This view of the subject is greatly confirmed by a comparison of the act alluded to, with that of deglutition (p. 640, note), and others demonstrably belonging to the reflex function. We know that some reptiles remain in coitu after the head is removed. This is then an act of the reflex function alone. It may take place without sensation, as in cases of disease of the medulla spinalis.

I may state, in conclusion, that all the functions of the muscular system which remain after the sources of the motive influence of the voluntary and respiratory motions are removed, with the exception of those of the heart, and other muscles which contract upon the principle of excited irritability, depend upon the reflex function.

The principles of the movements in the animal economy, viewed in an anatomical and functional point of light, may now be enumerated thus:

1. The cerebrum, or the source of the voluntary motions.
2. The medulla oblongata, or the source of the respiratory motions.
3. The medulla spinalis generally, the middle arc of the reflex function.
4. The nervo-muscular fibre, or the seat of the irritability.
5. The sympathetic, or the source of nutrition, of the secretions, &c.

It is not pretended that this arrangement is either strictly accurate or complete. These principles of action are, besides, frequently and variously combined, and much ulterior investigation is required to ascertain the share and fix the limit of each in various compound operations of the animal economy.

The reflex function of the different portions of the medulla presides over their corresponding organs: the medulla oblongata presides over the larynx and the pharynx; the lumbar and sacral portion of the medulla spinalis presides over the sphincter ani, the cervix vesicæ; and the intervening portions of the medulla give tone and equilibrium to the corresponding portions of the muscular system, and what LEGALLOIS has so vaguely designated "*life*," to the corresponding regions of the body. But the operation of the reflex function is by

no means confined to parts corresponding to distinct portions of the medulla. The irritation of a given part may, on the contrary, induce contraction in a part very remote: the irritation of teething may induce spasmodic action or relaxation of the sphincters: the irritation of the nostrils, in the case of a young hedgehog, when so languid that voluntary motion and respiration had ceased, induced as energetic contraction of the most distant part of the panniculus carnosus and of the muscles of the posterior extremities, as irritation of the posterior extremities or tail themselves.

It would seem, from what I have observed in the young of the hedgehog and of other animals, when languid, torpid, or *dying*, that the voluntary motions cease first, then the respiratory motions, next those of the excited reflex function, and, lastly, those of the irritability; the last act of the irritability being that which induces the cadaveric rigidity. After all evidence of irritability has ceased, it is probable that the functions of the sympathetic may still continue.

Such is the order, then, in which this series of functions disappear in death; an order which is inverted when the same functions and their appropriate organs gradually came into existence, in the fœtal and natal states, and in the progressive series of the animal kingdom. The movements of the fœtus in utero, are entirely phenomena of the reflex function: they occur in the anencephalous as well as in the perfect fœtus*. This function and the irritability constitute, indeed, the principles of life and motion in the *fœtal state*.

The functions, in *sleep*, seem to be diminished, and that in the same order. This is particularly seen in the deep lethargy of the hedgehog. The animal becomes quiescent; then it nearly ceases to respire; then the action of the panniculus carnosus yields to partial relaxation; lastly, the heart beats with a reptile slowness. In ordinary sleep, the muscles which retain the eye open lose their powers, and the eyelids close by an act of the reflex function, just as they are kept closed in the anencephalous infant. The eye is only partially closed, even during sleep, in cases of extreme languor and exhaustion, with diminished energy of the reflex function. Volition is first impaired, and the eyelids close; the reflex function next fails, and the eyelids close partially only.

It appears probable that the facts of this paper may lead to some important additions to our knowledge of anatomy, by inducing an accurate inquiry into

* See M. Lallemand's Observations Pathologiques, p. 68.

the origin, course, connexion, and distribution of the subcutaneous, or submucous, and muscular nerves, which constitute the arcs of the reflex function. There can be no doubt that a system of nerves takes its origin from the lower portion of the spinal marrow, to supply the sphincters and the organs of generation, which may be compared to those which concentre in the medulla oblongata. The medulla is also, in its whole course, the source of nerves which supply the limbs, the tail, and the panniculus carnosus, in those animals which possess these structures respectively.

It was observed in one frog that the strychnine applied to a single posterior extremity induced general tetanus. General tetanus, in the human subject, is the effect of the local wound of a nerve. These facts demonstrate the strict connexion and unity of the different parts of the nervous system.

The anatomy of the reflex function must be particularly studied in the medulla oblongata; in the portions of the spinal marrow which give origin to the nerves of the anterior and posterior extremities; in that of the intermediate space which supplies the trunk; in that which is the source of the nerves of the sphincters, the ejaculators, &c., and in that which supplies the tail; and, lastly, in reference to the several columns of which the spinal marrow is composed. I think the investigation of the anatomy will, for various reasons, be best pursued in the hedgehog.

It is gratifying to me to state that no part of these experiments has inflicted pain, beyond that of prompt decapitation, or division of the spinal marrow. This is true, at least, if the conclusion be correct, that when the head is removed from the body, sensation and volition cease, whilst the reflex function and the irritability alone continue; and it may be satisfactory to the humane to know that the motions of the eel, for example, after the head is removed, are not motions arising from sensibility, but from another principle, as distinct from feeling as the irritability of the mere nervo-muscular fibre. This fact will suggest the propriety, as well as the means of avoiding such monstrous cruelty as that of skinning eels alive. This will be effectually done by first removing the head, however the animal may afterwards move on the application of stimuli, and *appear to feel.*

V. *Recapitulation.*

To avoid misapprehension, I think it right, in conclusion, very briefly to recapitulate the claims of this paper:

1. Many of the facts which depend upon the reflex function have long been known to physiologists:

2. But these facts only extend to the excited action of the reflex function, seen in the limbs, and even they have been erroneously ascribed to sensation and volition, or instinct:

3. The facts of excited movements of the larynx, pharynx, sphincters, and ejaculators, and of the panniculus carnosus, have not been shown to be allied to these, and to be dependent on the same individual function of the nervous system:

4. It has not been shown that this function, in its natural state, constitutes the principle of equilibrium and tone, in the whole muscular system, and the principle which presides over the orifices and sphincters of the internal canals:

5. And certainly not, that this principle, morbidly affected, constitutes, in its different forms, the diseases arising from dentition, and the diseases termed tetanus, hydrophobia, chorea, paralysis agitans, certain forms of epilepsy, of tremor, of asthma, &c. &c.:

6. Nor that the same individual function is augmented or diminished to a fatal degree, by certain poisons.

7. This series of facts has not been duly associated and shown to belong to *one* particular *order*:

8. The principle of action in this order of facts has not been demonstrated to be at once excited, and reflex, in its operations, to be essentially connected with corresponding portions of the medulla oblongata and medulla spinalis, and to be independent of the brain:

9. Nor has it been clearly distinguished from the other sources and principles of muscular motion existing in the animal economy, viz. volition, the motive influence of respiration, and irritability, or shown to constitute, with the irritability, the principle of life in the fœtal state:

10. The reflex function appears, in a word, to be the *complement* of the functions of the nervous system hitherto known.

I trust it will be found, from this brief recapitulation, that the foregoing paper may have done some little service to physiological science. I consider the subject as but sketched,—the investigation as but just begun. One part of this inquiry is altogether untouched,—the influence of the mind and emotions, and the corresponding parts of the nervous system, upon the organs which are the subjects of the reflex function. The muscles of voluntary and respiratory motion are alike under the influence of the reflex function; and the muscles over which this function more peculiarly presides are impressible through volition and respiration: other muscles, which are especially attached to the reflex function of the lower portion of the medulla spinalis (p. 661), are apparently under the influence of the cerebellum*. Mental emotions modify the reflex function: they induce sickness, relax the sphincters: they also aggravate the diseases of this function, inducing the attacks of epilepsy, of the croup-like convulsion, &c.

* See SERRES, Anatomie Comparée du Cerveau, tome ii. p. 601, &c.