On Reciprocal Innervation of Antagonistic Muscles.—Seventh Note.

By C. S. Sherrington, F.R.S.

Physiology Laboratory, University of Liverpool.

(Received February 28,—Read April 6, 1905.)

In a previous note* on this subject, instances were pointed out in which the passive posture already obtaining in a limb influences the character of the spinal reflex elicitable from the limb. It was there shown how passive flexion, for instance, favours reflex extension. On resorting to postures assumed and maintained not passively but actively a like influence is evident.

A reflex described in the previous note gives good illustration of this. Light pressure applied to the *planta* of the spinal dog evokes a brisk extension of the limb at hip, knee, and ankle. The pressure applied is such as resembles that which the weight of the dog would, in its own step, apply to the *planta* on contact with the ground. This reflex—which may be termed the "extensor thrust"—employs the antagonist muscles to those employed by the well-known flexion reflex provocable by noxious stimuli applied to the *planta*, *e.g.*, by a prick. This latter reflex, the flexion reflex, although it throws into action a group of muscles different from that thrown into action by the extensor thrust, yet exerts a marked influence over that reaction. If the extensor thrust be compared as elicited before and after a prolonged flexion reflex, the "thrust" reflex is found more facile and vigorous just after the flexion than it was before it.

Again, if the crossed extension reflex of the limb be examined before and after a prolonged flexion reflex a similar alteration is evident in it. When a carefully adjusted electrical stimulus is at regular intervals applied to the afferent path of one limb and the resultant extensor reflex of the crossed limb is noted, it is found that if in one of the intervals a flexion reflex of the latter limb is induced and maintained for 15 seconds or more, the extensor reflex becomes altered in consequence. For a period immediately following the flexion reflex the extension reflex is increased. The intensity of the reflex is heightened its duration is prolonged, and its latent time is reduced. If the testing stimulus be subliminal the threshold value of the stimulus required by the reflex is found lowered. In short the activity of the flexion arcs

* 'Roy. Soc. Proc.,' vol. 66, p. 67, 1900.

directly or indirectly induces in the extension arcs a super-excitability as tested by crossed extension just as when tested by the extensor thrust.

But although this after-effect of the activity of the flexion arcs upon the antagonistic arcs, both direct and crossed, is one of increase of activity, the primary effect is, as shown previously, one of depression. Thus the crossed extension reflex is temporarily inhibited by the flexion reflex; the extensor thrust becomes inelicitable directly a pronounced flexion reflex sets in. Indeed, these mutually antagonistic reflexes are, like other similarly opposed ones, coupled together in such a way that provocation of the active state of discharge of one reflex checks the active state of discharge of the other reflex. It, therefore, becomes obvious from this, and other evidence given in the previous notes, that in such instances the spinal mechanism, temporarily depressed (inhibited), later enters into a state of exaltation manifested by enhanced tendency to active discharge, and by capacity to discharge with greater intensity than before. A like sequence is well seen when, using the knee jerk as index, the effect on the knee-extensors of stimulation (mechanical, kneading, etc.) of the antagonistic hamstring muscles freed from their attachments is observed. The depression (inhibition) of the antagonists is pronounced, but on discontinuing the stimulation the knee jerk regains not merely its previous briskness, but becomes temporarily more brisk and ample than before. The same is seen when the stimulation is direct faradisation of the afferent nerves from the hamstrings, or when, instead of using the "knee jerk" as an index to the *tonus*, the heightened reflex rigidity of the extensors in decerebrate rigidity is directly observed. In all these instances, and in others that can be given in a fuller communication than the present, there supervenes on the spinal inhibition a rebound effect of augmentation.* This intraspinal rebound effect becomes especially evident on cessation of a stimulus of inhibitory character of *prolonged* application. The rebound can be experimentally shown to ensue even during the actual application of the stimulus that initially caused inhibition if the application of that be long continued. The exaltation after-effect may ensue with such intensity that simple discontinuance of the stimulus maintaining the one reflex is immediately followed by "spontaneous" appearance of the antagonistic reflex. These phenomena are well shown by the opposed reflexes at the knee of the dog.

Thus, in the spinal arcs inhibited there supervenes on the state of inhibition a phase of super-excitability. In this after-effect central inhibition

* Sherrington, Schäfer's 'Text-book of Physiology,' vol. 2, p. 841, 1900.

presents resemblance to peripheral inhibition as exemplified, for instance by pure vagus action on the heart. The cardiac depression is followed by exaltation of excitability and conductivity of the cardiac tissue. "As to contraction force and conductivity, the after-effect is in the opposite direction to the primary effect."*

This spinal interaction between certain reflex centres, related to movements of opposed direction, resembles that known to hold between adjacent retinal points. The spinal phenomenon seems fundamentally akin to that of visual contrast,† as both Macdougall and myself have pointed out. If visual brightness be regarded as analogous to the activity of spinal discharge, and visual darkness analogous to the absence of spinal discharge, the reciprocal spinal action in the example last mentioned above has a close counterpart in the well-known experiment where a white disc used as a prolonged stimulus leaves as after-effect in the visual field a grey image surrounded by a bright ring (Hering's "Lichthof"). The bright ring has for its spinal equivalent the "spontaneous" discharge from the adjacent reciprocally correlated spinal "centre."‡

The "spinal induction" is obviously qualified to play a part in linking reflexes together in a co-ordinate sequence of successive combination. If a reflex arc A during its own activity not only temporarily checks the discharge-action of an opposed reflex arc B, but also as a subsequent result induces in arc B a phase of greater excitability and capacity for discharge, it predisposes the spinal organ for a second reflex opposite in character to its own in immediate succession to itself. I have previously pointed out the peculiar prominence of "alternating reflexes"§ in prolonged spinal reactions. These may be traceable largely to "spinal induction." It is significant that they are usually cut short with ease by mere passive mechanical interruption of the alternating movement in progress.

Much of the reflex action of the limb that can be studied in the "spinal" dog bears the character of adaptation to locomotion. This has been shown recently with particular clearness by the observations of Philippson.‖ In

* Gaskell, 'Schäfer's Text-book of Physiology,' vol. 2, p. 220, 1900; see also 'Transact. of VIIIth Internat. Med. Congress,' Copenhagen, 1884.

† Sherrington, 'Journal of Physiol.,' vol. 21, p. 33, 1897; Macdougall, 'Brain,' vol. 26, p. 177, 1903.

‡ For the influence of varying conditions on this experiment and an explanation offered important to the analogy suggested here, see W. Macdougall, "Young's Theory of Light and Colour Vision," 'Mind,' vol. 10, N.S., No. 37, pp. 25 to 30 of the reprint.

§ Croonian Lecture, 1897; 'Phil. Trans.,' B, 1898.

‖ 'Archives de Physiologie,' 1904.

describing the "extensor thrust" of the limb, I drew attention to its significance for locomotion. "Spinal induction" obviously tends to connect this "extensor thrust" as an after-effect with precurrent flexion of the limb. In the stepping forward of the limb the flexion that raises the foot and carries it forward clear of the ground though temporarily checking the reflex discharge of the antagonistic arcs of extension is, as it continues, so to say, sensitising them to respond later in their turn by the supporting and propulsive extension of the limb necessary to progression. In reflex sequences an antecedent reflex would thus not only be the means of bringing about an ensuing stimulus for the next reflex,* but in such instances as the above, will predispose the arc of the next reflex to react to the stimulus that will arrive.

In recently† attempting to deal with the factors that determine the succession of reflexes in time, I mentioned this factor, "spinal induction," but laid less stress on its potency than its phenomena now seem to me really to warrant.

* Loeb's "Ketten-reflexe," discussed in his 'Vergleichende Gehirnphysiologie u. Vergleichende Psychologie,' Leipzig, 1899, p. 96, and *seq.*; compare also Exner, 'Entwurf einer physiologischen Erklärung psychischer Erscheinungen,' Vienna, 1894, p. 102, and *seq.*, under "Successive Bewegungscombinationen"; also Wundt, 'Grundzüge der physiologischen Psychologie,' vol. 1, p. 181.

† Brit. Assoc., Cambridge, 1904. Address to Section I.