BRAIN.

PARTS II. & III., 1891.

Original Articles.

ON THE SENSORIMOTOR NERVE-CIRCUIT OF MUSCLES.

BY PROFESSOR A. CHAUVEAU.

THIS title was suggested to me by a reminiscence of the International Medical Congress, held in London in 1881. During the opening address of the Physiological section by Professor Foster; I was struck by what the speaker said of the manner in which Charles Bell understood the relations between the sensory and the motor nerves, that is, of his conception of the *nerve-circuit*. It is true that this expression could not establish itself, because its adoption would have assumed the existence of an unlikely physiological fact. It is indeed certain that the existent knowledge concerning the nervous system did not allow of the reality of a *nervous circulation*, or of a *nerve-circuit*, in the strict and definite sense of these words.

It is, nevertheless, quite certain that sensory nerves influence the action of motor nerves and *vice versâ*. I confess that I have often been tempted to express the general mechanism of their physiological relations by Charles Bell's locution, which is striking and picturesque. The mention made of it by Prof. Foster made me take the resolution to use it whenever I should give an account of the numerous experiments I have made, at different times, on the functions of the sensory nerves of muscles. This is what I attempt to do in the present paper, which, at the instigation of my friend, Dr. Waller, I have the pleasure to publish in the

country and language of Charles Bell—a fact which accentuates the intention to pay thereby a deserved homage to the memory of one of the founders of neurophysiology.

I shall deal in the present essay on muscular nerves only. All muscles are supplied with motor and sensory nerves: though this fact is rarely demonstrable anatomically, it is always so physiologically in health or disease. For instance, it is easily demonstrated in the case of voluntary muscles by squeezing of nerve twigs which spend themselves completely in these organs; such an excitation produces always pain, and sometimes reflex movements, if the subjects have been prepared for the manifestation of such a reaction.

This muscular sensibility has been much studied, even from the psycho-physiological point of view; for it is the primordial condition of what is called the muscular sense. But this property used to be considered as only a case of the general sensory mechanism. Nobody thought of otherwise connecting the sensory with the motor function. One used to say that the contraction excited by the latter utilised, for its regulation, the sensibility given to the muscle by the former. The two nerves were then considered as two isolated physiological systems, acting simultaneously side by side.

Now when, after Charles Bell, we use the expression *nerve-circuit* to designate this arrangement, we imply in some way the existence of one and the same conducting system, composed of two parts, centrifugal and centripetal, intimately connected together. Can the study of the sensory and motor nerves of muscle be influenced in its results, if these conductors are thus united into a single physiological system? One would be tempted to expect from this union nothing but a difference in the mode of presenting facts. But I hope to show that both the acquisition and the interpretation of facts, gain by the adoption of Charles Bell's view of the nerve-circuit.

And first: What anatomical idea can be framed of this circuit? We know absolutely nothing of the relations existing between the terminal filaments of the sensory nerve

tubes, and the muscular tissue itself. Still there is room for believing that these tubes have no direct relation with muscular elements, and for supposing that they contribute in forming the pre-terminal anastomoses or networks of the motor nerves in the muscular system. In the case of voluntary muscles, be it so or otherwise, it is easy to conceive as a circuit the sensorimotor nerve apparatus of the muscular fasciculus.

Under the hypothesis of a juxtaterminal unity of the two kinds of nerve fibres, we may picture to ourselves the circuit in the following manner among others: starting from the motor cell, which is the origin of the centrifugal tube, it would reach through the latter the anastomosis next to the terminal plate. Thence through the centripetal tube supposed to end in this anastomosis, it would return to the sensory group of cells in the medullary centre, finally merging into its starting point through the commissure connecting the motor and sensory cellular groups.

In the unlikely case that special sensory endings should be discovered along the muscular fasciculus, the circuit would be completed through the muscular substance itself, between the motor and sensory nerve endings. I consider this case as unlikely for two chief reasons: the first is, that in voluntary muscle (with which we are at present concerned), the true nerve-endings are now well-known, and universally considered to be motor only (terminal plates and ramifications, Doyere's eminences). The second, which would be sufficient in itself, is that in very short muscles, each primitive bundle carries but one such nerve-ending, very rarely accompanied by a small satellite attached to the same cylinder as the chief organ. But I wish to guard myself against any definite conclusion upon this difficult point, which calls for further histological investigations.

The concept of a nerve-circuit is still more admissible in the case of visceral muscles. Every kind of nerve fibre supplying them ends in networks studded with nerve cells, which, perhaps, send fibrils in to the unstriated muscular elements.

If the nerve-circuit is really constituted as just stated,

the elementary muscular organs are not placed in its course, but are merely *tangent* to it, either directly or through terminal structures, such as plates, fibrils, &c. This remark is important, because this tangential disposition complicates the problem of neuro-muscular interconnections. But since our present knowledge does not allow us to explain even the transmission of excitations from nerve to muscle, its mechanism does not become less intelligible by the admission that the nerve-endings do not directly and separately connect the muscles to the two kinds of nerves, but to the common circuit formed by the union of these nerves near their peripheral end.

How shall we proceed to study experimentally, by laboratory methods, the properties and functions of the two portions of the sensorimotor circuit? We have to determine the influence of each upon muscular action. Hence we shall first study the results of excitation of each portion before section; then after division those of excitation, both of the central and of the peripheral end. We shall next investigate the effects of interruption in the centrifugal, and in the centripetal portion; and finally, compare the effects obtained in each case.

Such is the programme of all analogous experiments. Let us add to it, if possible, a study of the commissures which, in the cerebro-spinal axis completes the circuit by connecting together the central ends of the centrifugal and centripetal paths. But how shall we fulfil this task? And where shall we find suitable organs to work upon? We require organs in which the sensory be quite distinct and isolated from motor fibres. I have, hitherto, found but two such, one belonging to the locomotor system, the other to the visceral; but these have sufficed to carry out my scheme with reference to the nerve-circuit of both sets of muscles.

1.—ON THE SENSORIMOTOR NERVE-CIRCUIT OF VOLUNTARY STRIATED MUSCLES.

The nerve supplying the sternomastoid muscle of the horse enters it through a slit close to the terminal tendon. Following the nerve upwards from this point it is seen to

divide. The larger branch joins the external branch of the spinal accessory, of which it forms one of the divisions. The other is supplied by the inferior branch of the second cervical pair. The disposition of these two nerves is generally simple; sometimes, however, they become plexiform at their point of union.

The first is the motor branch of the muscle; the second is purely sensory. Squeezing of the combined nerve near its point of entrance produces pain, but after division of the second branch gives rise to no sign of sensation whatever.¹ I may add that excitation of the peripheral end of this branch never gives rise to contraction of the muscle.

Thus we have here present the fundamental anatomical condition required by the experimental and comparative study of the influence excited on a given muscular action by the two portions, centrifugal and centripetal, of its nerve circuit. The operative procedure required to expose them is so easy and simple that it need not be described here.

I shall not enter upon any details upon the actual experiments made. It will be enough to describe the results, which have been uniform, and of the exactness of which I am perfectly satisfied.

A.—*Comparative excitation of the centrifugal and centripetal portions of the sternomastoid nerve-circuit.*—This excitation has been carried out sometimes by squeezing, sometimes by single or repeated induction shocks.

(a.) *Excitation of the two branches, motor and sensory, without interruption of their continuity.*—Single induction shocks, of minimal strength, are suitable for this experiment. The two nerve branches must remain in contact with the subjacent structures (*M. Ant. rect. capitis major*) in order to avoid any electrical derivation. They are thus excited at the electrodes only, the points of contact being the only ones where the current has enough density, or where the potential is high enough, to act upon the nerve fibres.

¹ On a donkey I observed, after division of the second cervical branch, the persistence of some sensibility in the combined nerve. *Post-mortem* dissection however, showed the existence of a filament from the first cervical pair. I cannot say whether this disposition is usual in the donkey, nor whether it may not be exceptionally present in the horse.

(1.) *Centrifugal part of the circuit (motor branch).—*I have never observed along with the muscular contraction obtained any clear sign of pain, even on marked increase of the current strength. I had previously noted the difficulty of obtaining, in the horse, signs of recurrent sensibility on exciting the spinal accessory too near its point of origin.

(2.) *Centripetal part of circuit (sensory branch).—*The minimal excitation thus necessary to obtain muscular contraction does not generally provoke any reaction when applied to the centripetal branch; the current strength must be somewhat increased. Strange to say the first effect observed, in certain subjects, has been a contraction of the sternomastoid. It was then difficult to discriminate between the effects of the centrifugal and that of the centripetal branch; the latter, however, was not quite so immediate as the former. Stronger excitations bring about additional phenomena, of which we shall speak further on.

I need not say that the contraction obtained on excitation of the sensory portion is of reflex origin, and constitutes a remarkable phenomenon by its exclusive localisation of the muscle to which the nerve-circuit belongs. The following facts bear still further upon this important datum.

(b.) *Excitation of the motor and sensory branches, interrupted in their continuity.*—Let us now investigate what takes place when the peripheral and central ends of each of the two branches has been divided.

(1.) *Peripheral ends.*—Excitation of the motor branch still calls forth contraction; that of the sensory branch has no effect whatever.

(2.) *Central ends.*—The results are opposite; excitation of the motor branch having no effect, whilst that of the sensory branch is followed with contraction of the muscle. Sometimes, however, the reflex contraction, even when the stimulus is very slight, is accompanied with more generalised movements which are a sign of pain. Still the latter reaction does not usually appear quite so quickly as the localised reflex contraction, and thus the two can be discriminated. But the reflex contraction following an excitation of the sensory nerve is not always localised in the

sternomastoid. On increasing the intensity, it may extend to all the muscular apparatus innervated by the external branch of the spinal accessory, and invade other regions on the same side of the body. In the case of strong stimuli it may even generalise itself on the opposite side of the body. I have been able to clearly observe this effect in many apathetic, unimpressionable subjects, easily bearing pain without reacting by any general voluntary and disorderly movements.

(c.) *General review of the conclusions reached by excitation of the nerve-circuit in muscles of animal life.*—These results favour the nerve-circuit theory of the relations between the sensory and the motor nerves of muscles, and may be summed up as follows :—

(1.) Stimuli applied to the nerve-circuit travel in a centrifugal or a centripetal direction according to the part excited.

(2.) Whatever part be influenced, contraction of the muscle follows, directly in the case of the centrifugal, indirectly through the nerve centres in that of the centripetal arc of the circuit.

(3.) Interruption of the circuit beyond the excited point, that is in the path through which the stimulus has to travel, prevents the latter from reaching the muscle and make it contract.

(4.) Whatever be the strength of the excitation applied to the centrifugal arc remains localised in the muscle which it has reached directly, and never produces anything beyond its contraction.

(5.) When the stimulus applied to the centripetal arc is very weak, it is wholly reflected in the central cellular groups upon the centrifugal portion of the circuit, and then produces a contraction of the corresponding muscle only.

(6.) When the excitation of the centripetal branch is stronger it may diffuse itself in the medullary centre, and provoke a contraction of more numerous muscles, among which the first affected are always those which are innervated by the same group of motor cells as the muscle whose nerve-circuit is being excited.

These first results of excitation of nerves supplying voluntary muscles encouraged the study of the effects of *suppression* of the conductibility of the nerve-circuit. Experiments made in that direction, however, did not yield the expected results; still they are interesting, as we shall see when we discuss their physiological significance.

B.—*Influence of the interruptions in the nerve-circuit of the sternomastoid.*—Transverse section, with or without excision, of the motor and sensory branches of the nerve supplying the sternomastoid, is as simple an operation as their excitation. I had intended to study its influence upon both muscular nutrition and normal contraction. I have, however, not been able to fully investigate the latter point.

(a.) *Effects produced upon the physiological voluntary contraction of the sternomastoid by interruption of its nerve-circuit.*—The sternomastoid of the horse acts chiefly as a flexor of the head. In order to bring it into play a wisp of hay is placed in the manger fixed rather high. The animal raises its head, seizes the hay with its incisors, and in order to bring it down suddenly flexes the head upon the neck. The exploration with the eye, or rather with the hand, of this region shows what takes place, at least whether the muscle contracts or not.

It was hardly necessary for me to investigate again the well-known effect of section of the motor branch of the nerve; the whole interest of the experiments centred upon that of section of the sensory branch. For never, to my knowledge, had the results of total and exclusive sensory enervation of a muscle been observed before. In previous experiments, as we shall have occasion to see presently, the abolition of sensibility affected a whole region, such as a whole posterior limb, and included all tissues, skin as well as muscle. Here we abolished nothing but the function of the sensory nerve supplying the contractile organ, and the conditions in which we were placed could not be more favourable for the comparison of the two kinds of nervous functions. The results obtained have been identical, both in cases where the experiment was made extemporaneously and where the subject was observed for some weeks after-

wards. Whilst the muscle which has undergone motor enervation remains absolutely paralysed, that which has been subjected to sensory enervation continues apparently to contract normally. For instance, in a subject whose motor nerve has been cut on the left, the sensory on the right, the left sternomastoid is felt to remain flaccid, whilst the right becomes rigid on contraction, when the animal flexes its head on pulling hay out of the manger.

I have never met with any exception to this rule, hence we may assert that, contrary to what happens on section of the motor branch, section of the sensory branch does not abolish movement. But we may not go beyond this somewhat vague conclusion, for we do not know whether movement, though not abolished, is not in some way altered or modified. Notwithstanding repeated and careful observation of subjects in whom unilateral sensory enervation had been performed, I failed to obtain evidence of any alteration of function. Flexors of the head are numerous, and easily supply each other's place; moreover, direct observation of the muscular action by palpation is not a delicate enough method for the analysis of that function.

Hence we reach this indefinite conclusion, that after section of its sensory nerve the sternomastoid muscle does not lose its voluntary contractibility, but that it is impossible to say whether its voluntary movement is not more or less disturbed.

This result appears to be in complete contradiction with the facts observed by Claude Bernard after section of a series of lumbar sensory roots in the dog. The corresponding hind limb has its movements disturbed, and may even become incapable of supporting the body. Now this disturbance is not due to cutaneous anæsthesia, for it never follows section of the skin nerves.¹ The paralytic phenomena observed in

¹ Section of the cutaneous nerves of the extremities has often been performed in order to determine their functions in locomotion and station. I have performed the experiment on some horses and many pigeons. In every case I found that complete sensory enervation of an extremity does not appreciably disturb these functions. My experiments on pigeons deserve mentioning; they were carried out on tame specimens, very easy to observe. I used to make one of the feet completely anæsthetic by cutting around the tarsal articulation the four nerves supplying the toes, which could thus be

the dog are obviously due to the destruction of sensibility in the leg muscles through interruption of the centripetal branch of their nerve-circuit.

The accuracy of this explanation may be doubted because the conditions of the experiment are not simple. The traumatism is serious, and it is not always easy to appreciate the real motor disturbance in a dog's hind leg from the attitude given to the limb. I, however, fully adhere to it, and hope further on to demonstrate that there is no contradiction between the facts to which it is applied, and those furnished by my own experiments. The discussion of the part played by the sensory nerves in the muscular functions of the leg, will show why the necessity of their intervention was not manifested in my experiments on the sternomastoid of the horse.

(b.) *Effects produced upon the muscular nutrition by interruption of the nerve-circuit.*—Among the animals upon which these experiments have been performed some were preserved for several weeks, others even till complete cicatrization of the extensive wound. After sensory enervation the muscle always remained contractile, though it occasionally appeared as if its contractions became somewhat less vigorous as time elapsed. Was this a fact, or was I the victim of an illusion, natural enough under the circumstances? I resorted to post-mortem examination of the tissues to find out whether sensory enervation did not involve corresponding muscular degeneration, and examined two cases, six and seven weeks respectively, after the

pricked, squeezed, cut, burnt, without giving rise to the least sign of sensation. When the animal is placed upon the ground after the operation, it does seem to hesitate in the use of the enervated foot. This hesitation consists, at the moment of starting on to walk, in a repetition of the movement of placing the toes upon the ground. The animal looks as if astonished not to feel this contact, but once started it uses both feet equally freely.

It is especially during sleep that these animals show how completely the mechanism of station is independent of cutaneous sensibility, for they roost indifferently upon the normal and upon the enervated foot. I used to place my subjects during the night on a perch at my bed side, and every time I awoke I observed them by means of an arrangement for the sudden projection of light, before they had had time to change their position on being aroused. I had facilitated the observation by previously colouring differently the two feet. Persevered in during several months these experiments always gave uniform results; the animals, during sleep, used to stand about as often on the anæsthetic as on the normal extremity.

operation. Now, in neither did I observe any such degeneration. The muscle did not appreciably differ from its normal fellow in either colour, weight, and histological characters. I admit that these experiments do not prove that sensory enervation does not have any influence upon muscular nutrition, for in very old horses, such as were used by me, degeneration after total enervation always takes place very slowly. However, I must add that forty-seven days after motor enervation only, unmistakable changes were apparent in the muscle, which was paler than its fellow, and whose fasciculi were infiltrated with fatty granulations.

If, therefore, it is not possible to affirm that the sensory branch of the sternomastoid nerve exercises no action upon muscular nutrition, it is at least possible to affirm that it has infinitely less influence upon it than the motor branch. Further researches, made under more favourable conditions, must be carried out in order to settle this point.

C.—*Summary*.—Interruption of the sensorimotor nerve-circuit of muscles of animal life, has twofold effects upon muscular nutrition and function.

Upon nutrition ; (1) section of the motor branch always causes atrophy and fatty degeneration ; (2) section of the sensory branch does not appear to disturb nutrition, but this assertion requires to be controlled by further researches.

Upon function ; (1) section of the motor branch immediately paralyses the muscle ; (2) that of the sensory branch does not suspend response to voluntary stimuli ; (3) voluntary movement of the muscle after its sensory enervation appears to be normal, though it is impossible, owing to the nature of the experiments, to exclude all possibility of slight disturbances ; (4) these results do not appear to conform to those obtained by Claude Bernard, in the total sensory enervation of the dog's hind leg, but the contradiction is apparent only. The conditions under which he experimented are not so simple as those obtaining in our researches. We shall return to this point, which we mention here only to guard against any premature conclusion as to the non-participation of the centripetal branch of the circuit in the muscular acts

of locomotion. The results described in the next paragraphs justify our reserve on this point.

II.—ON THE SENSORIMOTOR NERVE-CIRCUIT OF INVOLUNTARY STRIATED MUSCLES.

In order to determine the effects of a rupture in the centripetal arc of the circuit on the physiological movement of the muscular organ (1) we should be able at will and with certainty, to excite that movement; (2) which must be always identical and known in all detail; and (3) be of easy observation.

Now all these conditions are united in an automatic, always similar, and well-regulated act, that of œsophageal deglutition. And very fortunately the observable (cervical) portion of this tube, receives in the horse its motor and its sensory supply from two different sources. I shall recapitulate the description I have given elsewhere of this arrangement.

The nerves of the cervical part of the œsophagus do not present any uniform arrangement in all mammals, but are arranged according to three types. In the rabbit as in man, motor and sensory fibres are intimately mixed in the recurrent nerve, and follow an ascending direction. In the dog, they are equally closely connected together, but are supplied by the pharyngeal nerve, and follow a descending course. In the solipedes they are completely separated, and take a descending and an ascending course respectively.

The descending nerves lying superficially on the sides of the œsophagus or embedded [in its substance, can be traced from the pharynx into the chest; and arise from the pharyngeal and external laryngeal nerves. The evidence showing that these are the motor nerves will be stated further on.

The ascending nerves are fine twigs supplied by the thoracic portion of the vagus or the recurrent nerve. They are themselves recurrent œsophageal nerves, disposed in no constant manner. Some are very long, sometimes reaching up to the origin of the tube; others, shorter, supply its thoracic extremity, and are of chief interest to us. They

are all centripetal nerves, as I have shown elsewhere, and shall point out again presently.

The ramifications of these sensory nerves obviously do not all go to the mucous membrane; some supply the muscular coat, forming, with the motor branches, the nerve-circuit of the œsophageal muscle in the cervical region.

Since, in the great majority of our present experiments, we cannot avoid acting on the sensory branches both of the mucous œsophageal membrane and of the nerve-circuit, we must first determine the part played to the sensibility of that membrane in the movements of deglutition, in order to eliminate from our results those not due to excitation or rupture of the muscular nerve-circuit.

Now we know that the functions of the mucous membrane of the cervical œsophagus do not influence the physiological movement of this portion of the tube. I showed that, in the horse, as in the rabbit and the dog, regular coördinated peristalsis occurs from the pharynx to the thorax during deglutition *à vide*. In the rabbit it is easy to demonstrate the fact, simply by dividing, with scissors, the œsophagus at its origin. The nerves being all ascending need not be considered. When, now, a movement of deglutition is set up, by seizing with a forceps the œsophageal stump that remains adherent to the pharynx, and pulling the latter backwards, one sees in the isolated œsophagus a continuation of the peristaltic movement, as if the organ had a bolus to convey. Sensory excitation of the mucous membrane by the bolus does not, therefore, take a direct part in the provocation and execution of this movement, at least in the cervical portion of the œsophagus.

In order to demonstrate this fact in the horse more care is needed, since we must avoid injuring the motor nerves adherent to the œsophagus. A wide slit is made at the origin of the latter, and a ligature involving the mucous membrane only is applied below the aperture. When now the animal is eating, the bolus can no longer penetrate into the œsophagus, but escapes at the outlet of the pharynx. Regular peristaltic movements are now observed throughout the cervical length of the tube; only the strength of con-

traction goes on diminishing from top to bottom, whence we conclude that the presence of food in the tube excites it only to give to its contractions the power necessary to drive forwards the alimentary bolus.

This proof of the non-intervention of mucous sensibility in the provocation and execution of coördinated deglutitional movements of the œsophagus, is quite peremptory. I will add still another, based upon an experiment showing that the excitation of the nerves of the mucous membrane does not cause any reflex movement of the œsophageal muscle. The value of this experiment will become evident when it shall be compared with a corresponding one, made upon the ascending branches which supply sensory filaments to both membrane and œsophageal nerve-circuit.

The experiment is as follows: the œsophagus having been rather extensively exposed on the left side, near the thorax, the muscular tube is slit longitudinally in the upper plane, care being taken not to injure the nerve branches. The mucous tube is thus brought into view, the nerve filaments supplying it being conspicuous on its surface. Excitation of these purely mucous filaments may easily be carried out by means of fine electrodes connected with an induction coil. Now I have never succeeded in thus producing the least reflex contraction¹ of the œsophageal muscle.

This preliminary discussion has prepared us for our experimental study. We know that by acting on the descending and ascending nerves, we act upon the centrifugal and centripetal branches of the circuit respectively. We may now proceed to observe, with perfect safety, the effects of excitation and interruption of the œsophageal nerve-circuit.

(a.) *Influence on the physiological coördinated œsophageal contraction, of interruption of the centrifugal and*

¹ This does not mean that the presence of an alimentary bolus arrested in the œsophagus, or of a foreign body introduced through a slit into it, cannot call forth more or less insensible contractions, alternately suspended and resumed, which aided by thoracic aspirations, end in causing a slow progress towards the stomach. But this is a phenomenon wholly different from true deglutition.

centripetal arcs of the nerve-circuit.—Let us take first the motor or centrifugal portion. It is easy enough to divide all the descending nerves at the origin of the œsophagus, and to observe the latter through long incisions made along the jugular furrow. One sees then that the cervical portion of the tube no longer contracts on deglutition. The bolus projected into the œsophagus by pharyngeal contractions soon come to a standstill, and remains stationary until another bolus pushes it down. This result was expected; still we must mention that in order to obtain it, we must divide all the descending nerves on both sides. Strange to say, unilateral section does not sensibly modify œsophageal deglutition: as if the whole of the œsophageal muscular elements were controlled by the nerves on each side independently, and excitation from the right propagated itself to the left, and *vice versâ*. Unilateral section of the motor nerves may deprive some muscular fasciculi of every supply, and so paralyse them; but the rest remain fully innervated. Thus the process of deglutition may be weakened—a fact difficult to ascertain—but is impaired neither as to its regularity nor its efficacy.

As to the effects of interruption of the centripetal arc of the œsophageal nerve-circuit, it is not easy to divide all the ascending œsophageal branches; I was so led to divide the trunk itself from which they arise (*viz.*, the vagus) below the point of origin of the motor branches.

Now after section of both vagi, though they contain no motor fibres to it, the cervical portion of the œsophagus displays profound disturbances in the coördinated movements of deglutition. These troubles are various. Sometimes the muscular tunic is paralysed, as after section of the motor nerves, but never in its upper third. The loss of power begins in the middle third, and becomes quite apparent in the inferior portion, where arrest of alimentary boli takes place either temporarily, or permanently, thus leading to obstruction along the whole œsophageal tract. Sometimes—chiefly in donkeys—the œsophagus becomes as it were ataxic, and contracts irregularly and almost simultaneously along its whole length. This happens especially

when the animal coughs, or when it is obliged to make some effort at deglutition.

Unilateral enervation appears at first sight to be as unefficacious in the case of the sensory, as it is in that of the motor, œsophageal nerves; for after section of either of the vagi the peristaltic contraction of the tube seems very little affected, when it is not quite regular. But the sequel shows that this operation profoundly modifies the process of deglutition. Arloing and Tripier found that, seven times out of twelve, in the donkey, division of one vagus is followed by complete obstruction, by food, of the œsophagus, from the pharynx down to the cardiac orifice, with or without filling and distension of the stomach. No doubt that in these cases the divided nerve has greater influence than its fellow upon the motor innervation of the terminal portion of the œsophagus, which becomes plugged, and thus arrests further boli still propelled by the upper portions of the tube. But division of the vagus having partly interfered with the action of the motor nerves upon these portions also, this disturbance eventually becomes apparent by œsophageal incapacity to force into the stomach the alimentary plug retained in the terminal portion of the canal.

Thus interruption of the nerve-circuit of the œsophageal muscle always determines serious disturbance in its physiological function: (1) Complete abolition if it occurs in the motor arc; (2) Sometimes complete abolition, sometimes motor incoördination, if it occurs in the sensory arc. Hence this centripetal portion of the circuit plays an important part in the normal action of the œsophagus.

(b.) *Comparative excitations of the centrifugal and centripetal portions of the œsophageal nerve-circuit.*—We excited in every case with rapidly intermittent induction currents, at the points previously selected for division of the nerves. The stimuli were applied either to the intact branches, or to their central and peripheral ends after section. We shall consider the results obtained in the latter case only, which are the most interesting.

(1.) *Excitation of the centrifugal portion (descending nerves).*—Excitation of the peripheral end brings forth tetanisation of the cervical part of the œsophagus.

Excitation of the central end remains without any effect. Still I am not certain whether it did not provoke in the animal a sort of attention, if not of anxiety, as if a few sensory fibres were contained in these nerves. These fibres possibly supply the upper part of the œsophagus and inferior pharyngeal constrictor muscle; and this would explain why the action of the upper part of the canal is not much disturbed, at least at the outset, by division of the vagus in the middle of the neck.

(2.) *Excitation of the centripetal portion (trunk of vagus in the mid-cervical region).*—The experiment is quite easy, but observation of the results is made sometimes difficult on account of the numerous other nervous elements excited, besides those of the nerve-circuit.

Such difficulties do not arise when the peripheral end is excited, for the stimuli must always be weak, too weak to produce stoppage, or even slackening, of the heart. We then obtain contractions of the stomach, and of the intra-thoracic portion of the œsophagus; the latter becoming manifest by a dragging, front to back, of the cervical portion which never itself displays any contractions.

Difficulties arise on exciting the central end, which process is accompanied with cough, nausea, forced inspirations, &c. Still one may generally observe what takes place in the œsophagus, especially if the stimuli are weak and short. Total tetanisation, more or less permanent and regular, simultaneous (at least to the eye) at all points, is always determined. This tetanisation appears after a certain delay; but is otherwise identical with that obtained by exciting the peripheral end of the centrifugal nerves.

The circular conduction of excitations is thus more clearly demonstrated here than in the corresponding experiment on the sternomastoid nerve-circuit.

(c.) *Elimination of the disturbing condition contained in these experiments.*—Though these results are clear enough, I have tried to reach the isolated centripetal fibres of the œsophageal circuit, that is the ascending branches which contain them. I thus hoped to eliminate all concomitant effects due to excitation of other elements of the vagus.

Though the task was laborious and difficult, I succeeded in obtaining perfectly unobjectionable results.

I have already stated that the portion of the cervical œsophagus, which is most influenced by section of the vagus at the stated spot, is that near the thorax. In order to observe the canal in that region and operate on its centripetal nervous twigs, it is necessary to make on the left side (the œsophagus being in the horse, strongly deviated to the left and placed by the side of the trachea) a long incision parallel to the jugular vein, and carried as low down as possible. It is in the lowermost part of the wound that we must look beneath the œsophagus and against the trachea, the ascending branch containing most of these twigs. Electric exploration is used in this search, to reveal the presence of the nerve by the œsophageal contraction it produces.

This contraction is not directly provoked, for if the nerve thus found be divided excitation of the peripheral end has no effect, whilst that of the central end brings about the result just as that of the intact nerve.

In this case the œsophageal tetanisation is the only phenomenon observed; the animal does not give any sign of pain, nor of cough or nausea, even on strong stimulation. The latter is, in any case, wholly reflected upon the centrifugal portion of the circuit, and thus brought to bear upon the muscle it supplies.

Several times, after finding this ascending branch, I slit up the muscular coat of the œsophagus in order to test the properties of the sensory fibres it supplies to the mucous membrane. The constant negative results of excitation of these fibres contrasted with those obtained by stimulating the branch itself.

Interruption of the continuity of this same branch has effects corresponding to those of its excitation. After its division I observed accumulation of food in the lower cervical tract of the œsophagus, the muscular layer of which was more or less paralysed.

To sum up, the results of the experiments just described confirm those previously described as following excitation or division of the vagus trunks. I will add that the left vagus

gives off most sensory branches to the cervical œsophagus, and more particularly the ascending branch on which the last experiments were made.

(d.) *Summary of results of experiments in the sensorimotor œsophageal nerve-circuit.*—(1.) The well coördinated movement of œsophageal deglutition lends itself admirably to the study of the respective influence upon muscular motility of the centrifugal and centripetal elements of the nerve-circuit. (2.) In the horse this study is made possible in the middle, and more especially the lower cervical portion of the œsophagus, by a peculiar disposition of the nerves. These portions receive their motor (descending) and their sensitive (ascending) nerves from two points of the vagus. It is thus quite easy to act separately upon these two branches of the nerve-circuit. (3.) Section of the centrifugal fibres produces complete motor paralysis. (4.) Section of the centripetal fibres always markedly disturbs the motor function, causing sometimes transitory and irregular paralysis, sometimes a peristaltic incoördination that interferes with the normal process of deglutition. (5.) Electrification of the centrifugal arc of the circuit produces œsophageal tetanisation. (6.) Electrification of the centripetal arc produces tetanisation, but after an appreciable delay. (7.) Tetanisation never occurs when, after division of the nerves, we excite the central end of the centrifugal arc or the peripheral end of the centripetal arc. (8.) We find here, therefore, a justification of Charles Bell's view; and the centrifugal and centripetal nerve fibres, connected together at their extremities by the original cells and their commissures or by the preterminal network, constitute a real circuit. Whenever this circuit be broken there is abolition or marked incoördination of the normal muscular action. Wherever it be excited there is muscular contraction. Finally, wherever it be interrupted during excitation the muscular effect continues or ceases, according as the division occurs above or below the point excited, that is beyond the course of the excitation or within that course itself.

(e.) *Concerning the intervention of the mechanism of the nerve-circuit in the function of the œsophageal muscle.*—

I have a remark to make concerning the intimate mechanism of this process. We have to deal with an automatic movement entirely withdrawn from the influence of the superior nerve centres. The action of the centripetal fibres on movement cannot, therefore, be explained by attributing to them the part of intermediaries between the muscle and the psycho-physiological centre for the muscular sense. In the present instance coördination depends only upon the action of the cell groups at the origin of the centripetal conductors. It is difficult to picture to oneself the intimate mechanism through which these sensory cells influence muscular action. But it has been well established that in order to act, these cells must be connected with the muscle through the sensory fibres, and with the motor fibres, through the original cells of these fibres in the nerve centres. A circular propagation of nervous influence is thus implicated, according to Bell's conception of a nerve-circuit.

III.—ON THE CAUSES OF THE DIFFERENCE BETWEEN THE RESULTS OF EXPERIMENTS ON THE STERNOMASTOID AND ON THE ŒSOPHAGEAL NERVE-CIRCUITS.

The two preceding sets of experiments have given us generally analogous results, which, however, seem to differ on an important point. Interruption of the centripetal arc deeply alters the physiological action of the Œsophageal muscle, but appears not to do so in that of the sternomastoid. This difference deserves closer study. We stated that we could not affirm that the sternomastoid, after its sensory enervation, fully preserves its normal function. At any rate, it is clear that if its action is disturbed this disturbance cannot be compared with that of the Œsophageal muscle. One might at first be tempted to attribute this difference to the fact that the two muscles are not of the same nature. Though both striated, one is an automatic organ, not influenced by the psycho-physiological centres, the other is a part of the voluntary locomotor system, influenced by these centres. Perhaps this system may work regularly in the absence of continuity in the centripetal arc

of its nerve-circuit, whilst this continuity is indispensable to the normal action of the striated or smooth visceral muscles, such as the œsophagus.

But this vague explanation is negatived by the above mentioned experiments of Claude Bernard, which demonstrate the necessity of continuity in the centripetal arc, for the normal action of muscles subjected to the higher centres. I do not believe that this conclusion be controvertible, but why then did not my experiments on the sternomastoid have the same result?

In Bernard's experiments it was necessary to divide all the sensory roots of the limb in order to deeply disturb locomotion, that is the coördinated and synergic contractions of the numerous muscles involved in standing and walking. If some of the roots escaped the animal preserved the use of its limb for these two actions. Let us suppose that among the nerve roots those only supplying one muscle, say the extensor of the toes, have been divided. Would its action have been impaired, or would it not rather have shown as little disturbance as the sternomastoid in our experiments? This question may perhaps be answered some day from physiological or clinical data. In the meanwhile the facts of the case seem to admit of another explanation.

It is certain that in locomotion the simplest movement requires the cooperation of numerous muscles, the contractions of which must be regulated, combined, coördinated. These muscles must be connected through their nerve circuit to the medullary groups of cells to which impulse is given from the higher centres. We may well admit that all these solidary organs are involved together in the willed movement, even those whose centripetal, that is unessential, nervous arc is broken.

Such is the explanation I should give of the phenomena observed by us in the sternomastoid. It is associated with other muscles in its motor functions, which are thus connected through their nerve circuits, with the same groups of nerve cells. Each muscle must always be connected with the motor group, but it is not necessary that every one communicate with the sensory group, for those

whose nerve circuit is intact are sufficient to bring about the action of all.

This is, no doubt, also the case with visceral muscles. Thus the muscular œsophageal layer is not a simple, but a complex organ, made up of numerous muscles. The nerve circuit of most of them is interrupted by division of the vagus or of the ascending nerves. Some still incomplete experiments lead me to believe that sensory enervation affecting but a very small number of œsophageal muscular bundles would not perceptibly disturb their function. To sum up, I think that the action of the centripetal arc obeys the same laws, both in voluntary and involuntary muscles.

IV.—ON THE CONNECTIONS BETWEEN THE TWO PARTS OF THE SENSORIMOTOR NERVE-CIRCUIT OF MUSCLES IN THE CENTRAL NERVOUS SYSTEM.

The physiological study of the cerebro-spinal connections between the central extremities of the centripetal and centrifugal arcs constitutes perhaps the most interesting and important point in the question before us. Unfortunately they are beyond the reach of experimentation, and can hardly be excited, or interrupted so as to break at their level the continuity of the nerve circuit. These connections lie deeply along the whole medullary axis; they consist of motor and sensory cell groups, which give rise to the corresponding centrifugal and centripetal nerve roots, and of the fibrillar or cellular elements binding the cell groups together, which constitute the true connections between the two systems.

In the absence of a special experimental study of these connections, we may utilise a certain number of collateral data of physiological and pathological origin. But I shall confine myself to very brief remarks on the excitation and suppression of these nerve elements.

(1.) *Excitation of cerebro-spinal cellular and fibrillar elements at the origin of peripheral nerve fibres.*—Concerning the excitability of the cells, which are the real origin of the motor fibres, I observed in a recently killed horse the results of their excitation. I used weak induction currents

applied through fine electrodes held near each other, and also scraping with the point of a needle. I shall mention only the clearest facts, elicited by excitation of the nuclei in the fourth ventricle, of the seventh and twelfth pairs. The movements produced in the facial and lingual muscles are identical with those following on the direct excitation of the corresponding nerve roots. When the excitation is spread over the whole cell group all the muscles are tetanised; when it is less strong and localised by maximum approximation of the electrodes, contraction occurs in those muscles only that are innervated by the region excited.

These facts show that both the intramedullary and peripheral portions of the centrifugal tract are endowed with similar properties. But it is of more interest to know what follows upon excitation of the sensory cell groups, which can easily be carried out in the spinal cord.

In this organ the grey motor column is surrounded with a thick layer of white matter, which prevents experimentation unless transverse section has been previously carried out. But the traumatism thus produced always brings about disturbances, among which is chiefly a great diminution of excitability of the deeper parts; hence we made use of the superficial position of the motor nuclei of the facial and hypoglossal nerves, in the experiments just described. Similar opportunities are afforded by the sensory grey columns of the cord, in the study of the excitability of the cells situated at the origin of the centripetal nerves; for the posterior horns are very superficial, and at the bottom of the posterior sulcus, nearly reach the surface, from which they are separated only by a very thin white layer in the intervals between the points of emergence of the sensory roots. The subjacent sensory cells can easily be excited by scraping this layer, or applying to it the electrodes.

This experimental condition is very favourable, since in all my experiments I always obtained results identical with those determined by excitation of the posterior roots themselves. I am speaking chiefly of results obtained on the horse, of which the cerebro-spinal axis lends itself well to these experiments, when the stimulus is applied after

division of the cord from the encephalon, and at some distance from the point of section. I shall describe the case where, after division between the atlas and occipital bone (artificial respiration being carried on), excitation is made between the last dorsal and first lumbar root. On gradually increasing the current, we observe:—

(1.) Very weak excitations cause contraction strictly localised in the spinal and abdominal muscles near the point of application. The stimulus is then wholly reflected upon the cells giving origin of the motor roots corresponding to the sensitive roots near which it is applied.

(2.) Excitations with stronger currents are diffused in the cord, above and below the excited spot, but on the same side only. Unilateral and more extensive contractions of the trunk muscles appear, owing to reflexion of the stimulus into a larger number of motor roots.

(3.) On further increase of current strength, the contractions may spread not only beyond the trunk muscles, into the upper and lower extremity, the diaphragm and the neck, but also invade the opposite side of the body. The effects of the localised excitation are thus remarkably generalised; the stimulus propagating itself to the ends of both lateral halves of the cord, and being reflected upon the motor cells along its passage on both sides.

Analogous results follow excitation of either of the two sensory roots between which the cord has been excited. These effects are exactly comparable with those following excitation of the sensory branch of the sternomastoid muscle.

The contractions are also localised in the muscles supplied by the nerve fibres, when the stimulus is weak; they irradiate either on the same side, or on both sides, when it is strong.

Hence we conclude that the central motor and sensory cell-groups which give rise to the centrifugal and centripetal nerves respectively, behave on stimulation as these nerves themselves; and that the theory of a nerve-circuit is thereby further justified.

I cannot present any experimental data as to the effect of

excitation of the inter-cellular commissures, though I frequently attempted to obtain them. This excitation is possible only on transverse sections of the cord, and I have already stated that the resulting physiological disturbance vitiates all its effects. Generally speaking, superficial pricking or scraping with a needle, under these circumstances, remains without any effect, whatever part of the grey or white matter be touched. In order to obtain a result, we must suddenly plunge the needle to the depth of three or four mm.; and even then we obtain it only if we come across either the central ends of motor fibres or motor cells. There then may follow some localised contractions in the dorsal and lumbar regions; in any other situation these needle pricks have no effect.

This negative result is apparent when the sensory spinal tracts are alternately excited on the surface of section and on the natural surface of the organ. Scraping the latter at the level of the sulci and posterior columns, at some distance from the cut end of the cord, nearly always calls forth fine reflex contractions, which stand in contrast to the negative result of irritation of the divided surface of these posterior columns and cornua. This sensibility of the posterior spinal surface in mammals is observed only when circulation is going on regularly. If artificial respiration be stopped, and the animal be bled, death ensues, and this sensibility disappears very rapidly. It vanishes with the last heart-beat. We have seen that it is different in the case of the motor system, both motor cell-groups and peripheral nerves preserving their excitability for a few minutes after death. Hence every movement obtained by exciting the cerebro-spinal axis of a recently killed animal shows that the stimulus has excited some motor element. These indications are given for the benefit of those desirous of investigating experimentally the present subject.

(2.) *Interruption of the sensorimotor circuit in the cerebro-spinal axis.*—I shall not enter now upon pathological details calculated to clear up this point, but will confine myself to recall a few facts. Our main interest lies in the effects of destruction of the central sensory system, cells and

fibres. Now we know that in *tabes dorsalis*, such a destruction, more or less extensive and complete, with preservation of the motor elements, produces locomotor disturbances which can be explained only as effects of central ruptures in the sensorimotor nerve-circuit of the muscles.

This is enough to demonstrate the function of this nerve-circuit; and I shall not say any more on this subject, in the absence of new experimental data, to elicit which would be a difficult, if not an impossible, task.

V.—ON THE APTITUDE OF THE MUSCULAR NERVE-CIRCUIT OF ANIMAL LIFE TO CALL FORTH COÖRDINATED MOVEMENTS INDEPENDENTLY OF THE PSYCHO-PHYSIOLOGICAL CENTRES.

Towards the end of Part II., when discussing the mechanism of coördinated oesophageal contractions during deglutition, I said that this act depends on the continuity of the nerve-circuit, and on the activity of the central sensorimotor cell-groups from which the two arcs arise. This activity is such that the cell-groups must be considered as exciting centre and automatic regulator of the organs and process of deglutition. There are many more such in the medullary axis, presiding over sub-conscious motor functions, and the coördinating functions of which are admitted with reference to manifestations of vegetative life. But it is less generally recognised that this axis is similarly endowed with regard to movements of animal life, or locomotion [proper. A few appropriate examples will show the similarity between these two classes of functions, so far as the mode of action of the nerve-circuit, and its cellular centres, is concerned in both cases.

We shall consider two cases of experimental movements in horses after separation of the medulla from the encephalon. These contractions are generally considered only as muscular jerks in no way connected with movements adapted to an end. No doubt many reflex actions in the locomotor system appear to be such; but in some we may easily trace distinct coördination.

(1.) *Artificial coördinated respiratory movements in horses after separation of the medulla from the encephalon.*—After atlanto-occipital division of the cord, artificial respiration is carried out. When the latter process is suspended, whether after minutes or hours, there is never any restoration of respiratory movements; and asphyxia rapidly supervenes with hardly ever the least inspiratory jerk during the final convulsions. We can, however, under the circumstances excite reflex inspirations sufficient to keep up respiration, without the assistance of the bellows. It is enough to stimulate the perforating branches of the intercostal nerves. Horses very uniformly and readily react to this excitation, as I had very frequent opportunities of observing in the laboratory on animals prepared in the way just described. At the beginning of the experiment, before any weakening of the reflex powers of the cord, it is remarkable to see how the least excitation of one of the perforating branches sets up inspiration.

Any stimulus is efficacious; mechanical shock, squeezing, electric shock, tetanising currents. With a single strong excitation, we observe (along with some other movements which I leave aside) a short and ample inspiration. Rapidly repeated stimuli fix the chest in inspiration during their whole duration. The use of the sledge induction apparatus enables us to give to these respiratory movements the perfect thoracic rhythm with its increasing and decreasing characteristics. The electrodes being left applied to the nerve, the secondary coil is made to slide to and fro in a well regulated manner, so as to obtain the requisite augmentations and diminutions in the tetanising current strength. It is strange to witness how exactly this process can reproduce the normal respiratory movements, and how easily life is thus maintained after spinal section. By occasionally changing the nerves and the points of application I have often maintained artificial respiration for half-an-hour or even longer.

The coördination of the respiratory movements so obtained is perfect. They are not mere reflex jerks, but genuine contractions regulated towards the carrying out of a natural function. This coördinated, purposive character is even

found in the short and sudden inspiration following a shock or instantaneous squeezing of the perforating nerve; such momentary stimuli acting upon the whole muscular respiratory apparatus. The chief muscle, the diaphragm, is thus thrown into activity not only in part or upon the excited side alone, but as a whole; and I have even seen subsidiary muscles, such as the external intercostals, contract at the same time.

These results show that the cord is capable of starting coördinated inspiratory movements, as for normal inspiration. This aptitude depends upon the cell groups belonging to the sensorimotor nerve circuit of the diaphragm, to mention only the essential muscle concerned. Under the influence of a special excitation these centres put forth their properties, along with those of their whole circuit, and the muscular function is thus carried on. In the present case the special excitation, which sets into activity the diaphragmatic nerve circuit, comes from a peripheral cutaneous nerve; under normal conditions it has a central origin: the medulla oblongata and the brain. Let us examine these two sources of excitation.

The bulb is the seat of what is correctly known as the respiratory centre, which sends off the rhythmical excitations necessary to keep up, during sleep and vigil, automatic respiration. After section of the cord, this centre cannot any longer act upon the cellular portion of the nerve-circuit of the inspiratory muscles; respiration then ceases suddenly, and cannot spontaneously recover itself unless the cells receive from elsewhere their needed rhythmical excitation—from the periphery, for instance, whence a stimulus could arise, more or less analogous to the experimental one through electrification or squeezing the perforating intercostal branches. It is no doubt to such an intervention that re-establishment of respiratory movements after spinal division is due, as Brown-Sequard, and Wertheimer have observed it to be the case in dogs under certain conditions.

Let us now consider the case where the brain itself takes part in the respiratory function—when more than its automatic maintenance is involved. When respiration is to be

slackened or accelerated, or made shorter or deeper, or used for special acts, such as vocalisation, coughing, sneezing, &c., we can understand that the higher centres enter into action to send specific excitations to the cell groups of the respiratory nerve circuits, either directly, or indirectly through the bulbar centre acting as a relay.

I only touch upon the surface of this difficult subject, avoiding all points not directly connected with this study. I hope thereby to present clearly the general ideas submitted to criticism on the respiratory nerve circuit, on the function of motor and coordinating centres fulfilled by the cell groups placed at the origin of this circuit; finally on the relations between these spinal centres, and excito-regulating centres in the bulb and brain.

(2.) *Coördinated movements in the horse's hind limbs after medullary division.*—I come to the second class of facts, showing the capacity of the isolated cord to call forth co-ordinated purposive movements, through the influence of the central cell groups of the muscular nerve-circuit. The present case, though somewhat more complicated, may be briefly stated, because we shall have but to repeat ourselves when we come to state the deductions from the analysis of the facts.

For our present experiment a lively and nervous subject is to be selected (donkeys are very suitable), and prepared as before. If the medullary section has been well done, and the artificial respiration is properly carried out, the excitability of the cutaneous surface is well marked throughout, but especially about the hind limbs, where the least touch calls forth lively and more or less generalised reflex movements. If the pastern of the limb on the side opposite to that on which the animal is lying, be suddenly seized, the limb is suddenly flexed upon the trunk, with some alternatives of flexion, as if the animal consciously intended to withdraw it from the pressure. Sometimes, especially in the donkey, if the pressure be strong and almost instantaneous, this flexion is immediately succeeded by an equally sudden extension, as if the animal were kicking an aggressor. Squeezing of the collateral digital nerves still more readily excites this movement.

Thus in the two cases, peripheral excitation does not call forth disordered jerks, but associated and coördinated contractions, giving the impression of a locomotor act analogous to that produced by the same excitation in the normal animal. It is interesting to note that this reflex kick occurs chiefly among bad tempered subjects, naturally disposed to kicking as a mode of attack or self-defence. It is, therefore, not in lower vertebrata only that such spinal reflex movements having all the characteristics of perfectly coördinated actions, are to be elicited.

The mechanism of these locomotor manifestations also is readily explainable. The sensory peripheral stimulus calls forth the combined activity of the cell groups of the nerve-circuits supplying the limb, the segments of which perform regular movements, through contractions associated towards a true locomotor act. Here again the nerve-circuit of the muscles carries within itself the principle of motor coördination, when its central or cellular portion—a true locomotor centre—is brought into play by an excitation. After division the spinal locomotor centres can receive artificial peripheral excitations only, without which the muscles remain inert. When intact the cord receives impulses from the medulla, and the three large encephalic ganglia (psycho-physiological centres); in other words excitations come from all the central portions which rule automatic standing and walking, as well as all voluntary modifications of these actions.

Such are the facts I had to bring forward concerning the capacity of the nerve circuit of voluntary muscles, for calling forth coördinated movements independently of the higher centres. I have been led into saying a few words concerning the physiological relationship between these centres, and the spinal ones considered as origin of the two arcs of the circuit; my intention in so doing was merely to throw more light upon the mode of action of this circuit, without ever intending to enter upon the great question of the psycho-physiological centres, and their connection with the locomotor function.

VI. — HYPOTHETIC VIEWS CONCERNING THE INTIMATE MECHANISM OF THE NERVE-CIRCUIT OF MUSCLES.

No subject in physiology lends itself less to the determination of the intimate mechanism of phenomena, than the function of the nervous system. This is perhaps why we content ourselves with little, and cling tenaciously to that little. The current prejudices concerning the part played in muscular contraction by sensory motor nerve functions, are opposed to the adoption of the nerve-circuit theory. One is used to look upon the motor and sensory muscular systems as independent, and one is disinclined to admit that sensory nerves may have, in addition to their proper function, a direct share in the execution of movements governed by the motor system. One readily conceives an excitation starting from the anterior spinal cells, travelling down the nerve and the motor plates, and giving start to the contraction. It is then only that one calls in the centripetal system; the sensory terminations (?) take cognizance of the incipient contraction; this impression is conveyed upwards to the regulating centres, which in their turn reflect it upon the motor cells; and these, finally, react in consequence, that is by regulating the contraction whose apparition they have already determined. I attribute greater simplicity to this mechanism, by admitting absolute simultaneity of collaboration among both motor and sensory nerves.

In order to frame a sufficient hypothesis concerning the synergy of both kinds of nerves in coördinated motion, we must keep in view the nature of the physiological relationship between both arcs at their extremities, where we assume them to be anatomically connected together. This relationship is such that an excitation is easily carried from the centripetal to the centrifugal conductor, through the central loop of the circuit, whilst no such transmission takes place through the peripheral loop, from the centrifugal to the centripetal conductor. Thus, this peripheral loop, or the muscular tissue which is tangent to it, may be considered as an insuperable barrier for excitations conveyed by the circuit; applied to the peripheral end of the centripetal

conductor, an excitation can reach the muscle only after travelling through the whole circuit, first upwards to the central, then downwards to the peripheral, loop. This is the fundamental fact to be remembered. Thus an excitation runs round the circuit in one direction only. Still there is reason to believe that the disturbance it sets up on entering the circuit is felt in both directions, for it is difficult to understand this disturbance to be other than a vibratory motion, giving rise to systems of waves which are propagated towards both extremities of the conductor. Some waves are *præpulsive*, going in the same direction as the excitation; others *retropulsive*, going in the opposite direction. This mechanism presents a certain analogy with what takes place in an air-filled tube, in which the same stroke of a piston produces in front a condensed half wave, behind a dilated half wave. Each of these is propagated in opposite direction to one extremity of the tube, as we supposed the case to be with reference to the *præpulsive* and *retropulsive* nervous waves.

In order better to define the action of this mechanism, let us consider the physiological event in which it has taken part, that is when an excitation impinges upon the nerve circuit in its central part. We may suppose that this excitation—whatever be its origin, brain, bulb, cutaneous nerves—first reaches that part of the circuit which stands between the centripetal and centrifugal cells. In the latter the excitation sets up a *præpulsive* wave forwards; in the former a *retropulsive* one backwards. Both these waves reach simultaneously the peripheral loop and exert their influence upon the muscular tissue that lies tangent to it; this influence is chiefly motor in the case of the *præpulsive*, chiefly co-ordinating in that of the *retropulsive* wave. For we have seen that if this simultaneous arrival of the two waves is not necessary to the provocation of muscular movement, it is essential to its co-ordination. Interruption of the centripetal conductor, by preventing the arrival of the *retropulsive* wave, does not necessarily paralyse the muscle, but it always interferes in some measure with the physiological adaptation of muscular contraction to the execution

of true coördinated movements. If one cannot foresee the essential cause of this disturbance, one has at least a clear notion that the lesion which produces it disables the centripetal conductors from transmitting to the muscle, under the shape of the retropulsive wave, the effect of the excitation experienced by the central portion of the nerve-circuit. We need say no more on this subject.

I might now review all cases of interruption or artificial excitation of the several parts of the nerve circuit, and show how the present theory adapts itself to our experimental results. But this would be superfluous. A general indication only need be given, concerning artificial excitation. Whatever be its point of application, it always calls forth a contraction if its præpulsive wave can reach the peripheral loop, and through it the tangent muscular fasciculus. The retropulsive wave has no share in the result, and to it is indifferent whether the centripetal branch of the circuit be or be not broken. For instance, if the motor nerve be divided and excited close to its termination the præpulsive wave will produce contraction just as well as if a retropulsive wave had circulated backwards round the whole circuit. Again, if after division of the sensory nerve close to its termination, the central end be excited, a præpulsive wave only is set up, sufficient to produce contraction. On the other hand, a retropulsive wave alone, set up by excitation of the central end of the centrifugal or the peripheral end of the centripetal conductor, never gives rise to any muscular contraction.

To sum up, the retropulsive wave intervenes only in the mechanism of coördinated movements, provoked by natural excitation of the spinal cells of the nerve-circuit.

We might institute a comparison between this physiological work, and the corresponding electric modifications it sets up in the nerves; but I must confine myself to the statement that the study of the negative variation yields inductions favourable to the theory of præpulsive and retropulsive waves, and so does that of the electrotonic state above and below the excited spot.

Such are the considerations which I had to present on a

possible manner of understanding the mode of action of the muscular nerve-circuit, that is to say the intimate mechanism of the cooperation of the muscular sensory fibres with the motor in the execution of movements.

Are these two kinds of fibres really so joined at their extremity as to form a circuit in which excitations give rise to waves in both directions? I may not affirm it; "*sunt verba*" may it be said of all what precedes concerning the possibility of such a mechanism. But this cannot be said of the facts which this attempt at synthesis is intended to bind together. Whatever fate be reserved for the theory herein exposed, interesting results will remain from the experiments undertaken to verify the theory of a muscular nerve circuit.

Addendum.—Among the new facts published in this paper, I may mention:

(1.) All results from experiments on the sternomastoid muscle; excitations and divisions of its motor and sensory nerves.

(2.) All experimental facts related to excitation and division of centripetal nerves of lower cervical oesophagus.

Some other facts had already been very incompletely mentioned in my previous publications, especially

(1.) Physiological respiration kept up by rhythmical excitation of perforating intercostal branches in the horse after spinal section.

(2.) Coördinated movements of the hind leg under similar conditions set up by excitation of the cutaneous nerves.

I do not believe I ever published before a large series of experiments made on the complete sensory enervation of one foot in the pigeon, and its effect upon standing and walking. But the facts elicited thereby have now lost the interest of novelty.

(Translated, from the original MS., by the Editor.)