On Reciprocal Innervation of Antagonistic Muscles. Twelfth Note.—Proprioceptive Reflexes.

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The following two reactions, observable in the extensor muscle of the knee, appear not without importance for the reflex co-ordination of antagonistic movements at that joint. They are reactions favourably studied in decerebrate rigidity. The cat is the animal in which, under that condition, my results have been chiefly obtained.

The reactions can be observed as follows:—In the decerebrate animal a preparation of the extensor of the knee is so made that by detachment of other muscles, or severance of other nerves, the vasto-crureus muscle, with its nerve-branch from the anterior crural trunk, remains the sole nerve-muscle component intact in the whole limb. The vasto-crureus is one of those muscles which, after decerebration, exhibits the marked tonus characteristic of decerebrate rigidity. This tonus of the vasto-crureus then maintains the knee in an attitude of partial or complete extension. The flexor muscles of the knee, together with all the other muscles acting on that joint, have been paralysed by section of their nerves.

I. If the nerve of one of the flexors, *e.g.*, of semitendinosus, be now faradised distal to its place of severance, the stimulation of the motor fibres in it causes contraction of the flexor muscle, the knee is consequently flexed; the flexor muscle, by its stronger contraction, bends the knee in spite of the tonic contraction going on in vasto-crureus, the extensor muscle. On discontinuing the faradic stimulation of the motor nerve of the flexor, the flexor muscle, of course, ceases to contract. It is then seen that, although the flexor is no longer acting, the knee still continues to remain flexed. In other words, the tonic contraction of the extensor of the knee, which prior to the contraction of the flexor kept the knee extended, ceases to do so after the movement of knee-flexion has been executed. Evidently the forced stretch given to the knee-extensor by the contraction of its antagonistic muscle has produced some change in the tonic condition of the knee-extensor. It has been previously shown* that centripetal impulses from the knee-flexor can cause a reflex inhibition of the knee-extensor. But in the experiment now described no centripetal impulse from the knee-flexor can have caused the

* Sherrington, 'Roy. Soc. Proc.,' vol. 52.

effect, because the nerve of that muscle had been severed above its place of stimulation; indeed, all the nerves of the limb had been severed except only that of the vasto-crureus (extensor muscle) itself.

The result, therefore, if traceable to centripetal impulses, is traceable to some among them which have their origin in vasto-crureus itself. In accord with this one finds (fig. 1, *L.r.*[1]) that on simply taking with the hand the desensitised limb below the knee, and gently but firmly flexing the tonically

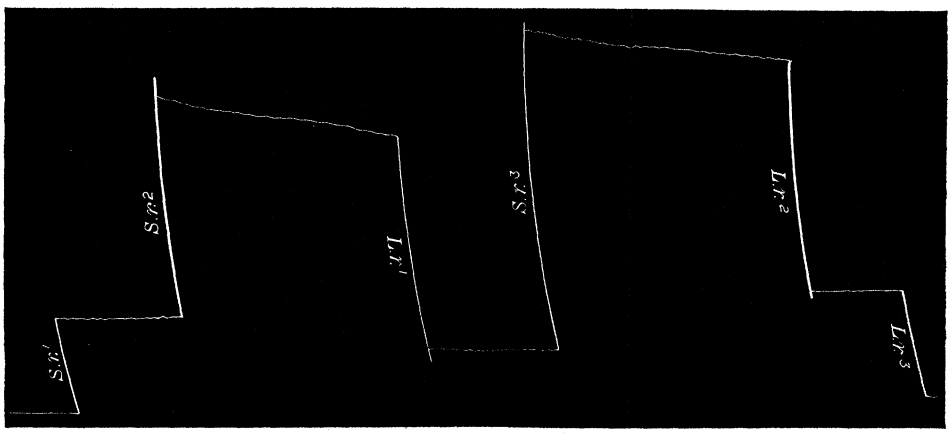

FIG. 1.

extended knee, the same result is obtained as that just described when the knee is bent by the flexor muscle. The forced movement, as executed by manipulation, experiences resistance from the tonic contraction of the extensor (vasto-crureus), but as the flexion movement is executed this resistance somewhat abruptly lessens almost to vanishing; on then discontinuing the forced flexion the limb is found to remain practically where the forced movement (figs. 2A, 4A, *L.r.*) had carried it. In short, the extensor muscle, in result of a forced stretch, assumes in permanence a new tonic length. This reaction of the extensor may, for brevity, be termed the "lengthening reaction."

The tonus exhibited by the extensor in decerebrate rigidity has been shown to be reflex in nature,* and to depend on afferent nerve-fibres arising in the extensor muscle itself.† The lasting increase in the tonic length of the muscle brought about by stretching it appears to be likewise reflexly produced. Evidence indicating this is as follows:—(1) The lengthening reaction is not obtained after severance of those afferent spinal roots through which pass the afferent nerve-fibres proceeding from the muscle (vasto-crureus) itself. (2) Together with the "lengthening reaction" of the extensor, itself stretched,

* Sherrington, 'Journ. of Physiology,' vol. 22, 1898.
† *Ibid.*

there is excited by the stretch a contraction in the extensor of the crossed knee. (3) There exist in the nerve of vasto-crureus afferent fibres which, under mechanical and electrical stimulation, cause relaxation of the vasto-crureus muscle itself.* (4) The increase of tonic length of the vasto-crureus muscle induced by the stretch is sometimes, under conditions favourable to

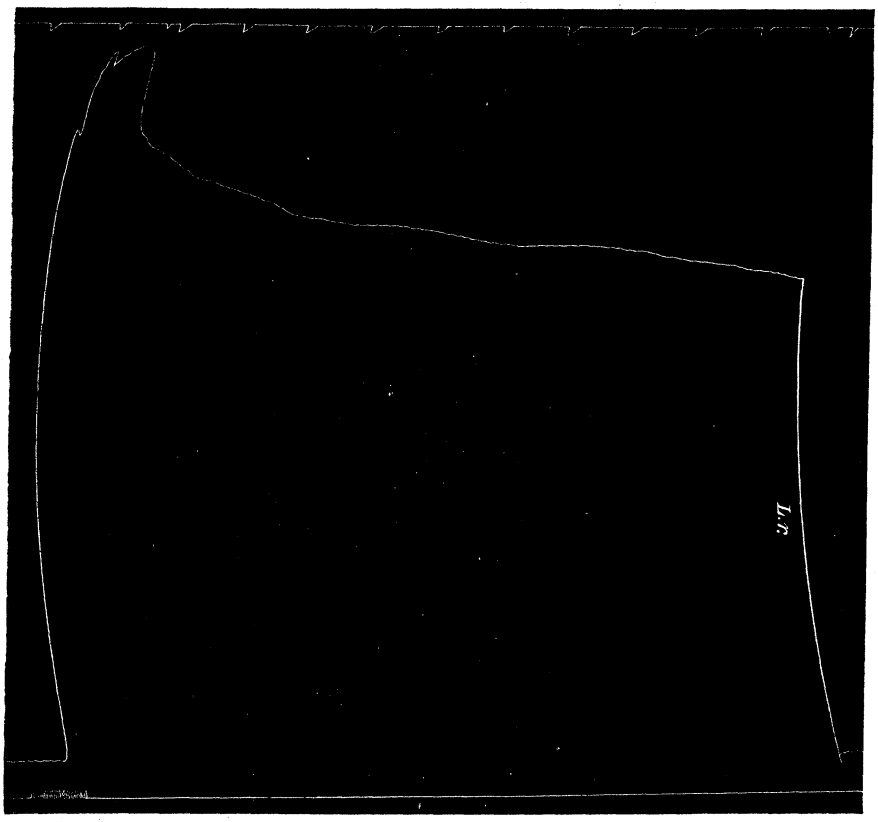

FIG. 2A.

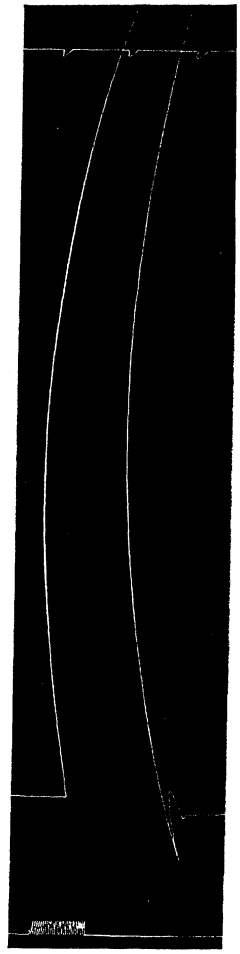

FIG. 2B.

reflex rebound† (successive spinal induction), followed by increased contraction of the muscle, just as is reflex inhibitory relaxation caused by afferent nerves known to act inhibitorily upon it. (5) Strychnine annuls the lengthening

* Sherrington, 'Roy. Soc. Proc.,' B, vol. 77, 1906.

† Sherrington, 'Roy. Soc. Proc.,' B, vols. 76 and 77; 'Journ. of Physiology,' vol. 36, p. 185.

reaction of vasto-crureus, as it annuls likewise other inhibitory relaxations of that muscle known to be reflex in nature.*

It appears, therefore, that the "lengthening reaction" of the extensor of the knee is a reaction excited by forced stretch of the muscle acting on the reflex tonus through receptive nerves arising in the muscle itself.

II. There is similarly observable in the decerebrate extensor muscle another reaction practically the converse of the foregoing. Suppose that in the limb of the decerebrate animal, prepared as above, the knee, in consequence of the "lengthening reaction" just described, is remaining flexed. Suppose, then, some skin-surface or afferent nerve appropriate for evoking reflex extension of the knee is stimulated either mechanically or by faradisation. The vasto-crureus, isolated as above, contracts, and in consequence the knee is extended. After cessation of the application (figs. 2 and 3, A) of the stimulus, the knee, instead of falling back into flexion, remains extended, and may remain so for many minutes. Light is again thrown on the nature of this persistence of the extensor effect by comparing with it the effect of passive manipulation of the limb. Suppose that, as before, the limb starts with its knee flexed. Then if the observer simply take the desensitised limb below the knee, and move it with his hand into a posture of extension at knee, on his releasing the limb the knee does not drop back into the flexed posture; it retains almost to the full the new extended posture given it by the manipulation (fig. 1, *S.r.*). Passive approximation of the ends of insertion and origin of the vasto-crureus has caused that muscle to assume a new tonic length, shorter than it exhibited before.

This same lasting change in the tonic length of the muscle results whether the initiatory approximation of the ends of the muscle be made by passive manipulation or by active contraction of the muscle itself. The maintenance of the extended knee-posture which follows a reflex contraction of vasto-crureus presents the same characters as the maintenance of posture following a simple passive lift of the knee. If during the application of the exciting stimulus, and for a second or two longer, the knee which the reflex would extend be mechanically prevented from extending, it does not on release assume the extended posture. Prevention of the shortening of the muscle in the first stage of the reflex prevents the occurrence of the long-maintained extension after-effect of the reflex, although that usually endures for minutes.

The conclusion indicated is, therefore, that the shortening of the muscle, produced either actively or passively, induces it to assume in relative

* Sherrington, 'Roy. Soc. Proc.,' B, vol. 76, 1905.

permanence a new tonic length shorter than that which it had previously. This reaction may for brevity be termed the "shortening reaction."

This reaction appears on grounds very similar to those advanced in regard to the "lengthening reaction" to be reflex, and to be traceable to reflex arcs arising in the muscle itself. (1) The "shortening reaction" of vasto-crureus is not obtained after severance of those afferent spinal roots through which pass the afferent nerve-fibres proceeding from the vasto-crureus muscle.

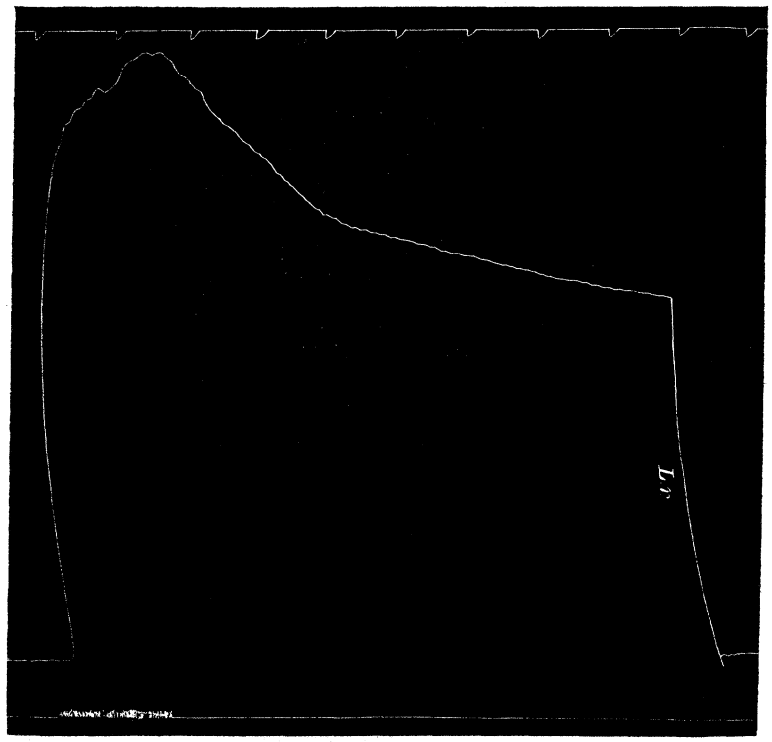

FIG. 3A.

Passive manipulation then fails altogether to elicit it. Where the afferent spinal roots of one vasto-crureus had been cut 20 to 80 days prior to comparing the reflexes from the two vasto-crurei in the decerebrate animal, the reflex contractions exhibited by the vasto-crureus with afferent fibres cut (fig. 2B, fig. 3B, fig. 4B) showed nothing of the long maintained tonic after-contraction exhibited by the fellow muscle whose afferent fibres still remained intact (fig. 2A, fig. 3A, fig. 4A). Reflex contraction of the muscle with its afferent nerve-fibres cut is, therefore, when evoked by slowly repeated stimuli, more clonic than is that of the muscle with its afferents intact (fig. 5, A and B).

(2) Among the afferent nerve-fibres proceeding from vasto-crureus are some which can evoke and maintain reflex tonic contraction of the muscle itself. That seems proved by the dependence of the decerebrate rigidity of this

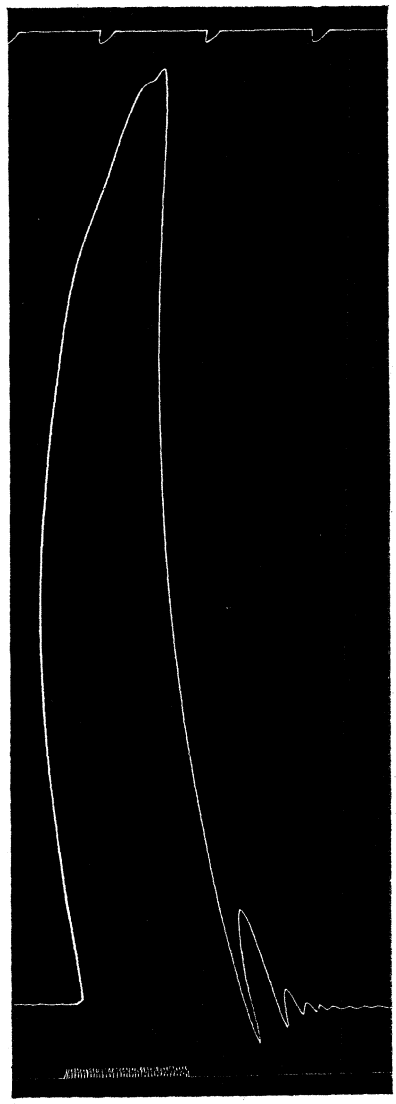

FIG. 3B.

muscle upon the afferent fibres of the vasto-crureus nerve.* (3) When the "shortening reaction" is elicited in the decerebrate animal it is in some

* Sherrington, 'Journ. of Physiology,' vol. 22.

experiments accompanied regularly by inhibition of reflex contraction of the crossed vasto-crureus. This can be well seen in the double vasto-crureus preparation, the animal being inverted and the extension of knee maintained by vasto-crureus against the weight of the limb below the joint; the occurrence of the "shortening reaction" in one vasto-crureus is then followed by the dropping of the opposite knee into flexion. This crossed inhibition,

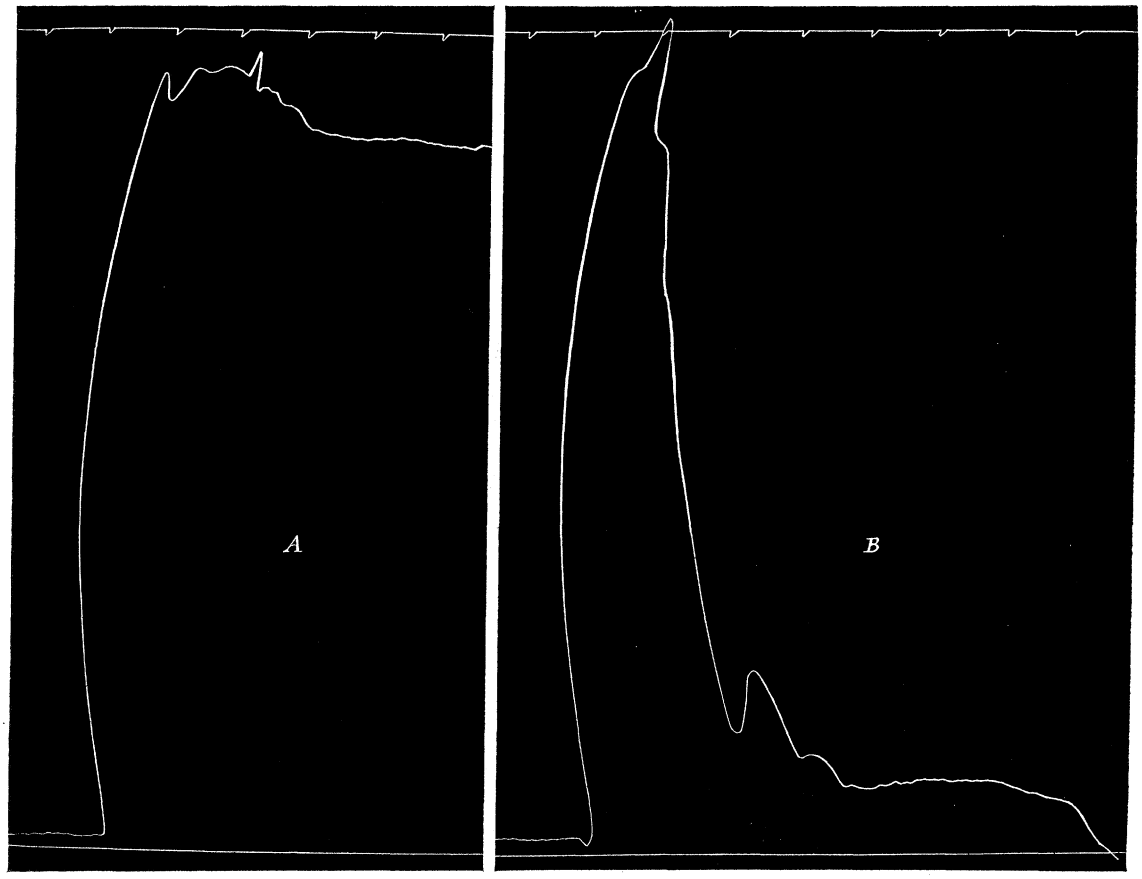

FIG. 4.

which obviously must be reflex, accompanies the elicitation of the "shortening reaction."

The evidence seems to warrant the conclusion that in the rigidity of the decerebrate vasto-crureus muscle the tonus of the reflex arc which maintains the rigidity of the muscle is regulable in two opposite directions by reflex influences which can be started from the muscle itself. Regulation in one direction is shown by the "lengthening reaction," which is a reflex excited by

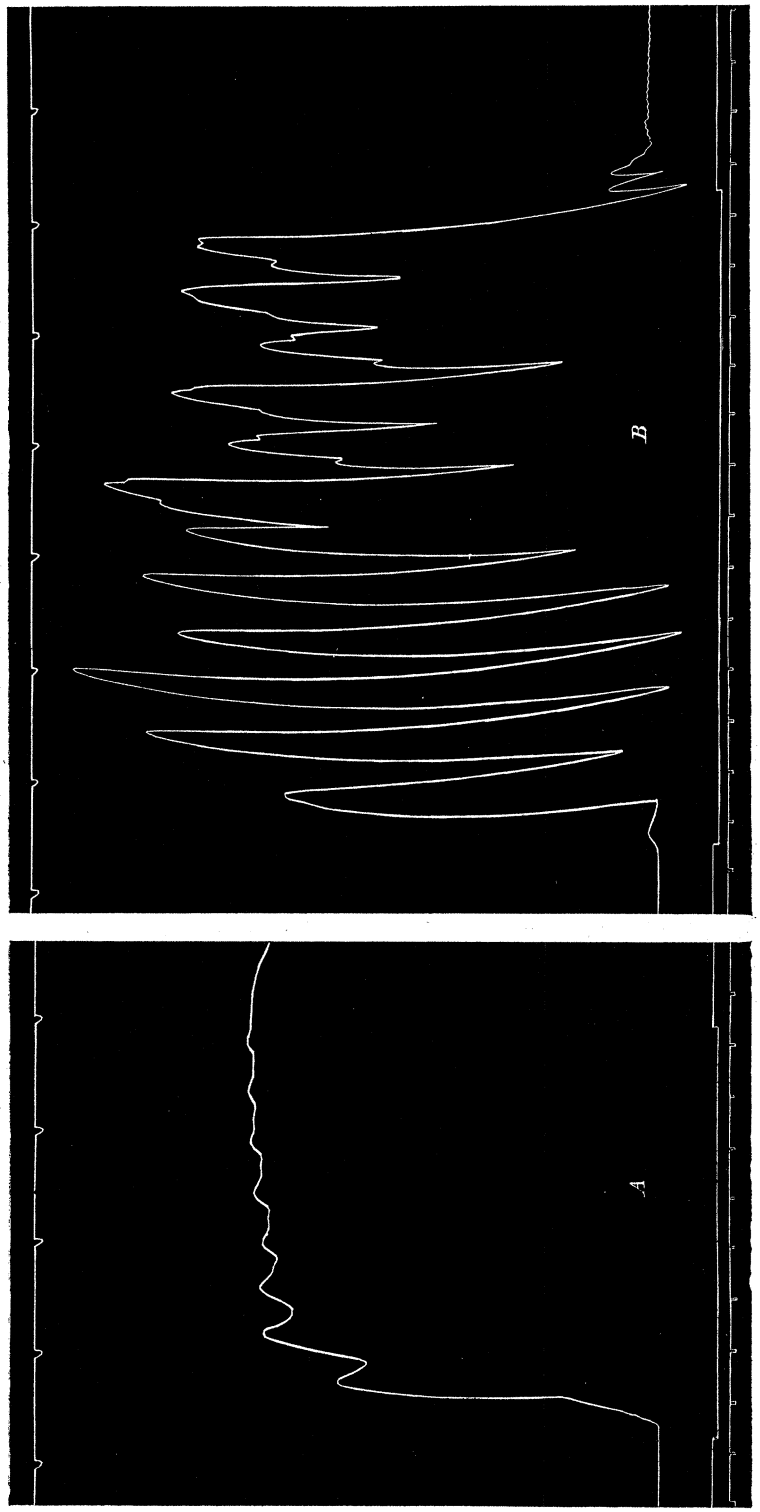

FIG. 5.

stretching the muscle; regulation in the other direction is shown by the "shortening reaction" which is a reflex initiated by approximating either passively or actively the ends of the muscle. By these means there is conferred upon the tonus of the extensor muscle a quality of plasticity. This plasticity enables the tonus to serve as an adjuvant to the reflex contraction of the muscle and also to assist the control of the muscle by its antagonist in the play of opposed movements succeeding each other at the joint upon which both muscles act.

III. The "lengthening reaction" and "shortening reaction" are readily studied in the vasto-crureus preparation above mentioned, but they are also well observable in other muscles exhibiting the rigidity of the decerebrate condition. If the preparation of the hind limb be modified so as to yield a gastrocnemius or soleus preparation, both reactions are evident in those extensors of the ankle. The preparation affords opportunity for determining a point less easily resolved by the vasto-crureus preparation. The nerve of vasto-crureus is credited with supplying a twig to the knee-joint and the question arises whether afferent nerve-fibres from the joint are not responsible for initiating the reactions described. To answer this, the isolation of the vasto-crureus from the knee-joint is required. When this is done, I find the reactions still obtainable. The afferents from the joint are therefore not essential for the reactions; they may, however, be contributory to them. In the case of the nerves to gastrocnemius and soleus, these do not supply twigs to either knee or ankle joint. The obtaining of the lengthening and shortening reactions in the gastrocnemius-soleus preparation shows, therefore, that in this case articular afferent nerves are not even contributory to them.

The "lengthening" and "shortening" reactions are also observable in the extensor muscles of both the shoulder and elbow; probably they are so also in the extensors of the neck and tail and the retractors of the head.

IV. These reactions observable in decerebrate rigidity are also obtainable after spinal transection in the dog. The extensor muscle of the knee exhibits considerable tonus in the dog after spinal transection in the thoracic region when time is allowed for subsidence of the spinal shock immediately consequent on the operation. In the knee-extensor of the spinal dog the "lengthening reaction" is easily obtained, and it is then more regularly than in the decerebrate cat accompanied by crossed extension at the opposite knee. The crossed extension of the opposite knee induced by passive flexion of the other knee has been observed by Philippson* in his spinal dogs and has been

* 'Travaux du Laboratoire de Physiologie, Institut Solvay, Bruxelles,' published by P. Heger, vol. 7, part 2, p. 31, 1905.

termed by him "crossed reflex III." The "shortening reaction" in the knee-extensor of the spinal dog is in my experience also readily evoked. To evoke it, the animal may be held up under the shoulders with the hind limbs hanging freely and the knee then gently raised by lifting it from under the lower end of that joint. This somewhat flexes the hip and extends the knee. A strong tonic contraction of the knee-extensor at once sets in and is usually long maintained. This reaction is frequently though not regularly accompanied by a movement of flexion at the crossed knee.

There is another crossed reflex, well seen in the spinal dog, which bears resemblance to the two just mentioned. A movement of extension of one hip causes a movement of flexion at the crossed hip. To evoke this all that is necessary when the dog is supported as described above is to allow one of the thighs to drop into extension. The opposite hip flexes almost immediately the extension of the other commences.

V. The reflex tonus of these skeletal muscles of the cat and dog is thus seen in these observations to be adjusted by a regulation which conforms, at least in regard to the results it ensures, with features observed by v. Uexküll in the tonus of the musculature of Echinus, Ophioglypha, and Sipunculus. v. Uexküll showed that in those cases stretching the muscle lessens the tonus in it. "Stretching brings about a fall in the tonus of the muscle; the stretched muscle has a lower level of tonus than the unstretched.* When an unstriped muscle is stretched it follows the stretch readily. When the stretch is removed the muscle does not quickly return to its previous length. It exists, therefore, after removal of the stretch, in a different state of excitation from before the stretch. For although it once more is loaded only with its own weight, it is nevertheless longer than before."† v. Uexküll assumes, if I follow him rightly, that a shortened condition of the muscle evidences greater tonus, a lengthened condition less tonus. That may be so, but at present I hesitate to assume it. Apart from this, which seems a difference rather of interpretation than of fact, this description quoted here from v. Uexküll applies fully to the case of the vasto-crureus in decerebrate rigidity. And v. Uexküll's observations on this feature of the tonus of muscles in Echinus, etc., have been found by other experimenters to hold good in the unstriped muscles of various other Invertebrata and in the unstriped muscles of various viscera in Vertebrates.‡ With this feature of behaviour of the tonus in unstriped muscle that of the tonus of the extensor muscles in the spinal dog and in the decerebrate cat conforms.

* 'Ergebnisse d. Physiol.,' part 2, 1904, and 'Zeitschr. f. Biolog.,' vols. 44 and 46.

† *Ibid.*

‡ *Cf.* Grützner, 'Ergebn. d. Physiol.,' part 2, 1904.

VI. These reactions and the other accessory crossed ones dealt with above belong, evidently by the mode of their elicitation, to that class of reflexes which have been termed *proprioceptive*. By proprioceptive reflexes are meant reflex reactions excited habitually by the organism acting as agent upon itself through its own organs applied as stimuli to its own nerves. In proprioceptive reflexes the organism applies itself as a stimulus to itself. By its own act, and in its own substance, it excites one or more of its own receptor organs. Other reflexes—and they form the major part of reflex action—are excited by environmental change acting through some environmental medium which impinges directly on the receptors of the organism. But the case of, for instance, the bending of the knee, regarded as an exciting stimulus, is different from those. In it the organism, by executing a movement of a part of itself, supplies by the alteration of the condition of that part a stimulus to certain reflex arcs, proprioceptive arcs arising in that part. The reaction thus excited from these arcs is causally related less directly to the environment than are reflexes excited immediately by the surrounding world; the proprioceptive reaction stands in secondary relation to an environmental cause. It is obvious that proprioceptive reflexes may be competent to extend and complete reflex actions, and cycles of reflex action, initiated primarily by environmental stimuli. They thus prolong, by intrinsic proprioceptive action, actions initiated by environmental stimuli of even transient operation.

It was pointed out elsewhere* that proprioceptive reflexes tend to be characterised by certain features: (1) to be tonic; (2) to ally themselves with, and reinforce other reflexes, exteroceptive and interoceptive; (3) to restore a posture which a phasic reflex has disturbed, and thus to contribute toward reinstating a previous reflex equilibrium which had been departed from, *i.e.*, to be compensatory. The reactions described in this note bear out and illustrate these proprioceptive functions. They are tonic. They tend to ally themselves to other reflexes. Taking the case of the extensor of the knee, suppose some environmental stimulus, impinging on the standing animal, impels it to take a step. The flexor of the knee, thrown into contraction, bends the knee; by so doing it stretches the knee-extensor and excites from it a proprioceptive reflex of relaxation (the "lengthening reaction"). This proprioceptive reflex of the knee-extensor is adjuvant to the contraction of the knee-flexor. Then, the phase of knee-flexion having passed, the phase of knee-extension sets in (induced perhaps by successive spinal induction); the knee-extensor contracts and the knee-flexor ceases to contract. The contraction of the knee-extensor shortens the extensor muscle,

* Sherrington, 'Integrative Action of the Nervous System,' London, 1906, chaps. 4 and 9.

and by so doing excites in it a proprioceptive reflex (the "shortening reaction"), reinforcing and subsequently maintaining its own contraction. The step has been taken, and both to the taking of it and to the resumption of it anew and to the ensuing maintenance of the standing posture, important contribution has been made by proprioceptive reflexes of the extensor muscle itself.

EXPLANATION OF FIGURES.

FIG. 1.—Vasto-crureus preparation; decerebrate cat. The base line shows the position of the leg when the knee is flexed. The first rise at $S.r.^1$ is due to lifting the leg below the knee into a less flexed position, and the horizontal line running to the right from that point shows the maintenance of the new posture by the tonus of vasto-crureus. The second ascent at $S.r.^2$ is due to a second passive lift of the leg below the knee; the horizontal line running to the right shows the increased degree of extension of the knee now maintained by the tonus of vasto-crureus. At $L.r.^1$ the knee was passively flexed nearly as far as the original degree of flexion, the horizontal line running to the right shows that the knee is now again maintained by the vasto-crureus in the new posture of flexion. The ascent of the line at $S.r.^3$ is again due to a passive extension of the knee; the horizontal line running to the right from near the top of the ascent shows the maintenance of the new extended posture of knee by the tonus of vasto-crureus. The descent $L.r.^2$ is due to a forced flexion of knee, and the horizontal line from its base indicates the maintenance of the new position of flexion by the tonus of vasto-crureus once more. The descent $L.r.^3$ marks a further forced flexion of the knee, bringing the knee to about the same degree of flexion as that from which it originally started; the final horizontal line shows how the tonus of vasto-crureus maintains the limb once more at this level. $S.r.^1$, $S.r.^2$, $S.r.^3$: "shortening reactions"; $L.r.^1$, $L.r.^2$, $L.r.^3$: "lengthening reactions." During the execution of each passive movement the recording surface was not allowed to travel.

FIG. 2.—Crossed reflexes produced in vasto-crureus by faradic excitation of the central end of the cut peroneal nerve of the opposite limb. Time marked above in seconds. Signal below marking the moment of application and the duration and frequency of repetition of the faradic stimulus. In A the record is from the left vasto-crureus, the afferent spinal roots through which pass the afferent fibres of the vasto-crureus nerve being intact; in B the record is from the right vasto-crureus, the afferent spinal roots of its nerve having been severed 30 days previously. A and B are both from the same animal and experiment and were taken within five minutes of each other. The tonic after-continuance of the reflex seen in A is absent from B. At *L.r.* in A the movement of the recording surface was stopped and the extended knee was forcibly flexed and then released; the recording surface was then allowed to proceed and the horizontal line of the tracing shows that the new length passively given to vasto-crureus was now maintained ("lengthening reaction"). If the "lengthening reaction" had not been made, the tonic after-continuance of the reflex would have gone on, probably for some minutes. Time marked above in seconds.

The intensity and duration of the faradic stimulation was practically the same for both reflexes: a 100,000 ohms resistance was in the secondary circuit in both cases.

In the reproduction of the records in the figures the reduction of size has been greater in A than in B; this difference can be judged from the time line.

FIG. 3.—Crossed reflexes produced in vasto-crureus by faradic excitation of the proximal stump of the cut popliteal nerve of opposite limb. Time in seconds above : below is signal line giving duration of the faradic stimulus. The intensity of the stimulus is the same for A and for B. A is the reflex contraction of the left vasto-crureus, B that of the right ; the spinal afferent roots containing the afferent fibres of the right vasto-crureus nerve had been cut 42 days previous to decerebration and examination of the reflexes. In B the tonic after-continuance of the reflex is wanting ; on cessation of the stimulus the muscle at once relaxes completely and its slackness is indicated by the vibratory swing at its return to the base-line. In A, on cessation of the stimulus, a tonic after-contraction similar to that of the "shortening reaction" succeeds the contraction caused by the exciting stimulus itself. This was allowed to continue for 8 secs. and then the recording surface was stopped and the muscle was (*L.r.*) forcibly stretched by hand to about the length it had at first before the reflex and then released ; the recording surface was then started again and the lever traced a horizontal line at the original level, showing that the "lengthening reaction" (*L.r.*) had taken place.

In order to make the comparison fair in regard to intensity of faradic stimulus the distance between the electrodes was in both cases the same, *i.e.*, 5 mm., and the nerve-trunk was drawn between the poles ; the distance of the secondary spiral from the primary was the same for both stimulations, and a 100,000 ohms resistance was in the secondary circuit. The duration of the stimulus was managed by hand and was longer in A than in B ; that difference does not account for the difference in the duration of the two reflexes. Time marked above in seconds.

FIG. 4.—Crossed reflexes produced in vasto-crureus by mechanical excitation (quick tightening of a previously loose thread-loop) of proximal end of cut anterior tibial nerve of opposite limb. A shows the reflex response given by left vasto-crureus muscle to this excitation of right anterior tibial nerve. B shows the response given by right vasto-crureus to the similar stimulations of left anterior tibial nerve. Both reactions are from the same animal and within four minutes' interval one from the other. The spinal afferent roots containing the afferent fibres of the right vasto-crureus nerve had been severed 52 days prior to the experiment. The tonic maintenance of the reflex, which in the case of the left (A) vasto-crureus lasted with little abatement for a couple of minutes, is absent in the reflex given by the right vasto-crureus (B). Time marked above in seconds.

FIG. 5.—Crossed reflexes produced in (A) the left vasto-crureus and in (B) the right vasto-crureus by stimulation of the popliteal nerve. Stimulation by a series of weak break shocks, marked by the lowest signal. The stimuli are admitted to the nerve for the period during which the short-circuit key in secondary circuit is open, marked by the upper signal line. The afferent nerve-fibres of the right muscle (B) had been severed 80 days previously ; those of the left muscle intact. Time above in seconds.