On Reciprocal Innervation of Antagonistic Muscles. Eleventh Note.—Further Observations on Successive Induction.

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(Received November 4,—Read December 5, 1907.)

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It was shown in previous notes* of this series that in the "flexion-reflex" of the limb the reflex inhibition of the extensor muscles is frequently followed by contraction of them. This contraction ensues immediately on cessation of the inhibitory stimulus, and is often more accentuated than was the contraction originally inhibited. The phenomenon was ascribed to a process of rebound in the central part of the nervous arc inhibited, and this process, on account of its seeming analogy with certain visual phenomena often called "inductive," was termed "successive induction."

The occurrence of this "successive induction" made it seem probable that under favourable conditions the reflex evoked in the limb by a single stimulus would be diphasic with a first phase of flexion followed by a subsequent phase of extension. The following observations show that this is in fact the case, and under appropriate conditions regularly so.

Among conditions requisite for the reflex's exhibition of this diphasic character is freedom of the preparation as far as possible from such depressing influences as "shock," deep narcosis, fatigue, etc. In purely spinal reflexes successive induction does occur; thus, it causes exaltation of activity of the extensor arcs to ensue after their inhibition during a flexion reflex; that was established by observations previously reported.† In those observations the reflex preparation used had been preserved over long periods subsequent to spinal transection, the depression due to spinal shock in the ordinary meaning of the term had had prolonged opportunity to subside. In the present observations the examination of the reflex has been proceeded to within a few hours of the transection, since it was found that the successive induction could be observed without recourse to long periods of recovery if the transection instead of being spinal was pontine, *i.e.*, through the anterior part of the hindbrain. The transection and

* 'Roy. Soc. Proc.,' B, vol. 76, p. 160; vol. 77, p. 478; vol. 79, p. 347; also 'Integrative Action of the Nervous System,' London and New York, pp. 21, 206, 1906.

† Sherrington, 'Roy. Soc. Proc.,' B, vol. 76, p. 161; vol. 77, p. 478; 'Integrative Action of the Nervous System,' p. 19; also article "Spinal Cord," Schäfer's 'Text-book of Physiology,' vol. 2, p. 841, 1900.

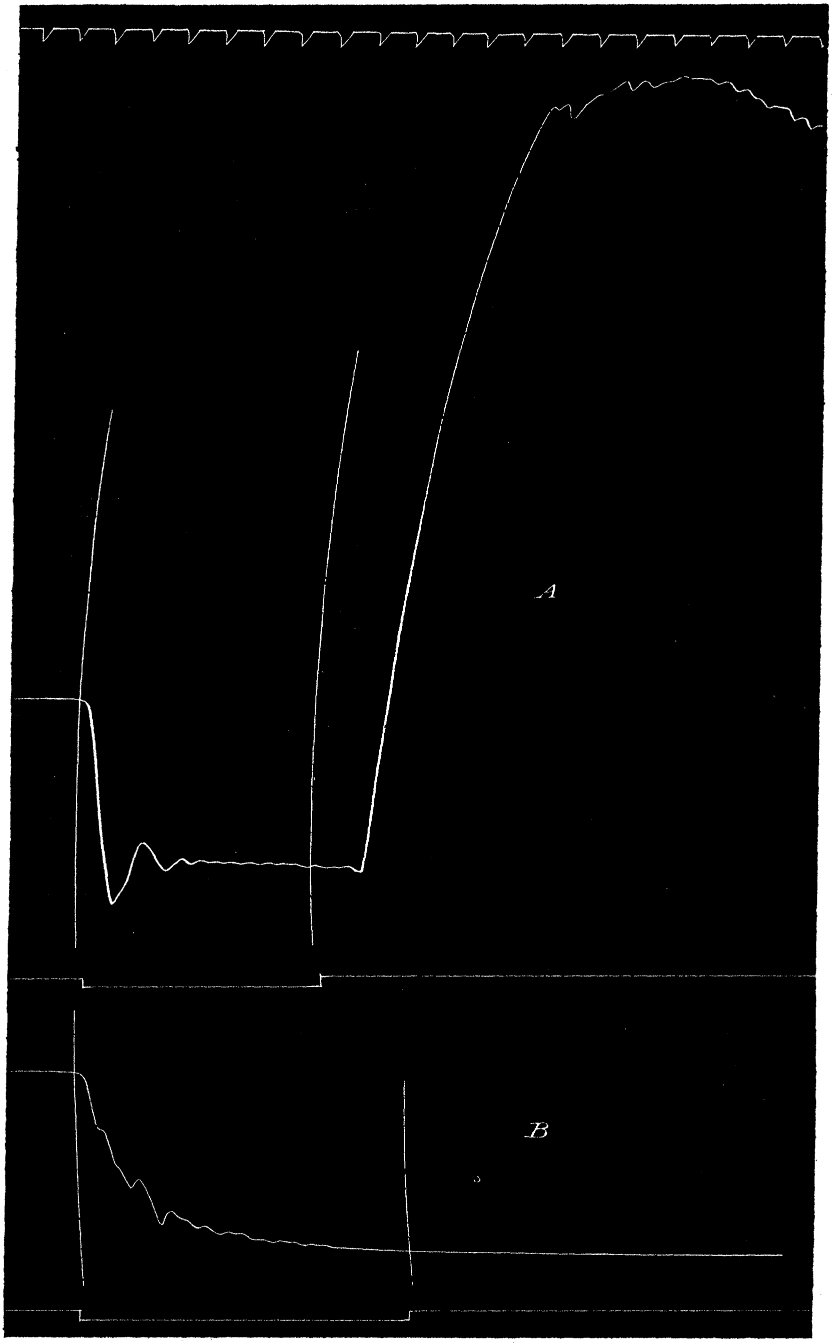

Fig. 1.

operation preparatory to that was carried out under deep chloroform narcosis. The brain anterior to the transection was removed. After this removal the chloroform narcosis was lightened. The "flexion-reflex," elicited from an afferent nerve or from some appropriate skin-point, is then found to be diphasic. The movement of active flexion is followed by a movement of active extension. During the active flexion the extensor muscles are relaxed by central inhibition; during the active extension the extensor muscles contract.

The contraction of the extensor muscle, *i.e.*, the discharge of the extensor motoneurones, never in my experience sets in during the actual delivery of the external stimulus used to excite the "flexion-reflex." So long as that stimulus continues the extensors remain inhibited (fig. 1).* It is only after withdrawal of that stimulus that the discharge of the extensor motoneurones occurs. The commencement of this discharge, judged by the muscle's contraction, follows withdrawal of the external stimulus by a time interval longer than that between commencement of external stimulus and onset of the inhibitory relaxation of the muscle. In other words, the latency of the contraction-phase is longer than that of the inhibition-phase (fig. 1, A, and fig. 8, A).

That the contraction of extensor muscle, *i.e.*, discharge of extensor motoneurone, never occurs *during* the continuance of the external stimulus, distinguishes the reaction from a rhythmic reflex such as the "scratch-reflex." In the scratch-reflex the phases of absence of discharge and of occurrence of discharge succeed each on the other in the motoneurone, *e.g.*, of extensor of knee, during unabated continuance of the external stimulus,† and with a period of alternation practically independent of the external stimulus. In the case of the "flexion-reflex" of diphasic character, the second phase, the phase of discharge of the extensor motoneurone, cannot apparently break through the state of inhibition characterising the first phase so long as the external stimulus is unremitted. The first phase may be termed, if desired, a refractory phase; but if so it is a refractory phase the duration of which depends on the external stimulus, whereas the duration of the refractory phase of the scratch-reflex is independent of the external stimulus.

* The time-marker records in fifths of seconds throughout all the figures. The signal marking excitation is below. All read from left to right. In all the records (figs. 1—9 inclusive), descent of the myograph line means relaxation of the muscle, and conversely its ascent means contraction of the muscle.

† Sherrington, 'Journ. of Physiology,' vol. 29, p. 58, 1903; vol. 31, p. xvii; vol. 34, p. 1; 'Integrative Action of the Nervous System,' p. 45.

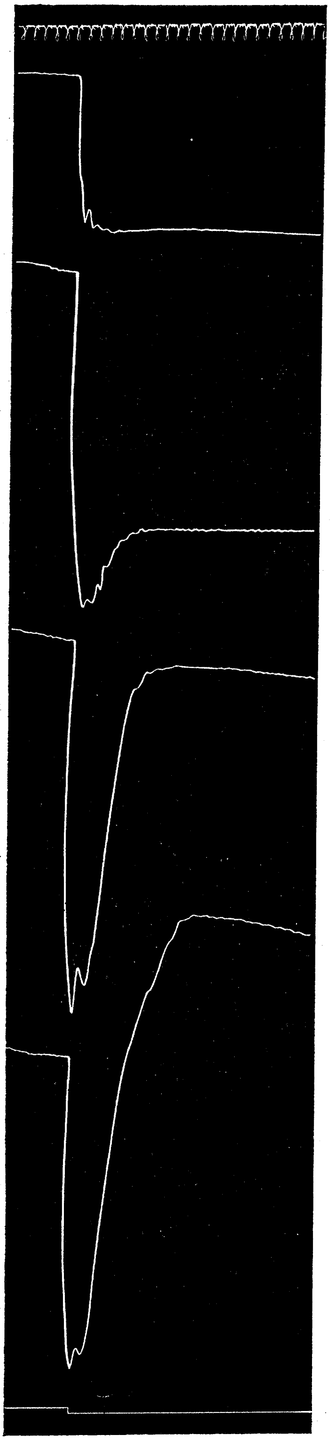

Fig. 2.

For the contraction-phase to ensue, not only must the external stimulus have ceased, but that stimulus must have possessed an intensity of above a certain minimal degree.

In fig. 1, the lower reaction B, showing no after-phase of contraction, was given by a weaker repetition of the faradic stimulus which in the same reflex preparation had shortly before caused the upper reaction A, showing marked after-phase of contraction. This influence of intensity is well shown when the stimulus is very brief, *i.e.*, a single make or break induction shock. When the shock is a weak one, inhibitory relaxation of the muscle is its only effect obvious in the preparation (fig. 2). When the shock is more intense, a phase of contraction follows the phase of relaxation (fig 2), and the contraction-phase becomes more marked as the intensity of the shock is made greater (fig. 2). With a quite strong induction shock, *e.g.*, a break shock unpleasant to the observer's tongue, the contraction-phase ensuing on the relaxation may reach a height much exceeding that of the contraction pre-existent to the inhibitory relaxation (fig. 2). Also, the contraction-phase may last several seconds, and be much longer than the phase of inhibitory relaxation which preceded it (fig. 2).

With longer and more complex stimuli, such as series of double shocks at an intermittence of 30 per second, a similar relaxation is even better evident (fig. 3). When the stimulus is quite weak, the reflex effect in the extensor muscle, *e.g.*, *vasto crureus*, is simply an inhibitory relaxation (fig. 3, A). As the stimulus is repeated with greater intensity, a phase of contraction follows on the phase of inhibition, and the contraction-phase increases with increase of the intensity of the stimulus (fig. 3, B, C, D). But the phase of contraction never

encroaches on the phase of inhibitory relaxation during the period of actual delivery of the external stimulus.

Further, with these stimuli other conditions governing the appearance and intensity of the contraction-phase become apparent. Of these, one is that a

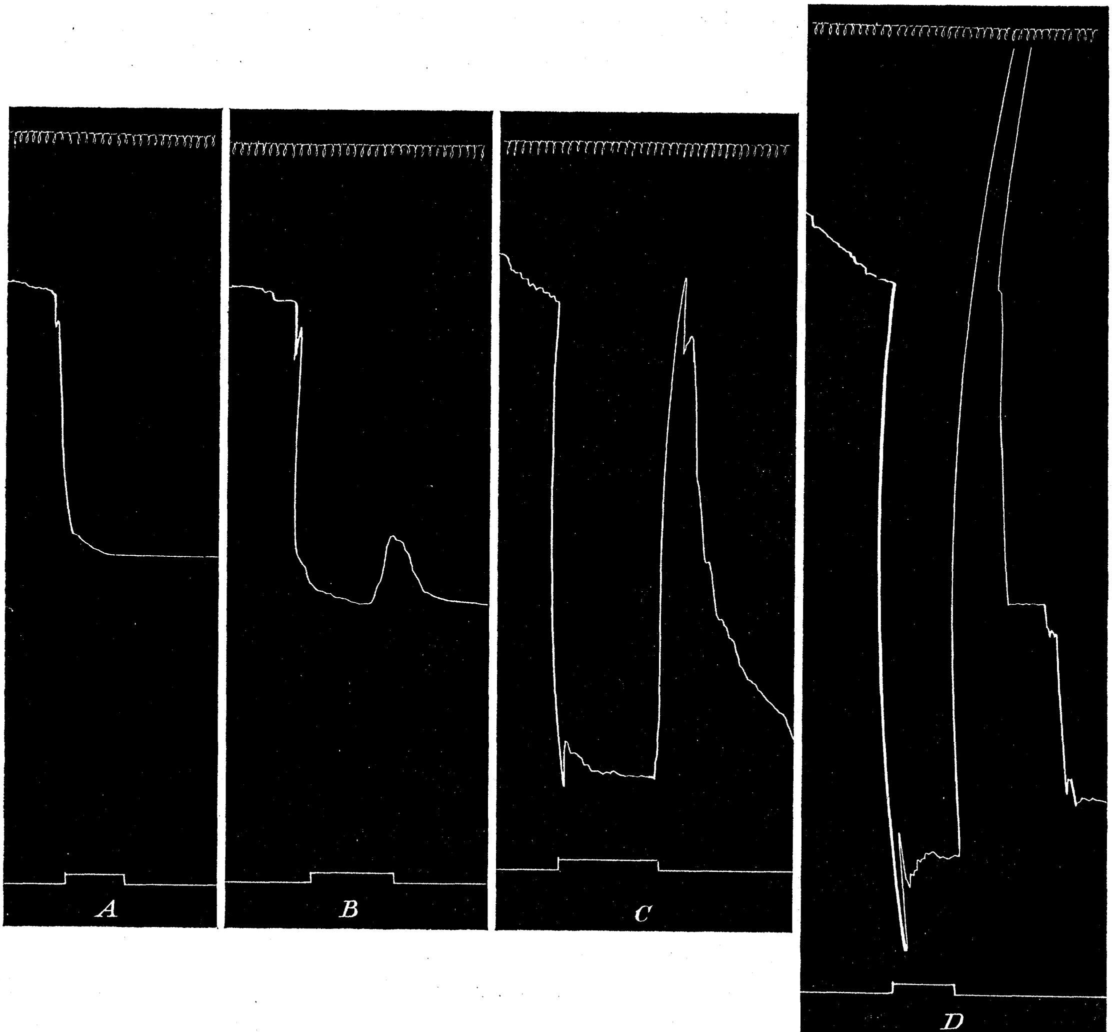

Fig. 3.

weak stimulus which, when brief, does not occasion a contraction-phase, does induce a contraction-phase if its duration be lengthened (fig. 4). Also, a stimulus which, when brief, occasions but slight contraction-phase, occasions more and more marked contraction-phase when its duration is more and more lengthened, up to certain limits. That it is less easy to evoke the diphasic

reflex by a single induction shock as stimulus than by a faradic stimulus, is explicable by the influence of mere duration of the stimulus upon the efficacy of a stimulus to induce the contraction-phase. The rule holds generally in reflex reactions that frequently-repeated small stimuli sum to a total effect equal to that of a single stimulus of much greater individual intensity. The above results amount, therefore, simply to this, that the phase of inhibition has to exceed a certain minimal value in order that a phase of contraction ensue from it.

In fig. 3 it will be noticed that the amount of lengthening of the muscle in the inhibitory phase of the reflex increases with the strength of the stimulus, as does the ensuing contraction-phase itself. Yet it is not at all necessary, in order to obtain the contraction-phase, or to obtain a marked contraction-phase, that the lengthening of the muscle in the precurrent inhibition-phase should have been extensive. The intensity of contraction-phase bears no close relation to the amplitude of the lengthening in the inhibitory phase. The amount of contraction-phase is independent in great measure of the extent of the fore-running inhibitory lengthening of the muscle. Thus, in figs. 4, 5, 6, and 7, the amplitude of the lengthening registered in the inhibition-phase was very small, yet the ensuing contraction-phase is marked in fig. 4, and is very great in figs. 5 and 6. The amplitude of the lengthening of the muscle, which takes place during the inhibition-phase, depends much on the degree of contraction present at the moment when the inhibitory stimulus is applied. If the muscle be then already fairly at relaxation length, the amount of further lengthening which ensues during the inhibition-phase may be small. The stimulus will then, nevertheless, if it have sufficient intensity or duration, be followed by large contraction-phase (figs. 5, 6, and 7). This seems important, because it indicates that the main predisposing factor for the after-coming contraction is not the peripheral relaxation of the muscle, but the central process of inhibition, and this the muscle only fully expresses under suitable mechanical conditions. We may suppose that the central change underlying this central inhibition increases with increasing intensity of stimulus—intensity including, as was argued above, duration (within limits) of stimulus. The amount of the after-coming contraction-phase seems, therefore, proportioned to the amount of the precurrent inhibition which takes place *centrally*. This argues in favour of regarding the contraction-phase as due to a central rebound from inhibition to excitation.*

It was said above that a stimulus, too weak when brief to evoke an after-phase of contraction, becomes effective when prolonged (fig. 4). The range of

* *Cf.* "Integrative Action, &c.," p. 212 ; 'Journ. of Physiology,' vol. 36, p. 191.

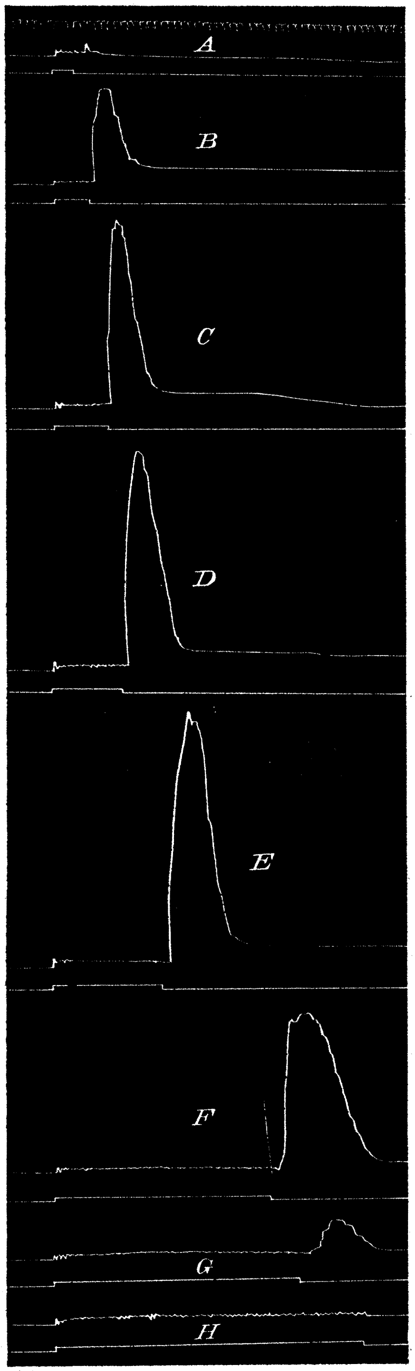

FIG. 4.

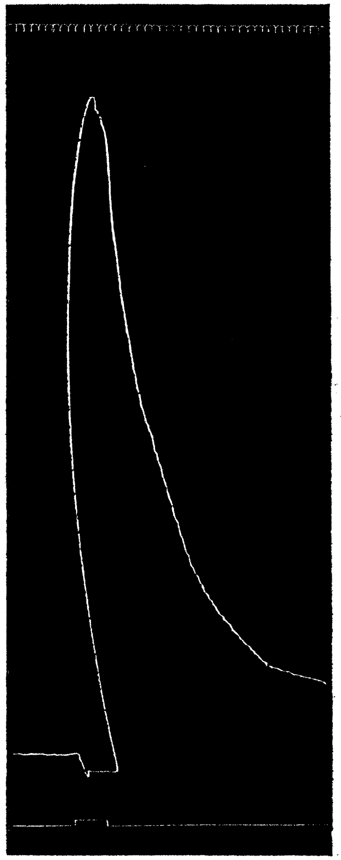

FIG. 5.

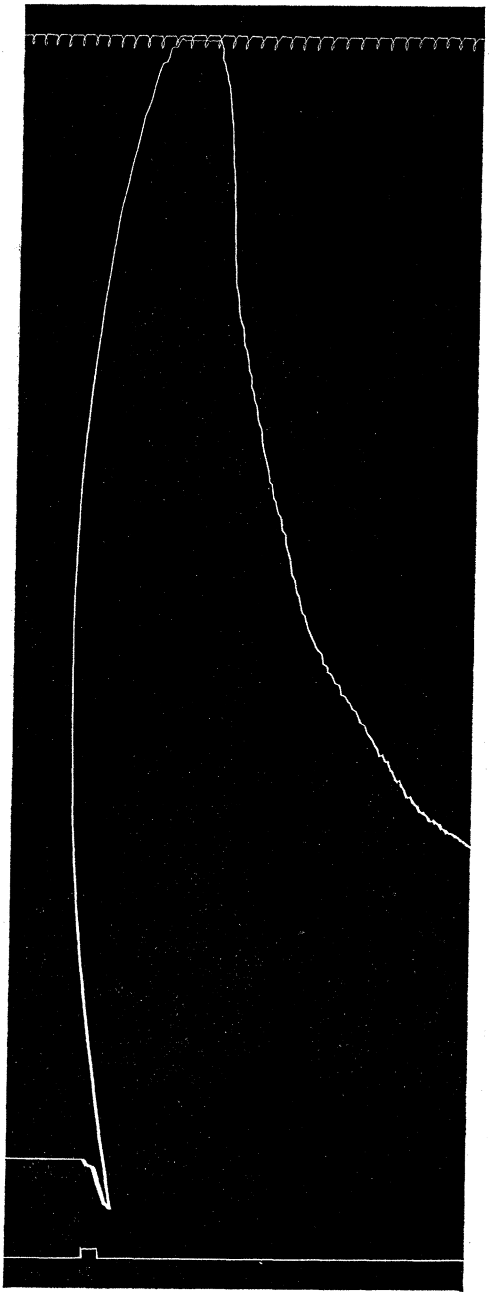

Fig. 6.

duration over which this holds good is wide, but it may be overstepped. An effective stimulus may, if much prolonged, pass unfollowed by contraction-

phase (fig. 4, H). There seems for each intensity of stimulus a duration which best favours the occurrence and intensity of contraction-phase (fig. 4). The length of this period varies with the condition of the reflex preparation as well as with the intensity of the external stimulus. In fig. 4 the reflex preparation was of relatively low activity. The relation existing between the period of the stimulus and the development of contraction-phase recalls the observations of Bowditch and Warren* on the time-factor in the influence of precurrent stimuli from various sources on the amplitude of the knee-jerk; also the relation observed by Yerkes† between precurrent stimuli and a reflex elicitable from the frog.

The contraction of the contraction-phase varies from a brief spasm (fig. 3) to a prolonged tetanus lasting many seconds (fig. 8, A and B). The con-

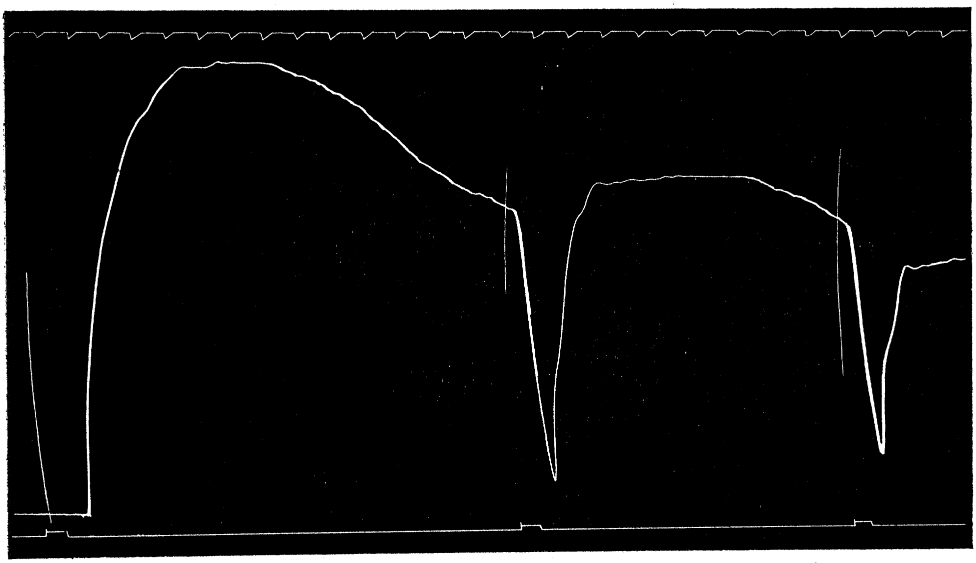

Fig. 7.

traction may be of great amplitude and power. When intense it reaches its maximum with considerable speed (figs. 1 A, 6, 7, 8, A and B). Its decline may be rapid (figs. 3, 4), but more usually is quite gradual (figs. 1, 2, 7). Its decline is always, in my experience, more gradual than its ascent, and usually very greatly so (figs. 1, 2, 7). This is a point of difference between it and certain forms of strychnine reflex as exhibited by the same extensor muscles, and it constitutes a distinction of some importance for determining the relation of strychnine reflexes exhibited by these muscles to the normal after-phase of contraction which they also show.‡

* 'Journ. of Physiology,' vol. 11, p. 25, 1890.

† Pflüger's 'Archiv,' vol. 107, p. 207, 1905.

‡ Sherrington, 'Journ. of Physiol.,' vol. 36, p. 191, 1907.

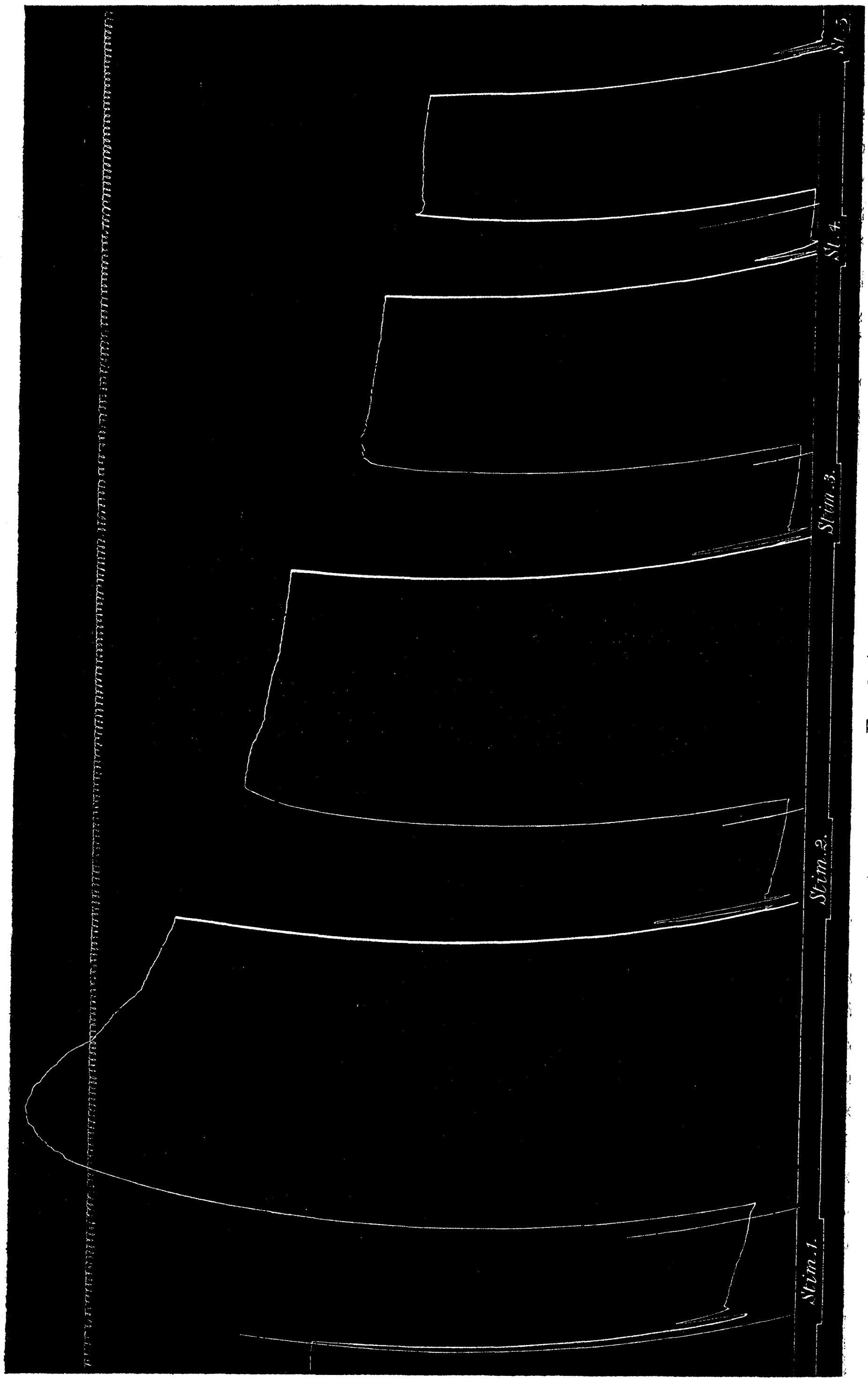

Fig. 8, A.

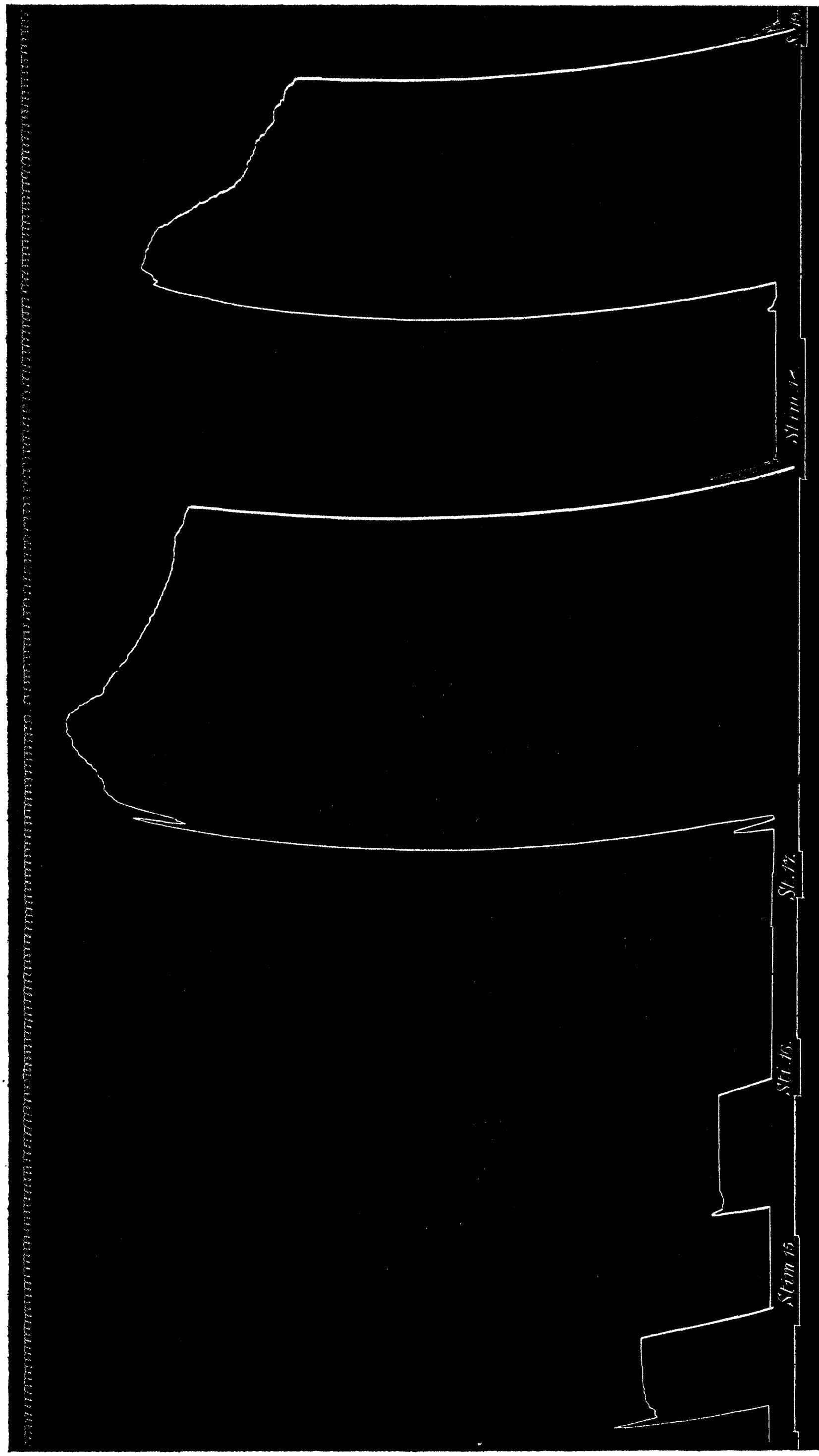

Fig. 8, B.

The contraction of the after-phase is extremely easily and rapidly cut short by a repetition of the stimulus upon which it followed. That stimulus inflicts on it with speed and certainty an inhibitory relaxation (figs. 7 and 8, A and B). Even the briefest repetition of the stimulus suffices. I have seen a repetition lasting only one-twentieth of a second cut it down. In fig. 7 is seen the effect of renewal of the stimulus for one-tenth of a second (fig. 7, third application of stimulus). The stimulus cuts it down by inhibitory relaxation, much as it cuts down a crossed extension reflex.*

On repetition of the original stimulus, the contraction of the contraction-phase is lessened or suppressed according to the intensity of the stimulus or the duration of its reapplication. On cessation of the reapplication the contraction-phase sets in again (figs. 7 and 8, A, B); subject only to the general conditions already mentioned as governing the contraction and to the condition that the reapplication has not been strongly repeated many times. The contraction-phase tires out more quickly than does the inhibition-phase. The contraction-phase that appears after a repetition of the stimulus does not seem to be simply a continuation or reappearance of the old contraction-phase that had been inhibited, for it often exceeds in intensity the intensity which the foregoing contraction-phase had at the moment when the inhibitory stimulus was renewed (fig. 7, second stimulation; and fig. 8, B). Nevertheless, the new contraction-phase has not so great intensity as the previous contraction-phase showed at outset (figs. 7 and 8, A). The fresh contraction-phase following each repetition of the inhibitory stimulus is on the whole somewhat less than the one preceding it (figs. 7 and 8, A, B), and the series of contraction-phases show progressive decline (figs. 7 and 8, A, B). Fig. 8, A, B, exhibits the first four and the last two of a series of 15 diphasic "flexion-reflexes" provoked in the extensor muscle (vasto-crureus) without pause between them. The external stimulus was not intense, and its intensity remained the same throughout this series, although the duration of its several applications was not exactly the same for each member of the series, since the short-circuiting key opened and shut by hand instead of automatically. The contraction-phase dwindled progressively in its repetitions, and on (fig. 8, B) withdrawal of the sixteenth stimulus no contraction-phase followed. The faradic stimulus was then (fig. 8, B) repeated with increased intensity, although with somewhat shorter duration. On cessation of this (seventeenth) stimulation, although little or no further lengthening of the already fairly-relaxed muscle had been obvious during the stimulation, a contraction-phase of considerable intensity at once followed (fig. 8, B). On repetition of the stimulus this was at once cut

* See fig. 3, in eighth Note of this series, 'Roy. Soc. Proc.,' B, vol. 76, p. 277.

down. On withdrawing the stimulus contraction-phase again appeared almost as intense as on the next previous withdrawal (fig. 8, B). By repeating and withdrawing the stimulus a new series was obtained. This declined more rapidly than the former one, and when its contraction-phases had died out a further strengthening of the stimulus induced a new and still more rapidly-declining series. It is clear, therefore, that in the first series the contraction-phase had been exhausted only relatively to the intensity of the external stimulus used in that series. A stronger stimulus was still able to evoke more contraction-phase. I have shown a similar relation to exist between fatigue of reaction and intensity of stimulus in the scratch-reflex of the spinal dog.* On the whole, in my experience the contraction-phase is relatively little resistant to fatigue. It will often disappear for a given stimulus in three or four severe repetitions of that stimulus. It seems to wear out more rapidly than does the inhibition-phase of the same reflex. It wears out especially rapidly when the reflex excitability of the preparation is low, *e.g.*, under shock, general exhaustion, etc.

It was said above that the contraction-phase is easily suppressed by chloroform narcosis. In the bulbospinal animal exhibiting extensor rigidity, a very considerable depth of chloroform or ether narcosis is required to abolish the rigidity. A depth of narcosis less than that required to abolish the rigidity of the muscles abolishes the contraction-phase of the "flexion-reflex" in them. When under deepening narcosis the stimulus for the "flexion-reflex" is repeated at suitable intervals, the contraction-phase following each inhibitory relaxation of the extensor muscle becomes less, and finally unobtainable before extinction of the decerebrate rigidity, and while the inhibitory relaxation of the muscle is still obtainable. Conversely, after chloroform narcosis has been pushed to the extreme of abolishing all reflex reaction, on lightening the narcosis the decerebrate rigidity reappears, and the reflex inhibitory relaxation of the extensors becomes demonstrable at a time when there is still no obtaining of the contraction-phase withdrawal of the inhibitory stimulus, occasioning no rebound contraction of the muscle.

Asphyxial conditions tend, as is well known, to augment some reflex reactions before finally paralysing them. The "flexion-reflex" is, as I have frequently seen in working with the spinal mammal, one of the reactions thus increased by impending asphyxia. It might, therefore, be thought that the appearance of the contraction-phase of the extensors in this reflex was attributable to a super-excitability, due to insufficient aeration of the blood from imperfect respiratory ventilation in the paralysed animal. This is not so; on the contrary, defective pulmonary ventilation and experimental

* 'Journ. of Physiology,' vol. 34, p. 42, 1906.

conditions tending to asphyxia depress the contraction-phase, and, if allowed to continue, soon abolish it.

The possible importance of "successive induction" as a coordinator of reflex actions seems obvious. If a reflex A not only temporarily inhibits a contraction B antagonistic to it, but also induces in the arc of B, as an immediately subsequent result, an excitation, we have a process qualified to link together simpler reflexes, so as to form from them reflex cycles of action such as characterise the reflex play of the limbs in locomotion. In a previous Note it was remarked that a difficulty in thus applying the experimental results then obtained lay "in the intensity and long duration" of the stimuli which have to be employed to produce the "successive induction."* "Such intensity and duration certainly do not occur in the course of the alternating reflexes"† as they occur naturally. The observations brought forward in the present communication remove that difficulty. Rebound contraction from "successive induction" is shown to be elicitable by stimuli of even momentary duration, *e.g.*, a single make or break shock; and still more readily by stimuli lasting even so brief a time as a twentieth of a second. The intensity of electric stimuli that evoke it need not be more than just perceptible to the tongue. Mechanical stimuli as well as electric also readily produce it.

The experiments afford, I think, convincing proof that in both fore limb and hind limb the ordinary "flexion-reflex," as expressed by the extensor muscles, is a diphasic reaction. The first phase is relaxation due to central inhibition, the second phase contraction due to central discharge. The first endures throughout the application of the external stimulus, the second immediately follows the withdrawal of that stimulus, and is due to a central rebound from the state of inhibition to a state of excitation. In the first phase of the reflex the extensor muscles abandon the maintenance of a posture, or the execution of a movement in which they were engaged; in the second phase they restore that posture to the limb, or reinstitute movement in the abandoned direction. The series of reflexes of fig. 8, A and B, is a series of "steps" executed by the limb under the sole action of a main extensor muscle of the knee (*vasto-crureus*). It has been shown‡ that in each reflex of such a series, the flexors§ contract during the application of the stimulus, that is, at and during time of inhibitory relaxation of the extensors.|| There-

* Sherrington, 'Roy. Soc. Proc.,' B, vol. 77, p. 495.

† *Ibid.*

‡ Sherrington, 'Roy. Soc. Proc.,' vol. 52, 1893.

§ For list, see 'Roy. Soc. Proc.,' B, vol. 79, p. 341.

|| For list, *cf. ibid.*, p. 342.

fore, in a series of reflexes such as that of which fig. 8, A and B, shows the extensor muscle's reactions, the active movements of flexion and extension, alternating one with another, do not require alternation of two external stimuli, one evoking flexion, the other extension. Such observations show that one and the same stimulus, intermittently applied, suffices fully for the double phases of the reflex movement. Contraction-phase ensues in the muscle antagonistic to the flexor in each pause of application of the external stimulus. In other words, a neural discharge, due to successive induction, produces after each reflex contraction of the flexor a compensatory contraction of the extensor, bringing the limb back to extension and keeping it there until renewal of the external stimulus again inhibits the extensor, and contracts the flexor. In this case, unlike the "scratch-reflex," the rapidity of succession of the phases of the cyclic reflex is in the hands of the external stimulus. If the rate of intermission of that stimulus is slow, the alternation of the phases of the reflex is likewise slow; if the repetitions of the stimulus follow quickly, the cycle of the reflex proceeds quickly. That is to say, the rate of stepping of the limb depends on the rate of recurrence of the applications of a single uniform stimulus which excites, during each of its applications, one phase of the reflex act, and is followed by the other phase.

Addendum.—December 3, 1907.

(With Herbert E. Roaf, M.D. Toronto.)

(Received December 4, 1907.)

Mention was made in the foregoing* of the possibility that not only complete withdrawal of the inhibitory stimulus, but likewise mere lessening of its intensity, might induce from the inhibited centre fresh motor discharge and consequent contraction of the muscles previously kept relaxed by reflex inhibition. This proves to be actually the case. To obtain this effect under the experimental condition, the reduction of intensity of the external stimulus has had to be considerable, and the reduction has been abrupt. The method adopted has been that followed in studying the influence of the intensity of the external stimulus on the power of the stimulus to break through reflex fatigue.† The resistance of the primary circuit has been suddenly altered by introduction of further resistance of known amount. With the current and inductorium used, no rebound contraction was obtained under our conditions of experiment when the resistance was increased by less than 30 ohms. Fig. 9 shows the effect of abruptly reducing the current

* *Cf.* also 'Journ. of Physiology,' vol. 36, p. 191.

† *Ibid.*, vol. 34, p. 42.

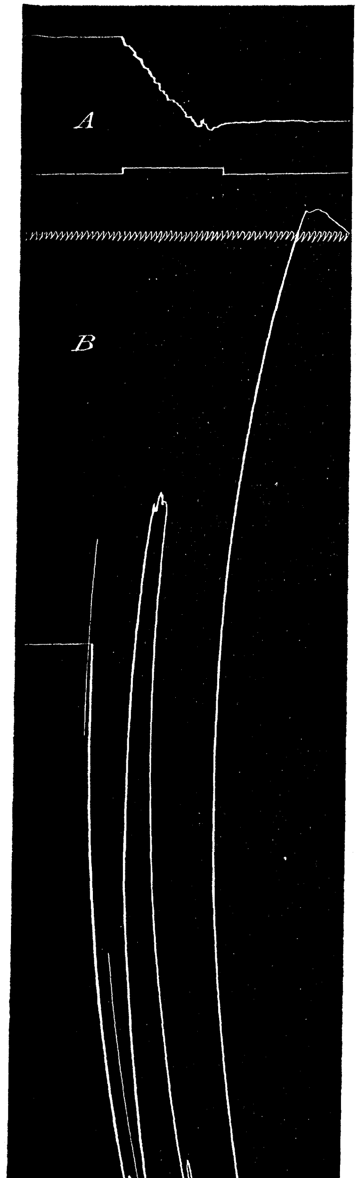

Fig. 9.

in the primary circuit by introducing 40 ohms additional resistance. The upper record (A) in the figure shows the reflex effect of faradisation of the afferent nerve with the secondary coil at 40 units of the Kronecker scale, and with the 40 additional ohms in the primary circuit. The effect is seen to be reflex inhibition, as is evidenced by a slight yet distinct relaxation of the vasto-crureus muscle. The stimulus was, therefore, above threshold value for producing reflex inhibition of the extensor arc. The lower figure opens with the effect of faradisation of the same nerve a minute later with the secondary coil unaltered in position (*i.e.*, 40 Kronecker units), but without the inclusion of the 40 additional ohms in the primary circuit. This stronger stimulus is seen to produce smart reflex relaxation of the extensor muscle. When that has reached its full amplitude and endured for something over a second, the extra 40 ohms are abruptly introduced (by un-short-circuiting them) into the primary circuit, and the faradic stimulus is thus reduced to the intensity it had in the upper trace of the figure, *i.e.*, to an intensity near, but distinctly above, threshold value under the experimental conditions of a minute before. The record shows that those conditions have now undergone a change, for now, instead of a weak inhibition, a strong extensor contraction sets in. This is the rebound contraction, and the change that has altered the conditions has been "successive induction" in the reflex preparation. The rebound contraction exceeds in intensity that obtaining prior to the inset of the original inhibition. The duration of the less intense faradisation, marked by the upper signal line, is continued for about a second, and then by short-circuiting the

additional 40 ohms from the primary circuit, the more intense faradic stimulus is recontinued. The strong inhibitory relaxation of the extensor muscle at once returns. Finally, on discontinuing this, there occurs once more a rebound contraction of the extensor muscle, and this rebound is more intense still. Such observations show that the central rebound from inhibition to super-activity on the part of the reflex arc of the extensor takes place in the face of a weak inhibitory stimulus applied to the arc at the time of the rebound.

The result seems to have bearings of some theoretical importance. Of these one appears as follows. When reflex contraction has proceeded, even for a short while, under the application of a full exciting stimulus a weak excitatory stimulus, which prior to the strong reaction was able to excite the reflex contraction though weakly, loses some of its efficacy and becomes less able to provoke its reflex; in other words, tends to fall below the threshold value and may become subliminal.* Such a change in excitatory reflexes is ascribed to, or rather described under, fatigue effects. In the case of the inhibitory reflex just mentioned, an inhibitory stimulus which, prior to the action of a stronger inhibitory, was able to produce reflex inhibition, fails to do so when repeated after the stronger stimulus has been producing inhibition for a short time. If in the case of reflex excitation, causing contraction, the phenomenon is permitted to rank as fatigue, the similar result observed in reflex inhibition indicates that a similar wearing out or blunting of inhibitory effect occurs, and can, under like terminology, be called fatigue. There is thus emphasised one more of several significant likenesses between the converse processes of reflex excitation and reflex inhibition.

Another bearing of theoretical importance which the observation allows is the following. The flexion reflex is in reality the reflex stepping of the limb, and such stepping is a rhythmic alternating reflex. The observations in the present Note indicate that instead of having to look for two different alternately-acting stimuli wherewith to explain the two successive phases of flexion and extension characterising the reflex, one stimulus (namely, that exciting flexion) is all that may be needed. But that stimulus has to be intermittently applied, extension by rebound contraction occurring in the intermissions of its application. The additional observations in this addendum show that it is not necessary for the stimulus to be actually intermittent; it will suffice if it merely suffer periodic decrements of intensity—provided the decrements exceed a certain amount. In other

* Good instances are seen with the scratch-reflex, *cf.* 'Journ. of Physiology,' vol. 34, p. 1.

words, in this reflex there is developed in the extensor neurones a slight refractory phase, slight because though effectively blocking a weak inhibitory stimulus, it fails before the insistence of a strong one. Thus analogy is at once revealed between this reflex and one superficially very different from it, namely, the "scratch-reflex." In the latter a feature of co-ordination is the occurrence of marked refractory phase. During the progress of the reflex the external stimulus which excites the contraction of the flexor muscles fails to excite them at rhythmically recurring periods owing to supervention of a refractory phase in the spinal centre. And the analogy is the closer since in the "scratch-reflex" the extensors of the limb as well as the flexors contract rhythmically,* and presumably their rhythmic contractions alternate with those of their antagonists. The recurrent refractory phase would therefore not only block the flexor excitatory stimulus, but at the same time block the extensor inhibitory stimulus. This is what it seems to be doing in the "step-reflex." The difference between the two reflexes becomes one of quantity and period rather than any essentially qualitative one.

The facts indicate that the reflex movement of stepping, with its two opposite phases of flexion and extension, can be excited by one single form of stimulus intermittently or even merely unequally applied, that stimulus being the one which directly excites flexion. This suggests an explanation for the striking inequality with which flexion and extension respectively are represented in the receptive field, both deep and superficial, of the limb itself. The direct stimulation, electrical or mechanical (*i.e.*, ligation), of any afferent limb-nerve, whether cutaneous or deep, excites as its immediate result flexion of the limb itself, not extension.† Somewhat similarly, in the motor cortex (especially of the hind limb) the primary representation of flexion greatly preponderates over that of extension. The explanation of

* By appropriate isolation the following muscles in the cat are seen to exhibit the characteristic rhythmic contraction constituting the scratch-reflex—*tensor fasciæ femoris*, *psoas magnus*, *gluteus minimus*, front portion of *gluteus maximus*, *pectineus*, *sartorius*, *semitendinosus*, *tibialis anticus*, posterior portion of *biceps femoris*, *flexor longus digitorum*, *adductor parvus*, *vasto-crureus*, *semimembranosus* and anterior part of *biceps femoris*. Although most of these are flexor muscles, some, *e.g.*, the three last mentioned, are extensors. These three can be seen to contract simultaneously together in the rhythm of the reflex. For the rhythmic abduction which accompanies the rhythmic flexion of thigh in the reflex *gluteus minimus* seems chiefly responsible, since that rhythmic movement persists when all muscles of limb except *gl. min.* have been paralysed by severance of their nerves. This list probably does not exhaust the whole set of muscles exhibiting the rhythmic contraction of the reflex.—C. S. S.

† 'Integrative Action of the Nervous System,' p. 291, 1906; 'Roy. Soc. Proc.,' B, vol. 76, p. 293, and B, vol. 79, p. 337.

this curious inequality may lie in the circumstance that reflex flexion of the limb of itself induces as a sequence to itself extension, so that no local stimulus is, in so far, required for extension. The same argument may also apply to the analogous inequality of jaw opening and jaw closing, both as locally elicitable reflexes and in their primary representation in the "motor" cortex.* At root of the inequality with which movements of opposite direction, forming complemental pairs, are represented, both in the fields of local reflex action and in the "motor" *cortex cerebri*, may lie "successive induction."

Address of the President, Lord Rayleigh, O.M., D.C.L., at the Anniversary Meeting on November 30, 1907.

Since the last Anniversary the Society has sustained the loss of twenty-five Fellows and three Foreign Members.

The deceased Fellows are:—

Thomas Andrews,
Sir Benjamin Baker,
Sir Dietrich Brandis,
Sir William Henry Broadbent,
Dr. Alexander Buchan,
Lord Davey,
Dr. August Dupré,
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The Foreign Members are:—

Marcellin Berthelot, Dmitri Ivanovitch Mendeleeff, Henri Moissan.

* *Ibid.*, and 'Journ. of Physiology,' vol. 34, p. 315.