Reciprocal Innervation and Symmetrical Muscles.

By C. S. Sherrington, F.R.S., Professor of Physiology, University of Liverpool.

(Received November 13, 1912,—Read January 23, 1913.)

(From the Physiology Laboratory, University of Liverpool.)

I. *Introduction.*

If we attempt to decipher the biological meaning of reciprocal innervation its various instances when marshalled together say plainly that one of the functional problems which it meets and solves is mechanical antagonism. Where two muscles have directly opposed effect on the same lever, "reciprocal innervation" is the general rule observed by the nervous system in dealing with them, and this holds whether the reciprocal innervation is peripheral as with the antagonists of the arthropod claw, or is central as with vertebrate skeletal muscles. Also where one and the same muscle is governed by two nerves influencing it oppositely, reciprocal innervation seems again the principle followed in the co-ordination of the two opponent centres, as has been shown by Bayliss* in his observations on vasomotor reflexes.

But the distribution and occurrence of reciprocal innervation extend beyond cases of mere mechanical antagonism. The reflex influence exerted by the limb-afferents on symmetrical muscle-pairs such as right knee-extensor and left is reciprocal.† Thus right peroneal nerve excites the motoneurones of left vastocrureus, and concomitantly inhibits those of the right. The reflex inhibition of the one is concurrent with, increases with increase, and decreases with decrease of, the excitatory effect on the other. Here the muscles are not in any ordinary sense antagonistic; not only do they not operate on the same lever, but they are not even members of the same limb, nor do they belong even to the same half of the body. They are, however, actuated conversely in the most usual modes of progression—the walking and the running step—though not always in galloping.

Similarly with other symmetrically paired limb muscles,‡ the limb afferents when tested for their reflex effect on such twin muscles commonly exert an opposite and reciprocal effect on the members of the pair. Here the bifurcation of the afferent path which leads to the reciprocal effect sits, so

* 'Roy. Soc. Proc.,' 1908, B, vol. 80, p. 339.
† 'Journ. Physiol.,' 1898, vol. 22, p. 398.
‡ 'Roy. Soc. Proc.,' 1905, B, vol. 76, p. 286.

to say, astride of the median longitudinal plane of the body, and a somewhat analogous case is that of the reciprocal innervation exerted by *cortex cerebri* on certain symmetrical muscle pairs in, for instance, the musculature of the eyeballs.* Stimulation of a point in the right cortex, while causing left external rectus to contract, causes right external rectus to relax, and conversely inhibits left internal rectus while exciting contraction of right internal rectus.

But in the case of such symmetrical muscle-pairs, though some circumstances and some afferents deal with the two members of the pair by "reciprocal innervation," it is equally clear that some deal with them by "identical innervation." Thus with the two vastocrurei, right and left, though most of the limb-afferents influence the two reciprocally, the genito-crural nerve influences them identically,† namely, excites concurrent contraction of both muscles, and it is clear that in their natural use both the muscles are sometimes thrown into contraction together and thrown out of contraction together, as happens in the gallop and in standing and sitting. Similarly with the lateral recti of the eyeballs, stimulation of certain brain points and certain voluntary acts which cause ocular convergence exert an identical influence on the two internal recti exciting both together, and similarly an identical influence on the two external recti inhibiting both. The relation of reciprocal innervation to the symmetrical muscle-pairs differs, therefore, from its relation to antagonistic muscles, in so far that in the former case it is only one of the ordinary modes of innervation obtaining for the muscle-pair, whereas in the latter case there is little evidence at present that reciprocal innervation of the muscle-pair is at all commonly under normal circumstances replaced by identical innervation.

Such symmetrical muscle-pairs present, therefore, the problem that sometimes they are co-ordinated by reciprocal innervation and sometimes by identical innervation. In the present observations it has been sought to see whether by experimental means in the purely reflex preparation they can be made sometimes to contract together or to relax together and at other times to behave reciprocally, the one member of the pair contracting concomitantly as the other relaxes.

II. *Change from Reciprocal Innervation to Identical in Symmetrical Extensors.*

When an afferent nerve of one hind limb is stimulated in the double (right and left) vastocrureus preparation (decerebrate cat), reciprocal innerva-

* 'Roy. Soc. Proc.,' 1893, vol. 52, p. 333.

† 'Journ. Physiol.,' 1910, vol. 40, p. 53.

tion is seen to obtain in the reflex effect on the two muscles. The muscle contralateral to the nerve exhibits excitatory contraction; the ipsilateral muscle inhibitory relaxation (fig. 1). This result holds good over a wide range of intensities of stimulation of the afferent nerve. The contralateral

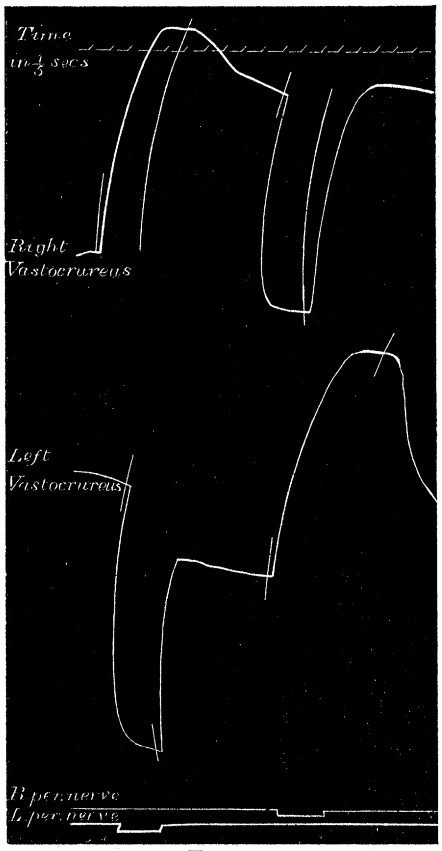

FIG. 1.

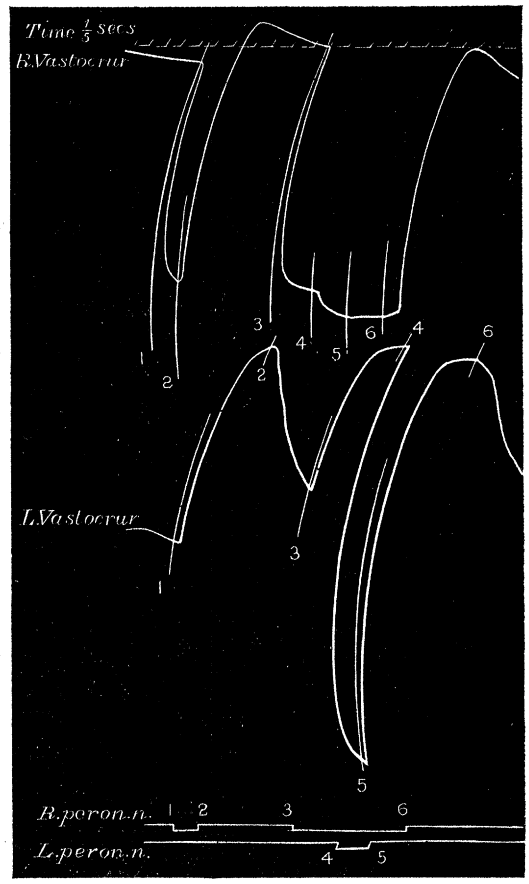

FIG. 2.

FIG. 1.—Reciprocal innervation of the extensor muscles, *vastocrurei*, of right and left knee, first from left peroneal nerve, then from right peroneal. Decerebrate cat. The inhibitory relaxations are in each case followed by post-inhibitory rebound.

FIG. 2.—Extensor muscles, *vastocrurei*, of right and left knee. The right peroneal nerve is first stimulated; then the same nerve again, and during its stimulation left peroneal is stimulated with same intensity approximately as right, and the left stimulus withdrawn, and finally the right. During the double stimulus both muscles exhibit inhibitory relaxation. Decerebrate cat.

excitation and the ipsilateral inhibitory relaxation increase *pari passu* as the intensity of the stimulation is increased.

But it is also possible experimentally to obtain simultaneous inhibitory

relaxation of both muscles followed by simultaneous contraction of them. If the preparation be carefully made, the condition of the twin isolated muscles remaining sensibly similar, and if similar right and left afferent nerves, *e.g.* right and left peroneal, be fitted with electrodes from similar induction coils similarly supplied and interrupted for faradisation and the intensity of the stimulation of the two nerves be kept as far as practicable equal, observations can be obtained as follows:—Suppose, as in fig. 2, right peroneal stimulated; right vastocrureus relaxes and left contracts; if then, while right nerve continues to be stimulated, left peroneal be stimulated in addition, right vastocrureus still remains relaxed and indeed may relax further, but left vastocrureus relaxes also. On then withdrawing the stimulation of left nerve left muscle contracts and right remains relaxed still, and finally on withdrawal of stimulation of right nerve right muscle contracts by rebound.

This shows that each of the afferent nerves employed taken by itself unfolds in response to stimulation an inhibitory effect on the ipsilateral muscle stronger than is its excitatory effect on the twin contralateral muscle. Stimulation of the right and left nerves concurrently if the stimulations be fairly equal in intensity causes therefore concurrent relaxation of both muscles. Thus when the stimulations of the two nerves are repeated synchronously, as in fig. 3, both muscles relax together at each repetition of the stimulation. Further at each discontinuance of the double stimulation both muscles exhibit synchronous rebound contraction. So that in response to the synchronously repeated and synchronously remitted stimulations both muscles relax and contract synchronously. If, however, the intensities of the two stimuli be markedly unequal the muscular reactions, right and left, though synchronous are, of course, reciprocal, not identical.

The identical form of reaction holds true over a wide range of intensities of stimulation, so long as the two stimulations, right and left, are kept of approximately equal intensity. The preponderance of ipsilateral inhibition over contralateral excitation obtains therefore both with moderate stimuli and with strong, the ratio between the intensities of the reflex inhibition and reflex excitation remaining apparently about the same for a wide range of stimulus intensities. The difference between the effect of synchronous double stimulation of strong intensity and of weak is in the main merely that with weaker stimuli the synchronous relaxations of the two muscles are weaker and are followed by less powerful rebounds than are strong, though the rebounds are still synchronous.

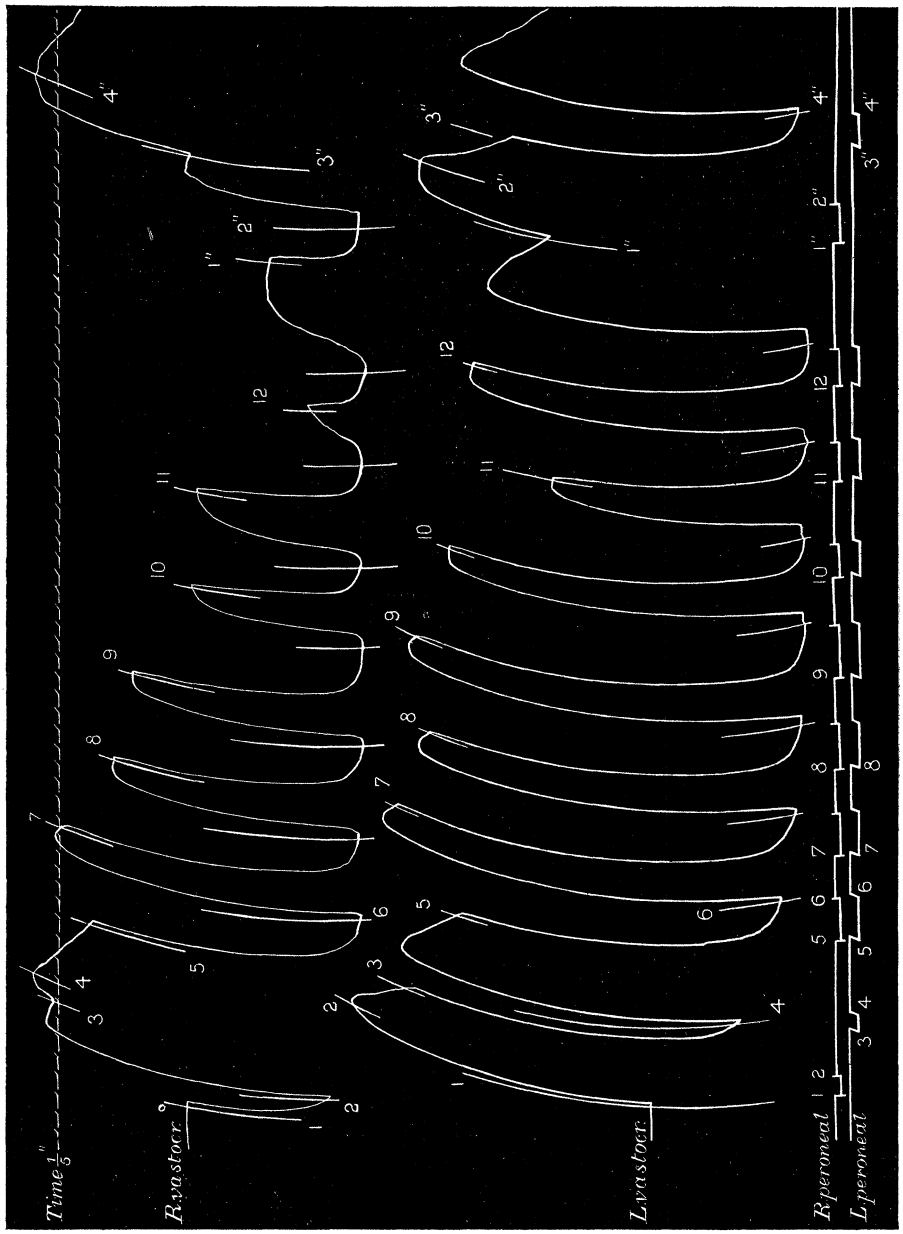

FIG. 3.—Extensor muscles, *vastocrurei*, of right and left knee. Stimulation of right peroneal, then of left, then seven stimulations of both nerves together, then of right alone, and finally of left alone. The intensities of stimulations right and left approximately equal. Decerebrate cat.

III. *Change from Reciprocal Innervation to Identical in Symmetrical Flexors.*

If instead of extensor muscles we take a pair of symmetrical flexors, upon them again reciprocal innervation is found to be the reflex result of stimulation of an afferent nerve of either limb. Thus with the two tensor fasciæ

femoris muscles, hip-flexors, the effect of stimulation of the central end of the peroneal nerve is contraction of the ipsilateral muscle and inhibitory relaxation of the contralateral (fig. 4). So also with psoas, and sartorius (fig. 5), and semitendinosus, the latter a flexor of knee. Yet with these flexors, although thus reciprocally innervated, it has been shown that, under certain circumstances, they exhibit identical reflex innervation, for instance when nociceptive stimulation is applied concurrently to both feet.* And

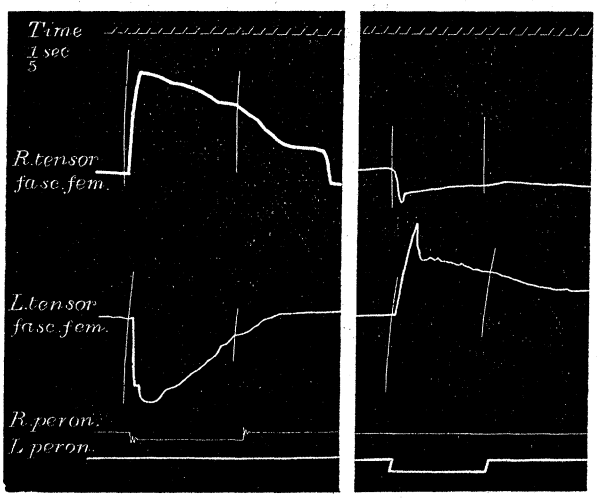

Fig. 4.

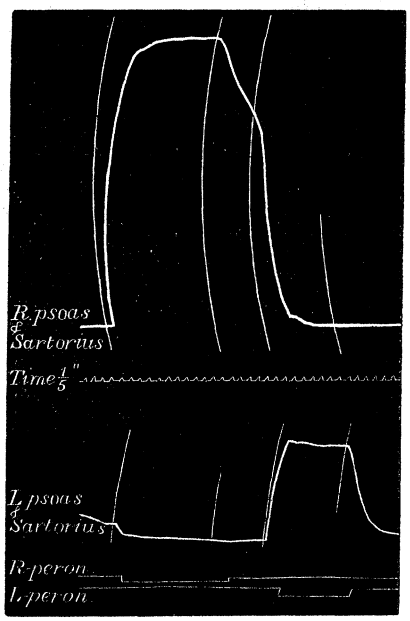

Fig. 5.

Fig. 4.—Flexor muscles, *tensor fasciæ femoris*, of right and left hips. Stimulation of right peroneal nerve, and then of left peroneal nerve. Decerebrate cat.

Fig. 5.—Flexor muscles, *psoas* and *sartorius*, of right and left hips. Stimulation of right peroneal causes contraction of the right muscles and inhibitory relaxation of the left. Stimulation of the left peroneal causes inhibitory relaxation of the right muscles and contraction of the left. Decerebrate cat.

when the two peroneal nerves right and left are concurrently stimulated with faradisation of approximately equal intensity, the two flexor muscles right and left both contract together (fig. 6) and exhibit fully identical reflex innervation. Here, however, the identical innervation presents itself in the form of concurrent contraction not of concurrent relaxation as was the case with the extensors. With the flexors, therefore, the excitatory effect of each

* Sherrington, in 'Schäfer's Handbook of Physiol.,' 1900, vol. 2, p. 840; 'Integrative Action of Nervous System,' p. 225, 1906.

afferent is stronger than the inhibitory effect, and the excitatory effect is ipsilateral. So that with both flexors and extensors the ipsilateral effect is

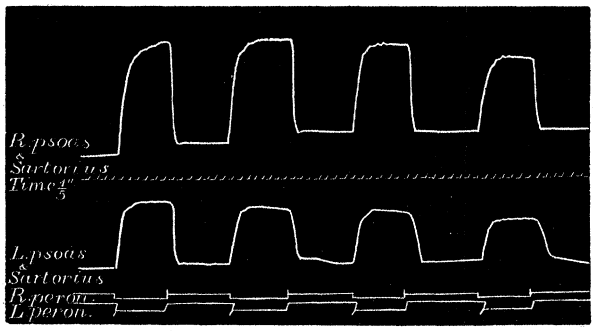

FIG. 6.—Flexor muscles, *psoas* and *sartorius*, of right and left hips. Stimulation of the right and left peroneal nerves together causes contraction of both the right and left muscles synchronously. The stimulation intensities right and left were approximately equal. Decerebrate cat.

the stronger, but in the case of the flexors it is excitatory while with the extensors it is inhibitory.

IV. *Algebraic Summation as a Factor in Producing the Change.*

In the case of these symmetrical muscles therefore the change from reciprocal reflex effect to identical is clearly explicable by algebraic summation of excitation and inhibition.* The result may be stated numerically. Right peroneal nerve under a stimulus whose intensity may be figured as 10, causes an excitation of the motoneurones of right flexor muscle of an intensity expressible as 10, and a weaker inhibition of the motoneurones of left flexor whose intensity may be called 6. It at the same time causes also an inhibition of the motoneurones of the right extensor of intensity 10, and a weaker excitation of the motoneurones of left extensor of intensity 6. Similarly, the reflex effect of the left peroneal nerve under a stimulus of like intensity is on the left flexor's motoneurones an excitation of value 10, and on right extensor's motoneurones of value 6, while left extensor's motoneurones it inhibits with value 10 and right flexor's motoneurones with value 6. Denoting (fig. 7) excitation by the prefix + and inhibition by the prefix −, the resultant reflex effect on the motoneurones of the muscles severally is, when both nerves are stimulated concurrently, + 4 for the flexor in each limb, and − 4 for the extensor in each limb. So that, if we suppose all the muscles to be previously in a condition of medium tonus the two symmetrical flexors then contract and

* 'Roy. Soc. Proc.,' 1908, B, vol. 80, p. 565.

the two symmetrical extensors exhibit inhibitory relaxation. It is to be noted that if the initial condition of the muscles be full repose, *e.g.* −10 in the above notation, then in the above instance the symmetrical extensors (as well as the flexors) enter upon a certain degree of contraction, namely −4, full relaxation being −10. In any case the double stimulus gives an identical reflex effect on the symmetrical muscles, though the reflex effect

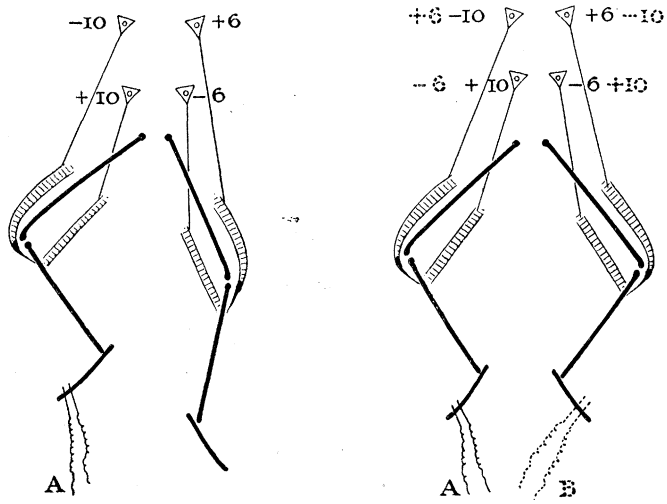

FIG. 7.—Explanation in text.

still remains reciprocal as regards the pairs of antagonistic muscles. Under the double stimulus the reflex effect becomes symmetrical and identical in the two limbs, although under either of the two components singly the reflex effects in the two limbs are diametrically opposed.

These results hold over a wide range of intensity of stimuli so long as the intensities of the stimuli right and left are approximately equal. This indicates that the intensity ratio between the ipsilateral and contralateral effects, both of inhibition and excitation, remains but little changed over a wide range of different intensities of stimulation. The absolute values rise and fall with increase and decrease of stimulation, but the relative values remain about the same, subject to two alterations which will be mentioned later.

The above observations therefore come under the rubric of algebraic summation in double reciprocal innervation. They show that double reciprocal innervation can change reciprocal innervation of *symmetrical* muscles into identical innervation of them. Double reciprocal innervation* applied to *antagonistic* muscles does not result in identical innervation of

* 'Roy. Soc. Proc.,' 1909, B, vol. 81, p. 249.

them, although it can bring about, it is true, the exhibition of some degree of contraction by both the antagonists at the same time.

The difference in intensity of reflex influence exerted on the ipsilateral and contralateral limbs respectively may have its biological meaning in the opportunity thus given for the limbs to exhibit either symmetrical reflex movements, or movements of opposed direction right and left, according as there is equality or inequality between their right and left stimuli.

V. *Symmetrical Rebounds.*

It will be noted that in the above attempt to change by experimental means the reciprocal innervation of the symmetrical muscle-pair consisting of right and left knee-extensor into identical innervation, success is reached as regards "immediate"* reflex effect only in so far as identical inhibitory relaxation of the two. Simultaneous contraction of the two in response to concurrent stimulation occurs occasionally with weak stimuli, especially where one of the nerves tends to give ipsilateral contraction. The identical contraction of the two which ensues, however, after their concomitant relaxation is, so to say, not an immediate but a "terminal"† reflex result, for it is due to post-inhibitory rebound.

Rebound contraction in one muscle of an antagonistic or of a symmetrical pair is so commonly associated with concomitant relaxation of the fellow muscle (fig. 8) of the pair that large identical rebound contractions

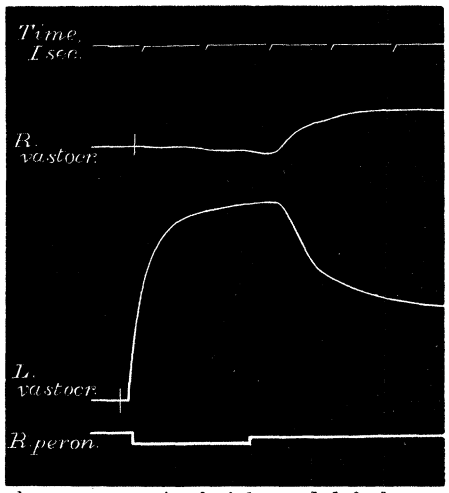

FIG. 8.—Extensor muscles, *vastocrurei*, of right and left knees. Stimulation of right peroneal nerve. The post-inhibitory rebound of the ipsilateral extensor is synchronous and reciprocal with the post-excitatory relaxation of the contralateral extensor. Decerebrate cat.

* *Cf.* T. Graham Brown, 'Quart. Journ. Exp. Physiol.,' 1912, vol. 5, p. 237.

† *Cf.* T. Graham Brown, 'Quart. Journ. Exp. Physiol.,' 1911, vol. 4, p. 331.

occurring concomitantly in the symmetrical muscles is not without interest. T. Graham Brown* has recently pointed out that in antagonistic muscles in many cases the terminal relaxation following an excitatory reflex may be regarded as of the nature of an inhibitory rebound, the converse of rebound contraction. It would seem, therefore, that the terminal rebound following a reflex of reciprocal effect on a muscle-pair is often itself of reciprocal character in the two muscles. In the symmetrical muscles dealt with in this paper the terminal effects when the reflex itself has been of reciprocal influence on the two muscles are quite usually of reciprocal character in the two muscles (see fig. 8). When, however, the character of the reflex itself has been changed, by the procedure described, from reciprocal into identical the terminal rebound also is changed from reciprocal into identical (fig. 3).

VI. *Factors Outside Algebraic Summation Involved in the Change.*

The above seems to me what the experiments clearly indicate as the main principle involved in the change from reciprocal innervation of symmetrical muscles to identical innervation of them when the stimuli are appropriately duplicated. This principle rests on the inequality of the excitation-potency and inhibition-potency respectively inherent in the components of the summed duplicate reflex. But the experiments have shown certain further features outside this principle. In the observations on the vastocrureus muscles, when the reflex inhibition due to the ipsilateral nerve is in progress, and stimulation of the contralateral nerve is then added, the effect of the latter is very occasionally not a mitigation but a distinct increase of the inhibitory relaxation (fig. 2, abscissæ 4, 5). A similar result is sometimes met with in the flexor, tensor fasciæ femoris, though there conversely in regard to the nerves used. A phenomenon comparable with these, although in the opposite direction, was reported previously by Miss Sowton and myself working with the knee-flexor, semitendinosus.† We noted that if the stimulation of contralateral nerve is relatively weak in comparison with that of the ipsilateral nerve, the former, if added when the latter is in progress, may, instead of lessening the reflex contraction due to the latter, actually increase it. In the observations of this paper a strong reflex inhibition of the extensor centre already in progress seems to convert a weak excitatory influence into an inhibitory one. In the previous observations a strong reflex excitation of the flexor centre seemed to convert a weak inhibitory influence into an excitatory one. And it has been the case in some of the present observations on the hip-flexors that the addition of a

* *Ibid.*

† 'Roy. Soc. Proc.,' 1911, B, vol. 84, p. 204.

strong contralateral stimulus to an already existent ipsilateral has increased instead of lessened the contraction (fig. 9), and this has been so not only during the application of the contralateral stimulus but still further on its withdrawal. A rebound contraction of the flexor muscle has then occurred,

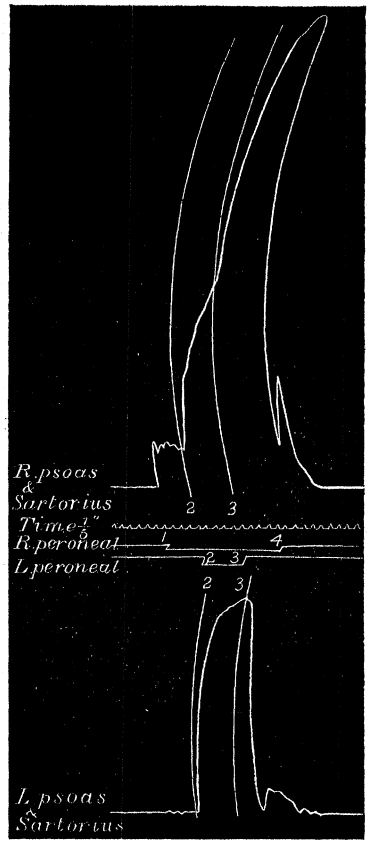

FIG. 9.—Psoas and sartorius muscles, flexors, of right and left limbs. Stimulation of right peroneal with a weak stimulus, coil at 24 cm. from primary; during this stimulation the left peroneal is stimulated for about one second with a strong stimulus, coil at 14 cm. from primary. The contraction of right flexors is increased during stimulation of left nerve, and on cessation of this stimulation a still further rebound augmentation of the right muscle's contraction occurs. Decerebrate cat.

adding itself to the contraction due to ipsilateral nerve, and causing a combined contraction of large amplitude.

It is obvious that such reactions though outside the main principle above stated work in the direction of assisting a double reciprocal innervation to change the reflex effect on the symmetrical muscles from reciprocal to identical character. The contraction of both flexors will be increased and so also the inhibitory relaxation of both extensors.

It seems, therefore, that in the combination of two reciprocal reflexes of opposite effect on the symmetrical muscles of the limbs there is, besides simple algebraic summation of the respective excitation and inhibition of the components, a further factor sometimes present. An actual reversal of the weaker element of one of the components appears to take place. Thus, the excitatory effect on the contralateral extensor tends occasionally to be reversed to inhibitory effect, and the inhibitory effect on contralateral flexor tends to be reversed to excitatory effect.

There remains the question whether identical concurrent contraction of the symmetrical extensor pair can be obtained as a direct reflex. With concurrent stimulation of both nerves, right and left, it can occasionally, when the stimulation is weak, especially if one or both nerves be then giving ipsilateral extensor contraction. Experiment shows that it can also be obtained by a procedure quite other than that followed for producing the identical innervation which has symmetrical relaxation for its result, namely by weak stimulation of the afferent nerve of one side alone, right or left. The range of intensity of stimulus over which reciprocal innervation of the muscle pair results from excitation of a limb afferent is wide and ranges from weak intensities without break right up to the very strongest. But with stimuli of little above threshold value the result changes in the decerebrate preparation. With these stimuli although the response in the contralateral muscle remains reflex contraction, in the ipsilateral muscle the response becomes reflex contraction instead of inhibitory relaxation. This alteration is that noted previously by Miss Sowton and myself.* That it is accompanied by concomitant contraction of the symmetrical extensor of the fellow knee shows that with change merely of intensity of the stimulus the reflex innervation of the fellow muscles alters from reciprocal to identical. The reflex contraction so obtained is weak but quite indubitable and clearly concomitant (fig. 10).

Over a range of stimulus-intensities running from threshold value up to weak or moderate, the exact limit upward varying with the condition of the preparation, the reflex result in the decerebrate animal passes from identical innervation (fig. 10, A) to an admixture of identical and reciprocal innervation (fig. 11), until with stronger stimuli reciprocal innervation is fully established (fig. 10, B). In the admixed form of result the reflex opens with bilateral contraction, *i.e.* contraction of both right and left extensor muscles, and then passes over into ipsilateral inhibitory relaxation, with contralateral pure contraction (fig. 11). This transition is speedier the less weak the stimulation. It is brought about by a change occurring, as noted by Miss Sowton

* 'Roy. Soc. Proc.,' 1911, B, vol. 83, p. 435.

and myself,* in the reaction of the ipsilateral muscle during the progress of the stimulation.

The statement was made above that the relative values of ipsilateral

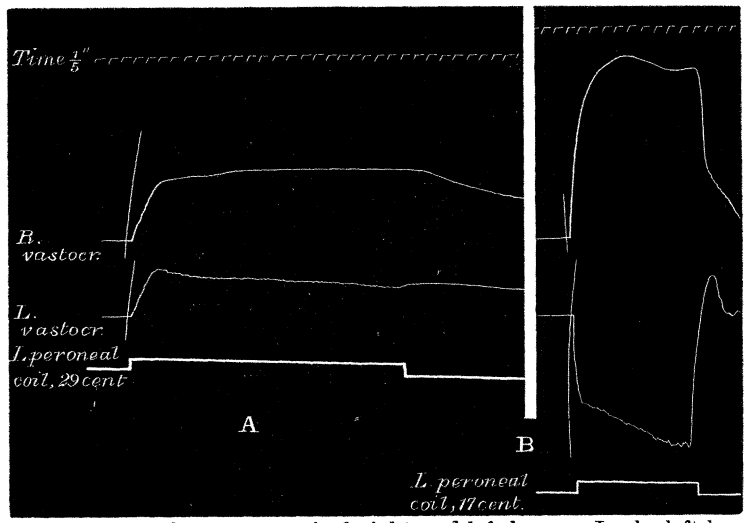

FIG. 10.—Extensor muscles, *vastocrurei*, of right and left knees. In the left-hand record the stimulation of left peroneal is weak and little above threshold value; in the right-hand record the stimulation of the same nerve is repeated, but with increased though still moderate intensity. Decerebrate cat.

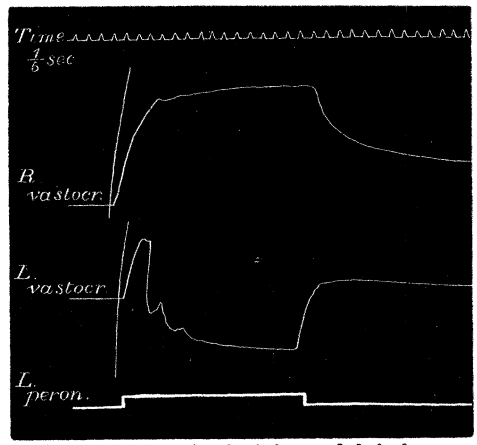

FIG. 11.—Extensor muscles, *vastocrurei*, of right and left knees. Stimulation of left peroneal with moderately weak faradisation. The reflex effect opens by being "identical" in the two muscles, but later changes to "reciprocal" as the stimulation continues. Decerebrate cat.

inhibition and contralateral excitation in the extensors remain about the same over a wide range of intensities of reflex stimulation, although the

* *Ibid.*

absolute values rise and fall *pari passu* with the stimulus intensity. What has just been said has to be remembered in relation to that statement. With decrease of stimulus intensity, as just said, a value of stimulus is ultimately reached, at which in the decerebrate preparation contralateral effect still remains excitatory, but ipsilateral becomes excitatory instead of inhibitory. The biological meaning of this may be that with these weak stimuli the reflex produced is that of standing, *i.e.* a local reflex contributory to the great compound reflex of standing, whereas, with stronger stimuli, the reflex produced is the nociceptive flexion reflex, or the flexion phase of a locomotor step-reflex.

With the flexor muscles of the hip, psoas, tensor fasciæ femoris, and sartorius, strong stimulation of one peroneal nerve sometimes excites contraction in these muscles in the contralateral, as well as in the ipsilateral limb. The contraction of the contralateral muscles is less strong than that of the ipsilateral. It tends to be followed on withdrawal of the stimulus by marked rebound contraction. The contralateral contraction of the hip-flexors recalls the contralateral contraction of the ankle flexor, tibialis anticus, noted by T. Graham Brown,* as sometimes occurring in both decerebrate and spinal preparations.

VII. *Summary of Conclusions.*

1. The occurrence and distribution of reciprocal innervation extends to cases of muscular co-ordination beyond those involving simple mechanical antagonism. Thus it is exemplified also in reflexes actuating symmetrical muscles, for instance, muscles symmetrically placed in the right and left limbs.

2. These muscles present the problem that, in reflexes, though often worked reciprocally, they are also often worked identically.

3. Experiments cited show certain ways in which the stimulations can be experimentally arranged to give either reciprocal or identical innervation of symmetrical muscles of right and left limb.

4. It is shown that algebraic summation of excitation and inhibition can explain this result.

5. It is further shown that there is evidence that other factors besides simple algebraic summation of the individual component reflexes have a share in changing the reciprocal innervation into an identical. A reversal of the weaker element of one of the components appears to occur. Thus, the excitatory effect on the contralateral extensor tends occasionally to be reversed to inhibitory effect, and the inhibitory effect on the contralateral flexor tends to be reversed to excitatory effect.

* 'Journ. Physiol.,' 1912, vol. 44, p. 125.