THE RULE OF REFLEX RESPONSE IN THE LIMB REFLEXES OF THE MAMMAL AND ITS EXCEPTIONS.

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A BROAD rule observable in the reflex movements elicited from the mammalian limbs by stimuli applied to afferent nerves of the limbs themselves is that the *movement in the stimulated limb itself is flexion while that in the crossed fellow limb is extension*[1]. But occasionally this paradigm is departed from[2]; and a standing exception is the "extensor thrust" which, although elicited by stimulation of the ipsilateral foot, is an extension reflex[3].

In all the following observations the cat has been the animal investigated. Usually the decerebrate preparation has been used, but in some cases the observations are in the high spinal (decapitate) or low spinal (otherwise decerebrate) preparations.

Movements at the knee. When the main joints and muscles of the hind limb are observed separately the rule is found to hold good for them severally; the occasional exceptions which occur can then be more particularly examined.

Thus in preparations in which the main extensor of the knee—*vastocrureus*—is isolated reflex contraction, instead of reflex relaxation, is found to occur not infrequently in response to ipsilateral stimuli in the decerebrate condition. This occurs especially in the case of weak stimuli[4], and when the electrical stimulus is the galvanic current and not faradic stimulation[5]. This ipsilateral contraction is never very strong, and it tends to pass over into inhibitory relaxation if the stimulus is continued or if it is increased in strength. If purely spinal

[1] This *Journal*, XL. p. 116. 1910.

[2] *Ibid.* XL. p. 55. 1910. *Quart. Journ. of Exp. Phys.* IV. p. 389. 1912.

[3] *Proc. Roy. Soc.* LXVI. p. 67. 1900.

[4] Sherrington and Sowton. *Proc. Roy. Soc.* B, LXXXIII. p. 435. 1911. [5] *Ibid.*

preparations (low spinal) are used in place of decerebrate the ipsilateral contraction of the knee extensor is not met with[1].

Again, the crossed reflex at the knee is occasionally flexion instead of extension. Observations with the isolated *semitendinosus*—a main flexor of the knee—show that sometimes increased reflex contraction of this muscle ensues on stimulating the afferents of the contralateral hind limb when the muscle is already in reflex contraction from stimulation of the afferents of its own limb[2]. The usual result is, however, diminution of the ipsilateral reflex contraction on applying the crossed stimulus.

Movements at the ankle. At the ankle joint too variations in the general rule occur. Judging from observations on the intact limbs the rule is more subject to exception. But to examine the rule for the ankle separately the muscles acting upon the hip and knee must be put out of action since the extensors of hip and knee can of themselves extend the ankle indirectly by their mechanical action.

The requisite conditions have therefore been ensured by isolation of the tendons of *tibialis anticus* and *gastrocnemius-soleus* of one limb; these muscles being respectively the main flexor and extensor at the ankle. The mechanical effect of all the other muscles of both hind limbs has been excluded by severing their nerves or their tendons, the limbs themselves being firmly fixed in strong steel holders. The tendons of the isolated muscles have been connected to the levers of a double myograph. To evoke reflex action in the recording muscles the internal saphenous nerves of both sides have been prepared and, as occasion required, faradised.

In decerebrate preparations the ipsilateral *n. saphenus* has yielded, as its most constant effect, contraction of *tibialis anticus*,—the flexor muscle—in accordance with the general rule[3]. This contraction of the flexor is, as a rule, unaccompanied by contraction of *gastrocnemius-soleus*—the antagonistic extensor. Several times, however, in the series of observations the exceptional result of contraction of *gastrocnemius* instead of *tibialis* has occurred—*tibialis* showing no contraction (Fig. 4). The contraction of *gastrocnemius* was usually preceded by a remarkably long latent period. It is to be remarked that we are referring here solely to the primary effects of the stimulation and are not entering upon the effects which follow the withdrawal of the stimulus. In the

[1] Sherrington and Sowton. *Proc. Roy. Soc.* B, LXXXIII. p. 435. 1911.
[2] This *Journal*, XL. p. 59. 1910.
[3] *Quart. Journ. of Exp. Physiol.* IV. p. 389. 1912.

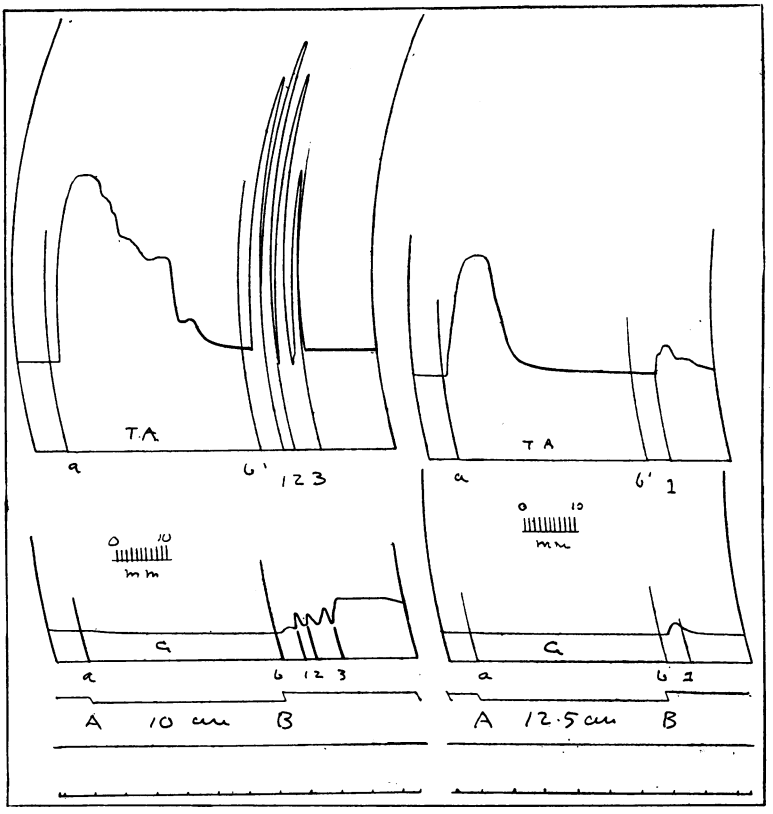

Fig. 1. Fig. 2.

Fig. 1. Antagonists at ankle-joint. Decerebrate cat, contralateral stimulus applied 6 hours and 21 minutes after decerebration. A contralateral flexion response.

In this and in all the other figures reproduced here the upper tracing records the movements of *tibialis anticus*, and the lower those of *gastrocnemius*. In either case the rise of the curve denotes contraction, and the fall relaxation, of the muscle. Between these tracings a millimeter scale has been drawn on the blackened paper. The *first* signal line gives the time relations of *contralateral* stimuli. The beginning and end of stimulation are denoted by the letters *A* and *B*. Corresponding ordinates lettered *a*, *a'*, *b*, *b'* have been drawn on the two tracings with the drum stationary. These therefore mark on the tracings approximately the beginning and end of stimulation. The *second* signal line gives the time relations of *ipsilateral* stimuli. The letters then used are *X* and *Y* (and *x*, *x'*, *y*, *y'* for the ordinates). The lowest line is a time tracing and records seconds.

Fig. 2. Antagonists at ankle-joint. From the same experiment as Fig. 1, but after the preparation had been converted to the low spinal condition by severance of the spinal cord in the lower thoracic region. A contralateral stimulus applied 6 hours and 49 mins. after the decerebration and 14 mins. after section of the spinal cord. The reaction is that of contralateral flexion.

cases of ipsilateral extension mentioned above the effect was in some cases obtained with minimal strengths of stimulus, and increase of the strength of stimulus led to the appearance of contraction of the flexor and abolition of the extensor contraction[1].

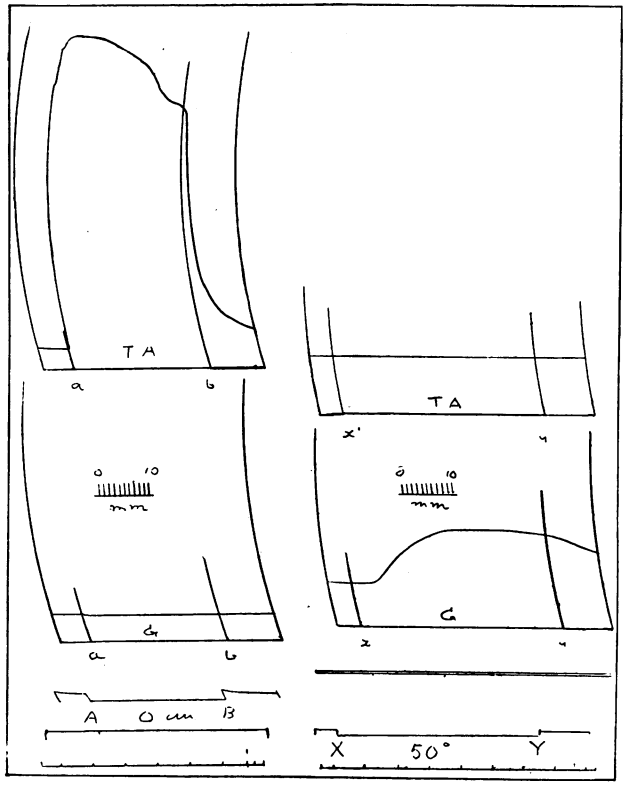

Fig. 3. Fig. 4.

Fig. 3. Antagonists at ankle-joint. Decapitate cat, contralateral stimulus applied 6 hours and 1 min. after decapitation. A well marked and sustained contralateral flexion response.

Fig. 4. Antagonists at ankle-joint. Decerebrate cat, weak ipsilateral stimulus applied 5 hours and 54 mins. after decerebration. The response is one of ipsilateral extension and stronger stimulation evoked ipsilateral flexion. The latency of the reaction is comparatively great.

The contralateral saphenous nerve has, in the majority of the observations, yielded contraction of *gastrocnemius-soleus* without contraction of *tibialis anticus*—thus exemplifying the general rule.

[1] *Quar. Journ. of Exp. Physiol.* IV. p. 361. 1912.

Occasionally, however, it has evoked the converse effect (Fig. 1); namely contraction of *tibialis anticus* without contraction of *gastrocnemius*[1]. This exceptional reaction has occurred under stimuli stronger than those sufficing to evoke *tibialis* contraction from the ipsilateral afferent, and the contraction has been usually—but by no means always—less well maintained than in the ipsilateral reflex. In some cases not only has no contraction of the *gastrocnemius* muscle accompanied this *tibialis* contraction but the *gastrocnemius* has shown obvious inhibitory relaxation (Fig. 3); reciprocal innervation of the antagonistic muscles was therefore clearly at work but in a direction opposite to that of its usual response.

Taking the series of observations as a whole contralateral flexion as an exception to the general rule of contralateral extension has been less infrequent than has been ipsilateral extension as an exception to the general rule of ipsilateral flexion.

With the isolated ankle muscles, just as with the isolated knee muscles, the exceptions to the rule of ipsilateral flexion have been confined to decerebrate preparations, and have never been clearly met with in purely spinal preparations[2]. But the spinal preparations have yielded instances of contralateral flexion of ankle breaking the general rule of contralateral extension[3] (Fig. 2). And these instances were furnished by the same preparations which in the decerebrate condition prior to spinal transection had also furnished exceptions similarly breaking the general rule. The spinal transection was made in the posterior thoracic region.

Conclusions.

The rule of ipsilateral flexion and contralateral extension holds, in the great majority of cases, for the reflex response of the hind limb to stimulation of the ipsilateral and contralateral limb afferents proper. It is, however, subject to a certain amount of variation in which the reverse of the rule occurs either in one limb or the other. These two types of exception do not tend however to occur in one and the same preparation.

One type of exception, namely ipsilateral extension instead of ipsilateral flexion, has been met with only in decerebrate preparations and not in spinal. With weak stimuli it seems to be a not uncommon phenomenon at the knee.

[1] *Quart. Journ. of Exp. Physiol.* iv. p. 360. 1912.
[2] *Ibid.* p. 340. [3] *Ibid.* p. 345.

Contralateral flexion in place of contralateral extension has been met with in spinal preparations as well as in decerebrate, and those particular preparations which yielded it sometimes do so both in the decerebrate and in the purely spinal conditions. Contralateral flexion appears to be less infrequent at the ankle than is ipsilateral extension of that joint.

The rule shows that the usual reflex condition of the limb centres both in the decerebrate and in the purely spinal preparation is such that the stimulus provokes flexor contraction upon one side and extensor contraction upon the other. The "neural balance"[1] as regards the limb-pair taken together may therefore be described as being in that case equally disposed to flexion and to extension although oppositely weighted in the two limbs. In those exceptional preparations which yield ipsilateral extension instead of ipsilateral flexion the effect of the stimulus is that both limbs extend. In this case the neural balance seems for some reason to be dominantly disposed or weighted towards extension. And this appears to happen only in decerebrate preparations; and in decerebrate preparations there is, as is well known, the marked tonic activity of the extensor muscles which constitutes decerebrate rigidity.

On the other hand, in those exceptional preparations which yield contralateral flexion in place of contralateral extension the effect of the stimulus is that both limbs flex. In this case the neural balance seems for some reason to be dominantly weighted towards flexion, and it is noteworthy that the same preparations which exhibit this tendency in the decerebrate condition may also exhibit it when rendered purely spinal.

The expenses of this research have been defrayed in part by a Grant from the Carnegie Trust.

[1] *Quart. Journ. of Exp. Physiol.* IV. p. 273. 1911.