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Significance of Supraspinal Control of Reflex Actions by Impulses in Muscle Afferents

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Work of the Sherrington school first demonstrated the importance of proprioceptive reflexes from muscle afferents in the reflex taxis of the limb[1]. Subsequent investigation has been directed to discover the contributions by the various afferent systems from muscles.

Large afferents from muscle spindles (Ia fibres) are discharged by a slight stretch of the muscle. These impulses exert a monosynaptic excitatory action on motoneurones and may thereby give rise to a reflex discharge of impulses. By operation through an interneuronal relay inhibitory actions are evoked in other motoneurones by the same impulses. These excitatory and inhibitory actions have been found to be distributed to different motor nuclei according to an intricate pattern, suggesting that the Ia system subserves coordination of movements[2].

Large afferents from Golgi tendon organs (Ib fibres) are adequately stimulated by contraction of the muscle. Impulses in Ib fibres from extensor muscles inhibit motoneurones to the muscle of origin and to other extensor muscles, whereas flexor motoneurones receive excitation[3]. However, the pattern does not conform entirely with the flexion reflex. For example, Ib impulses from a flexor muscle do not evoke excitation in neurones to its own muscle.

Finally the reflex actions by the small afferents from muscle spindles (12 – 4 μ), i.e. group II fibres with flowerspray ending[4] and also of the small group III fibres ($< 4\ \mu$), which probably respond adequately mainly on nociceptive stimulation, are those of the general flexion reflex[5]. The actions by impulses in group II fibres are of particular interest. A slight stretch of the muscle will cause a discharge in these fibres, the threshold for stretch being only slightly higher than for the Ia fibres with annulo-spiral endings on muscle spindles[4]. Thus there are two systems of afferents from muscle, which are activated adequately in the same way, but with entirely different connections to motoneurones. The question thus arises: The intricate pattern of Ia actions is seemingly very suited to subserve co-ordinated movements, yet how can it assert itself in the reflex control of movement among the often very large but non specific actions by group II impulses?

The investigations of the synaptic actions of muscle afferents discussed above were carried out in animals made spinal through section of the cord. One possibility is that reflexes in spinal animals are not representative for the intact animal. Strong evidence has already been presented to show that interneurones mediating reflexes from muscle afferents are controlled from suprasegmental structures[6].

We have therefore compared synaptic actions by the various systems of muscle afferents in decerebrate cats before and after section of the spinal cord. It has been a consistant finding that the actions by group II and III muscle afferents which are so conspicuous in the spinal animal, are almost completely absent in the decerebrate preparation. They appear immediately when the cat is made spinal by section of the cord either in the upper cervical or upper lumbar region. In the curves of Figure 1a single gastrocnemius volley conditioned a monosynaptic testing reflex that was evoked by an afferent volley in the nerve to the knee-flexors, biceps posterior and semitendinosus. With all strengths of stimulation to the gastrocnemius nerve there were no actions before the cord section, but large facilitations appeared immediately afterwards. This occurred not only for the effects evoked by stimulation of the gastrocnemius nerve at 3·0 and 15·5 times threshold for the nerve, which would activate group II and III afferents respectively, but also for the facilitatory action from stimulation at 1·6 times threshold.

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This stimulus was just maximal for group I and the facilitation would be caused by Ib impulses. The interpretation is that the interneurones which are involved in mediating excitatory action to motoneurones by group Ib, II and III impulses, were inhibited by impulses descending from suprasegmental structures.

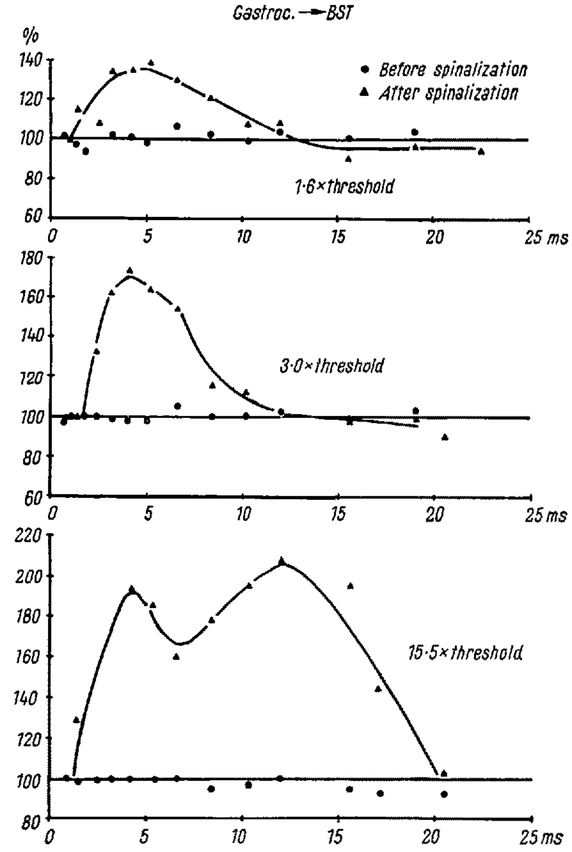

Fig. 1.—The effect of a conditioning volley in the nerve to gastrocnemius upon a monosynaptic testing reflex that was evoked by an afferent volley in the nerve to biceps posterior-semitendinosus (BST). The upper curve illustrates the action of a gastrocnemius volley which would be maximum for group I (1·6 times threshold); the lower show the effect of inclusion of group II (3·0); and group III (15·5 times threshold). The two sets of points at each strength were obtained just before (●) and just after spinalization (▲). In all curves the black line at 100% indicates the mean size of the unconditioned monosynaptic reflex.

The curves in Figure 2 show how the monosynaptic reflex from gastrocnemius was influenced by single conditioning volleys evoked at various strengths of stimulation in the nerve to flexor digitorum longus. After spinalization large inhibitory actions appeared in the two lower curves, being caused by group II and III afferent impulses respectively. Thus it is clear that interneurones mediating group II and III inhibitory actions on motoneurones of extensor muscles are also tonically inhibited from higher centres.

In the upper curve of Figure 2 stimulation at 1·55 times threshold was just maximal for group I and the inhibitory action appearing with spinalization presumably was evoked by impulses in Ib fibres. It has been a regular finding that the Ib inhibitory actions increased with spinalization, but usually these actions were observed before spinalization. It is of particular interest that, whereas in the spinal preparation the Ib inhibitory action from flexor digitorum longus usually was larger than those elicited from gastrocnemius or plantaris, the reverse occurred in the decerebrate preparation. This is demonstrated in Figure 3, where there are intracellular records from two plantaris motoneurones A–C before and D–G after the animal was made spinal. With increasing strength of stimulation to the flexor digitorum longus nerve there was hardly any change in the decay of the excitatory postsynaptic

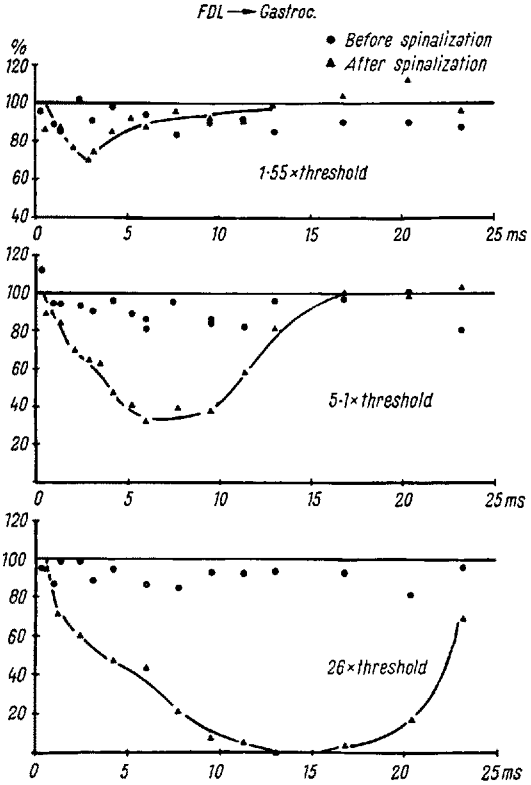

Fig. 2.—This is similar to Figure 1 but the monosynaptic testing reflex was evoked by volleys in the gastrocnemius nerve and the conditioning volleys in the nerve to flexor digitorum longus (FDL) at maximum for group I (1·55); on inclusion of group II (5·1) and group III (26 times threshold).

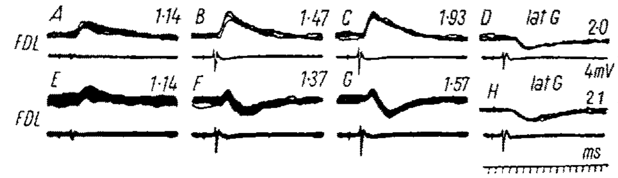

Fig. 3.—These intracellular records from plantaris motoneurones were obtained A–D before and E–H after spinalization. A–C and E–G show the effect of increasing the strength of stimulation of the flexor digitorum longus nerve. The figures indicate the strength of the volley with respect to the threshold of the nerve. D and H are the responses to an afferent volley (maximum for group I) in the lateral gastrocnemius nerve.

potential (A–C), showing that there was little or no inhibitory action. However, after spinalization the usual large inhibitory postsynaptic potential appeared in records F and G. On the other hand the inhibitory potential caused by Ib impulses from the lateral gastrocnemius-soleus nerve appeared before as well as after section of the cord.

It has been assumed that the functions of the Ib systems in the reflex taxis of the animal would be protective, i.e. too strong a contraction of the muscle would be prevented by autogenetic inhibition[7]. However, the pattern of connections in the spinal animal suggests an additional function of the Ib action. The large inhibitory action exerted by Ib impulses from flexor digitorum longus would appear with the active plantar flexion of the toes, at the height of the extension phase of the step and could be of importance for terminating the extension phase and initiating the flexion phase of stepping.

If impulses from flexor digitorum longus normally were a contributor in the reflex regulation of stepping, these inhibitory actions would clearly require control from higher centres, for example during voluntary contraction of the flexor digitorum longus or during running. A control at the interneuronal level would certainly be most effective. Such an inhibitory control presumably exists, although less pronounced, for Ib inhibitory actions from other muscles than flexor digitorum longus.

The functional implication of the suprasegmental control of interneurones mediating group II and III impulses may be a different one. Attention was drawn above to the co-existence in the spinal preparation of the entirely different pattern of synaptic actions caused by the two types of muscle spindle afferents, groups Ia and II respectively. In the present experiment there was no evidence that the synaptic linkage between Ia fibres and motoneurones was controlled from higher centres. On the other hand, with the interneurones mediating the group II and III actions, there exist very effective inhibitory control mechanisms from supraspinal centres. It may tentatively be suggested that in normal locomotion there is assistance by reflex actions from the Ia and Ib systems, but on account of this inhibition at the internuncial level impulses in group II and III fibres are largely without synaptic actions on motoneurones.

Zusammenfassung

An decerebrierten und spinalen Katzen wurden diverse somatische Afferenzen in ihren synaptischen Wirkungen auf Vorderhornzellen verglichen. Bei der decerebrierten Katze waren deren erregende und hemmende Wirkungen stark herabgesetzt oder nicht nachweisbar. Somit werden Zwischenneurone im Reflexbogen durch supraspinale Zentren tonisch gehemmt. Die Bedeutung dieser Kontrolle für die Reflexregulierung wird besprochen.

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Selective Depletion of Nor-Adrenaline in the Adrenal Medulla of the Rat After Administration of Reserpine (Histochemical Research)

Recent research (Carlsson and Hillarp[1], Kroneberg and Schümann[2], Molinatti *et al*[3]) has demonstrated that the alkaloids of *'Rauwolfia serpentina'* cause the liberation of catechol amines by the adrenal medulla of animals of different species.

In the rat, the administration of reserpine causes a definite modification of cellular chromaffinity; alongside various groups of cells completely devoid of pheochrome substance, the remaining glandular parenchyma preserves a normal degree of chromaffinity (Molinatti *et al.*[3]). As demonstrated by Hillarp *et al.*[4] and Eränkö[5], adrenaline and nor-adrenaline in the rat's medulla are contained in two distinct types of cells. Therefore the particular behaviour observed in this animal has suggested to us that under the action of reserpine only one of the two cathechol amines is selectively secreted.

This investigation therefore was carried out in order to examine the possible differences in behaviour of adrenaline and nor-adrenaline. The latter may be demonstrated histologically by means of Hillarp-Hökfelt's reaction[6], which consists in the formation of a pigment insoluble in

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