

The Intrinsic Factors in the Act of Progression in the Mammal.

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I. *Introduction.*

Whilst the act of progression is being performed, the several limbs exhibit rhythmic movements of flexion and of extension. When any limb is in contact with the ground, it extends, and thus serves to propel the animal forwards. At the end of this act the limb is lifted from the ground by a movement of flexion, is carried forward, and finally is again placed upon the ground to repeat the cycle. During these phasic acts the dynamic balance of the neural centres is disturbed by two different kinds of peripheral stimuli.

In the first place, the discontinuous contact with the ground, and the synchronous distortion of the skin of the foot—determined by the weight of the animal then carried in part by that limb—produce changes in the activity of exteroceptive end-organs therein embedded, and discontinuous augmentations and diminutions of the stimuli originated in them.

In the second place, the backward and forward movements of the limb, and the activity of the muscles which execute them, produce changes in the state of the proprioceptive organs situated in the muscles, joints, and tendons which take part in the act.

The act of progression is one richly co-ordinated. Yet it has long been known that movements of the hind limbs, certainly those of progression, may be present in the "late spinal animal." A mechanism confined to the lumbar part of the spinal cord is therefore sufficient to determine in the hind limbs an act of progression, which is probably very nearly a normal one. As reflex movements of the hind limb, exactly similar to movements

integrated in the act of progression, may be obtained by the artificial stimulation of exteroceptive or of proprioceptive end-organs, the suggestion has naturally arisen that the act of progression may be entirely determined by cyclic variations of the stimuli which arise in peripheral sense organs, and are themselves conditioned by the movements which they engender—in other words, that the act of progression is automatic and conditioned by the integration of reflex movements which follow each other successively, and each of which determines the stimulus which calls the following movement into being.

In discussing the nature of progression, Philippson* has laid stress upon the stimulation of the skin as a factor in the determination of the act. Before this, Sherrington† had observed that in the spinal dog and cat, the ipsilateral flexion reflex may be evoked, soon after the trans-section, by pressure so directed upwards upon the pads of the foot that the toe-joints are extended—the stimulus being comparable to the pressure of the ground in progression. But later, when the shock of the operation has passed, the same stimulus will evoke the ipsilateral extension reflex—the “extensor thrust”—if the stimulated limb be in a state of flexion. If it be extended, the reaction is one of flexion as before. Philippson believes that this reflex plays an important part in the mechanism and determination of progression. He supposes that the first contact of the limb with the ground evokes the extensor thrust. This reaction is reinforced by the crossed extension which accompanies the flexion of the opposite limb. These two determine an increase of pressure of the foot upon the ground, and this peripheral exteroceptive stimulus then causes a reflex flexion of the same limb and an extension of the opposite limb, which then is about to come, in its turn, into contact with the ground. The former limb is now flexed and carried forward while the latter is in contact with the ground, and the stretching of the skin thus caused in the inguinal region determines the appearance of extension in the flexed limb. This extension brings the limb on to the ground, where the contact determines the extensor thrust. And so the cycle begins again. On this hypothesis, it is, however, difficult to explain the mechanism of Freusberg's‡ “mark-time” reflex. There the “late spinal” dog, when suspended free from the ground, performs movements of progression with its hind limbs. Philippson thinks that here the crossed extension due to the ipsilateral flexion, combined with the inguinal stretching

* ‘L'autonomie et la centralisation dans le système nerveux des animaux,’ Bruxelles, 1905.

† ‘Roy. Soc. Proc.,’ 1900, vol. 66, p. 66.

‡ ‘Arch. f. d. ges. Physiol.,’ 1874, vol. 9, p. 358.

of the skin and with the action of association paths in the lumbar cord, are sufficient to produce the phenomenon in the absence of contact with the ground.

The difficulty in explaining this phenomenon has been emphasised by Sherrington.* He points out that, in the intact animal (cat, dog), severance of all the sensory nerve trunks directly distributed to all four feet up to and above the wrists and ankles scarcely impairs the act of progression. He also notes that reflex stepping is not annulled, or even obviously impaired, by severance of all the various cutaneous nerves of the limb. And stretching of the prominent fold of skin which runs along the outer edge of the groin cannot be of essential importance in the act, because cocainisation of this region does not interfere with reflex stepping. The extensor thrust may also be abolished—by that division of the sensory nerves of the foot described above—without noticeably changing the acts of the walk and trot. He therefore concludes that the intrinsic stimuli for reflex stepping of the limb are not referable to any part of the skin of the limb.

In continuation of his work on proprioceptive reflexes,† Sherrington finds in the sensory end-organs of the muscles themselves the seat of the intrinsic stimuli for reflex stepping.‡ He considers that the mode of process in reflex walking is as follows: The spinal step is a rhythmic reflex which may be excited by continuous stimuli applied either to the cross-section of the divided spinal cord or to various peripheral points outside the limb itself. The generating stimulus is continuous, but the movement of the limb is determined by the alternate action of two antagonistic reflexes. The primary stimulus sets one of these in action. This act generates in that limb a proprioceptive reflex antagonistic to itself. The proprioceptive reflex interrupts the primary reflex, and in this interruption abolishes the stimulus which engendered itself. The primary reflex is then reconstituted and again calls forth the interrupting reflex, and so on. The secondary reflex is determined by the combination of three main factors—centripetal impulses from the deep structures moved passively by the primary reflex (joints, etc.); centripetal impulses from the muscles which move actively in the primary reflex; and the central change underlying “rebound.” The phenomenon of “reflex reversal” and the “extensor thrust” may also play a part.

Of particular significance is this factor of “central rebound.” Sherrington§

* ‘Journ. Physiol.’ 1910, vol. 40, p. 28.

† ‘Roy. Soc. Proc.’ B, 1908, vol. 80, p. 552; ‘Q. Journ. Exp. Physiol.’ 1909, vol. 2, p. 109.

‡ ‘Journ. Physiol.’ 1910, vol. 40, p. 28.

§ ‘Roy. Soc. Proc.’ B, 1905, vol. 76, p. 160; ‘Roy. Soc. Proc.’ B, 1906, vol. 77, p. 478.

has noted that the flexion reflex, for instance, is often terminated after cessation of the exciting stimulus by an active phase of extension; and that the individual muscles which are in a state of inhibition during the application of the stimulus contract suddenly after its termination. That this phenomenon is not due to a proprioceptive stimulus generated in the muscles which take part in that primary flexion reflex—or at any rate is not solely conditioned by such a stimulus—is shown by Sherrington's observation* that the rebound contraction—"successive spinal induction"—may be obtained in the de-afferented preparation.

Another point of interest and importance is the partial similarity of the act of progression with that of the scratch. Sherrington† has noted this similarity, and the present author‡ has shewn that in the anaesthetised rabbit the one state may immediately follow upon the other, and that there is indication in some cases that the two may blend for a time. This partial similarity is suggestive. Sherrington§ found that in the scratch-reflex the flexion of the thigh did not completely relapse during each brief extension of the phasic act—that there was always a certain amount of maintained flexion. In certain states, as the present author|| was able to shew for the guinea-pig, the two factors in the scratch may be separated. And of these two factors one is a state of maintained flexion while the other is a discontinuous inhibition of that state. In the scratching phenomenon described by the present author¶ as occurring in the guinea-pig under anaesthesia there is an alternation of the state of scratching from one hind limb to the other. At any one time the state of maintained flexion complicated by rhythmic inhibition is accompanied in the crossed hind limb by a state of maintained inhibition of flexion. He has suggested that the rhythmic inhibition during maintained flexion and the maintained inhibition of flexion which immediately succeeds in the same hind limb may be expressions of one and the same activity; and that they may, in effect, be conditioned by variations in the mutual influence of interacting spinal centres. The suggestion in reality is that the locus of the inhibitory factor is central, and that it is not of essential peripheral origin from proprioceptive stimuli. For the scratch this is in accordance with a previous observation of Sherrington** that the

* 'Q. Journ. Exp. Physiol.,' 1909, vol. 2, p. 109.

† 'Journ. Physiol.,' 1910, vol. 40, p. 28.

‡ 'Q. Journ. Exp. Physiol.,' 1911, vol. 4, p. 151.

§ 'Journ. Physiol.,' 1906, vol. 34, p. 1.

|| 'Q. Journ. Exp. Physiol.,' 1910, vol. 3, p. 21; 'Q. Journ. Exp. Physiol.,' 1911, vol. 4, p. 19.

¶ 'Q. Journ. Exp. Physiol.,' 1910, vol. 3, p. 21.

** 'Journ. Physiol.,' 1906, vol. 34, p. 1.

de-afferented hind limb of the cat may be made to scratch. Although this is perhaps not conclusive—in view of the possible influence of stimuli which arise in the opposite hind limb—he and the present author have recently demonstrated at a meeting of the Physiological Society a cat in which scratching may be elicited although both hind limbs have been completely de-afferented.

The phasic alternation of maintained flexion in the scratching phenomenon of the guinea-pig under anaesthesia in many ways resembles the phasic alternation of flexion in the act of progression, and has suggested for some time to the present author that the act of progression may, too, be essentially a central and not a peripheral phenomenon.

II. *Operative Procedure.*

In these experiments the animal used was the decerebrate cat, and the movements of the isolated *tibialis anticus* and *gastrocnemius* were recorded. Before decerebration a loose ligature was placed round the spinal cord at the level of the 11th, 12th, or 13th pair of thoracic spinal roots; and all the posterior spinal roots caudal to, and including, the 6th lumbar root were divided upon the side of the recording muscles. In the limb of that side all the other muscles were put out of action by the severance of their motor nerves or of their substance; there remained in action only the muscles supplied by the branches of the popliteal nerves in the leg, and these, besides having their tendons cut, were de-afferented by the section of the lumbar roots. The long saphenus nerve, a purely afferent one, was left intact for another purpose. In the opposite hind limb all the muscles were de-afferented by the section of their nerves or by the section of their substance; there remained of the nerves of that limb only the long saphenus nerve.

In effect this procedure completely de-afferented the two hind limbs, including the muscles whose movements were to be recorded.

To record the muscular movements the leg was firmly fixed in steel clamps, and the recording muscles wrote upon the myograph by means of light aluminium levers to which their tendons were attached by threads.

An interval of about five hours was allowed to elapse between the end of the operative procedure described above and the experiment about to be described.

It is hardly necessary to state that up to the time of decerebration the animal was kept completely under the influence of the anaesthetic.

III. *Movements of Progression in the Low Spinal Preparation in which the Muscles are not De-afferented.*

Before passing to the consideration of the movements of progression in de-afferented muscles it is well to examine briefly the movements which occur in the same preparation when the muscles have not been de-afferented. The procedure of operation was that described above, with the exception that the lumbar posterior spinal roots were not divided.

When such a decerebrate preparation is rendered a low spinal preparation by the rapid severance of the spinal cord at or about the level of the 12th thoracic segment the recording muscles shew movements undoubtedly those of progression.

Three periods may be distinguished in typical instances of the reaction thus evoked as movement at the ankle.

Immediately after the section of the cord there is a period during which the flexor muscle, *tibialis anticus*, remains more or less in a state of maintained contraction. The maintenance of this contraction is not perfect. There are usually phases of incomplete relaxation. These become more frequent and more complete towards the end of this period, and at its termination the relaxation phases are complete but rather irregular in rhythm. During the first period the extensor, *gastrocnemius*, plays little part, and may exhibit no movement at all. Towards the end *gastrocnemius* begins to exhibit movements synchronous with the relaxations of *tibialis anticus*.

In the second period the movements of the antagonistic muscles are very regular and alternate. The flexor record demonstrates regular phases of contraction separated by regular phases in which the muscle remains relaxed. The extensor record exhibits contractions of the muscle synchronous with the relaxation phases of *tibialis anticus*. These contractions are of rapid initiation and short duration. They seem to commence at the moment in which the movement of the flexor changes from contraction to relaxation, and they resemble the "extensor rebound" observed after the cessation of a state of extensor inhibition.

In the third period of the reaction the movements of the flexor become smaller in extent and appear at greater intervals of time. There is a change in the type of movement of the extensor. The extensor record changes completely in appearance. The muscle tends to remain in a state of contraction, and this is broken by phases of relaxation which are synchronous with, but commence before, the contractions of the flexor.

This third period of the reaction is the terminal one. The movements of the flexor cease. The extensor remains in a state of contraction, still, however,

complicated by phases of relaxation. These finally cease, and the reaction terminates with the extensor in a condition of maintained and unbroken contraction.

IV. *Movements of Progression in the Low Spinal Preparation in which the Muscles are De-afferented.*

When the spinal cord is severed in the same manner in the de-afferented preparation movements of progression may be obtained, and these are similar to the movements observed in the preparation in which the afferent nerves of the recording muscles are intact.

In the record illustrated (see figure) the cord was cut approximately at the point marked X in the figure on the signal line below (X, X also on the two tracings). The first period lasts approximately up to the ordinates marked 1. The upper tracing shews a state of maintained flexion broken by more or less incomplete relaxations of short duration. The contraction of *gastrocnemius* shewn in the lower tracing is unusual. The second period lasts approximately up to the ordinates marked 8. The acts of flexion and extension are very regular. Examination of the ordinates 4, 5, 6, and 7 shews that the commencement of flexion is accompanied by *gastrocnemius* relaxation; the change from contraction to relaxation at the top of the *tibialis anticus* "beat" is accompanied by a contraction of *gastrocnemius*; this does not last up to the point at which flexion recommences. This contraction of *gastrocnemius* strongly resembles the contraction of "rebound." The third period commences at or about the point marked by ordinates 8, and persists up to the end of the record. After the contraction of *gastrocnemius* marked by ordinates 9, the curve begins to rise slowly. This is broken by a relaxation which commences before the *tibialis* contraction marked by ordinates 10. This flexion movement is small, and is not accompanied at its change to relaxation by a contraction of *gastrocnemius*. Thenceforth the *gastrocnemius* tracing exhibits only periods of relaxation synchronous with the *tibialis* contractions, and no rebound contraction. After ordinates 12 the *gastrocnemius* remains in maintained contraction.

The records thus shew the same three periods observed in afferent-present reactions.

In the first period the maintained contraction of the flexor muscle—complicated by more or less incomplete phases of relaxation—is present. This at first has sometimes been accompanied by little or no movement of the extensor; in other cases this latter movement has been present.

The second period seems to be characterised by a greater regularity than is usual in preparations in which the afferent arcs are unbroken. The movement

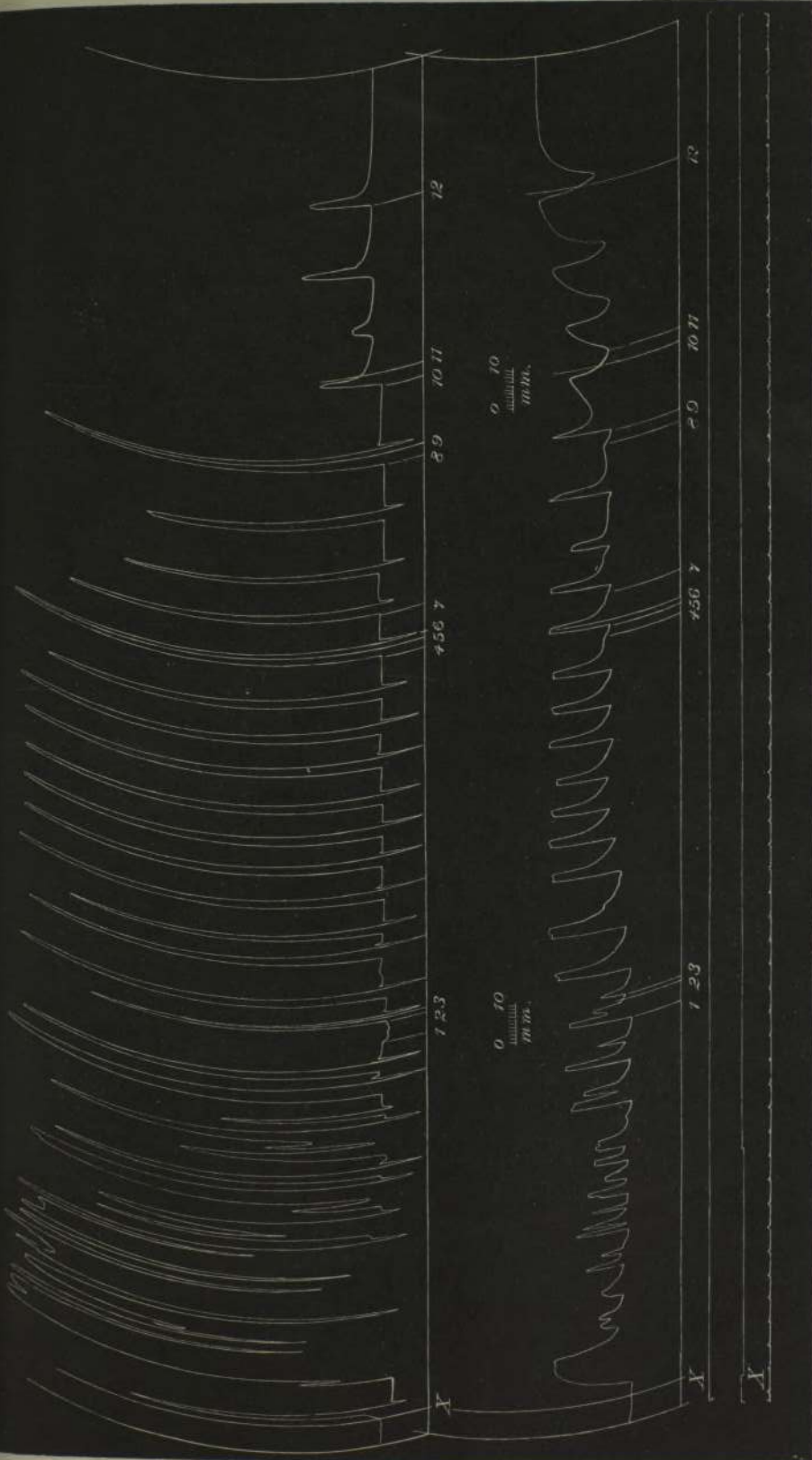
Tibialis
anterior.Gastro-
cnemius.Signal,
Seconds

FIG. 1.—Decerebrate cat, June 19, 1911. Recording muscles de-afferented and paralysed, and all others de-afferented and paralysed. Record of movements of progression as evidenced in *tibialis anterior* (upper tracing) and *gastrocnemius* (lower tracing) upon cutting the cord completely across between the levels of origin of the twelfth and thirteenth pair of thoracic spinal roots. The cord was cut six and a half hours after the decerebration. In the tracings the rise of the curve denotes contraction, the fall relaxation; the record is to be read from left to right; seconds are marked below; ordinates, marked 1, 2, 3, etc., mark corresponding points in the two tracings; and millimetre scales have been reduced in proportion with the record.

of the extensor is strongly reminiscent of rebound contraction. It does not persist for the whole of the duration of the synchronous flexor relaxation, but relaxes soon. There is then sometimes an additional relaxation synchronous with the contraction of the flexor. The termination of this flexor contraction is then succeeded by the extensor contraction—and so on.

In the third period of the reaction the rebound-like contraction of the extensor disappears and is replaced by a condition of maintained contraction which is broken by relaxations synchronous with the flexor contractions. These are much smaller than before and gradually disappear. The transition of the type of flexor contractions is sometimes sudden. The period finally ends with a maintained and unbroken contraction of the extensor.

It may be said that there is no great difference between the movements of progression as evidenced in the de-afferented muscles and those not de-afferented. The greater regularity of the movements as observed in the former preparation may possibly be due to the absence of the peripheral part of the mechanism. But it is also possible that the difference is an accidental one; for records as regular have been obtained from the preparation in which the muscles are not de-afferented, although the average regularity is less.

V. *Conclusions.*

These experiments show that the *phasing of the acts of progression is determined neither by the peripheral skin stimuli nor by the self-generated proprioceptive stimuli of the muscles which take part in them.*

The section of the spinal cord generates an arrhythmic stimulus. This causes the contraction of certain limb muscles. In the preparation used, of these the recording muscles are the only mobile parts of the two limbs. The characteristic alternating contraction of the two antagonists cannot be determined by their own contraction and the consequent setting up of a series of refractory phases in the activity of the centres by means of the stimulation of a sensory apparatus contained in the muscles, because the afferent nerves which arise in these muscles were put out of action in the preparation used. Not only must the locus of the changes which condition the refractory phase of progression be in the spinal cord, but *the mechanism which determines them must also be central.*

There are, therefore, two points of interest in connection with the mechanism of progression—the question of the nature of the central changes in activity, and the question of the part played in the act by the proprioceptive mechanism. The stimuli which arise in the skin probably play but a small part in the act, and then are of importance only in certain of its types and not in all.

The evidence given by the records throws some light upon the problem of the nature of the central activities. In a typical example there is first a period in which a state of maintained flexion, although a broken one, is the predominant feature. The terminating period of the reaction is one characterised by maintained extension—at the end unbroken. Between these there lies a period in which the phasing of the act is most perfect. This period—lying as it does intermediate between those of maintained flexion and of maintained extension—may be regarded as a period of balance.

Any hypothesis regarding the nature of the central activities must at present be tentative, but this appearance of "balance" supports a view put forward by the author in previous papers.* As regards the act of progression the central mechanism may be regarded as consisting of antagonistic centres. In one hind limb it may be supposed that the one of these determines a state of maintained flexion and a concomitant state of maintained inhibition of extension, while the other determines a state of maintained extension and a concomitant state of inhibition of flexion. It is inessential at present whether the lumbar centres are two in number and situate in opposite sides of the spinal cord; or whether they are four in number and situated in antagonistic pairs on each side of the cord; or whether they are more than four in number.† All that it is desired to insist upon here and now is that the centres are paired, and that each pair consists of antagonistic opposites.

If this be granted, and if there be presumed some such state as "fatigue"—in its broadest sense—accompanying the expression of activity of either of the antagonistic centres, it is possible to frame a tentative hypothesis of the nature of the central changes which condition the phasic act of progression.

It may then be supposed that some neural disturbance rearranges the conditions of activity of the antagonistic centres in such a manner as to destroy their balance. The one centre then expresses its activity in a movement—for example, flexion—of the limb, and at the same time inhibits the activity of its antagonistic centre. But this expression of activity is accompanied by a state of "fatigue," which progresses in extent and tends to restore the balance of the centres. At the same time the inhibition of

* 'Q. Journ. Exp. Physiol.,' 1910, vol. 3, p. 21; 'Q. Journ. Exp. Physiol.,' 1911, vol. 4, p. 19.

† For instance, there may be antagonistic factors (contraction and relaxation producing) in one and the same centre. Thus the activity of such a centre as that for *tibialis anticus* might be exhibited either as contraction or as relaxation of the muscle.

the other centre by the first decreases in efficiency. The point then arrives when the second centre is no longer inhibited efficiently. But there is then following upon the inhibitory depression an exaltation of its activity—"rebound." The balance is therefore not only regained but overshoot. The exhibition of activity by the second centre then determines the contraction of the antagonistic group of muscles, and at the same time there is an inhibition of the activity of the first centre. The "fatigue" which accompanies this activity of the second centre then sets in. The balance is restored, but again overshoot. And so the act proceeds.

The phenomenon of rebound, which Sherrington* has shewn to be of central locus, may play a very important part in the swinging of balance between the spinal centres. And the phenomena which underlie the phasic act of progression may be likened to the beating of a pendulum. The activity exhibited may remain for a time flexion, may then swing back to the neutral point of spinal balance, but may overshoot this and become extension activity, may then swing back past the neutral point into flexion activity—and so on.

There remains the question of the part played by the proprioceptive mechanism in the act.

There can be no question of its importance nor of its suitability to augment the central mechanism. It cannot, however, be regarded as determining the refractory phases in the act. Its part must be regulative, not causative.

A purely central mechanism of progression ungraded by proprioceptive stimuli would clearly be inefficient in determining the passage of an animal through an uneven environment. Across a plain of perfect evenness the central mechanism of itself might drive an animal with precision. Or it might be efficient, for instance, in the case of an elephant charging over ground of moderate unevenness. But it alone would make impossible the fine stalking of a cat over rough ground. In such a case each step may be somewhat different to all others, and each must be graded to its conditions if the whole progression of the animal is to be efficient. The hind limb, which at one time is somewhat more extended in its posture as it is in contact with the ground, in another step may be more flexed. But the forward thrust it gives as its contribution to the passage of the animal must be of a comparatively uniform degree in each consecutive step. It may only be so if it is graded by the posture of the limb when in contact with the ground, and by the duration of its contact with the ground. This grading can only be brought about by peripheral stimuli. Of these we must regard

* 'Q. Journ. Exp. Physiol.,' 1909, vol. 3, p. 109.

the proprioceptive stimuli from the muscles themselves as the most important, and *the part which they play is essentially the regulative—not the causative.*

This work has been done during the tenure of a Carnegie Fellowship, and the expenses of the research have been defrayed by a grant from the Carnegie Trust.

Summary.

1. By means of a stimulus (namely, section of the spinal cord) central in application, although remote from the local centre, the act of progression may be induced in muscles de-afferented by the cutting of their appropriate posterior spinal roots. It occurs thus after all the muscles of both hind limbs have been de-afferented, and all but the recording pair have been put out of action by motor paralysis.

2. The act of progression as exhibited by these muscles and thus induced scarcely differs, if indeed it differs at all, from the act similarly induced when the afferent arcs of the recording muscles have not been broken.

3. In either case the reaction, as evidenced in movement at the ankle-joint, shews three periods. In the first the record is characterised by a state chiefly of maintained flexion. In the last there is a state characterised by maintained extension. Intermediate between these there is a period of "balance," in which the movements of progression are most perfect.

4. *The rhythmic sequence of the act of progression is consequently determined by phasic changes innate in the local centres, and these phases are not essentially caused by peripheral stimuli.*

5. *The proprioceptive stimuli which are generated by the contraction of muscles taking part in the act (when the appropriate posterior spinal roots are intact) play a regulating and not an intrinsic part in the act. Their chief importance may be in the grading of the individual component movements to the temporary exigencies of the environment.*
