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Observations on 'Intact', De-Afferented and De-Efferented Muscle Spindles.

By

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The muscle spindles are controlled by the gamma efferents, as discovered in this laboratory by LEKSELL (1945) and confirmed and further elucidated by KUFFLER and HUNT (see summary 1952). GRANIT and KAADA (1953) showed that the spindles can be excited and inhibited from various foci in the brain. We have continued their work, especially with regard to supraspinal control of tonus.

The scope of this control measured as the difference between maximum excitation and inhibition obtained from one inhibitory and one excitatory focus in the brain, both affecting the same sensitive spindle, was found to be as great as 160 impulses per second. Hence the supraspinal governors are extremely potent and cannot be regarded as trivial. A mechanism of this order must be of corresponding physiological importance.

De-afferentation was used in both decerebrate and chloralosedial animals in order to find out whether supraspinal control required segmental afferents. This was found not to be the case. In several preparations the spindle frequency was not markedly influenced by de-afferentation except at high initial tension when often an increase was noted and ascribed to the release from the segmental inhibition described by HUNT (1951).

De-efferentation, however, led to a sudden drop of spindle frequency owing to denervation of the external loop through the

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muscle. At the same time the discharge became regularized and, at all initial tensions, stabilized significantly below the value of the spindle in possession of its gamma efferents. This experiment, too, was carried out over a large range of tensions from zero upwards. Even at zero tension the activated spindle (intact or de-afferented animal) had a higher frequency than the de-efferented spindle.

The experiments on de-afferentation demonstrate a striking difference in the behaviour of the ordinary motoneurones and the gamma motoneurones belonging to the spindle's intrafusal muscle fibre. The ordinary or alpha ventral horn cells fall down to a very much lower level of excitability after de-afferentation which, indeed, is the essence of the classical observation of SHERRINGTON on the decerebrate animal that de-afferentation removes the tonic contraction in the hind limbs. The gamma efferents, however, continue to discharge. This is particularly well shown by testing with the aid of tonic neck reflexes and comparing motor effect and muscle spindle activity. In such tonic activities the spindles are intimately engaged, excited or inhibited as the case may be, when the neck reflex upon the hind limb is elicited. After de-afferentation the spindles repeat their previous performance but the parallel reflex motor activity disappears or is very much depressed.

What is the reason for this difference between alpha and gamma cells in their reaction to de-afferentation? The simplest explanation is that the de-afferentation removed the facilitating effect of the spindle afferents that provided the turning point in these reflexes as well as the permanent supraspinal tonic facilitation. SHERRINGTON's argument, as is well known, was that de-afferentation removed the peripheral arc of the postural reflex responsible for tonus. But at that time it was impossible to forecast that the central influence from as distant a source as the brain itself had an important link in an external loop of control on the discharge of the muscle spindles. By de-afferentation one does not merely remove a peripheral segmental reflex arc but also the spinal and supraspinal control. When testing with tonic reflexes after de-afferentation one will therefore find the spindle afferents still respond in a manner which aids these reflexes while the muscle itself is quiet because the impulses from these important sources do not reach the ventral horn cells.

These remarks must not be interpreted to mean that all tonic

effects are mediated over the external loop consisting of gamma efferents → muscle spindles → monosynaptic arc → ventral horn cell. Instances were given of supraspinal tonic effects on the alpha ventral horn cells which could not be satisfactorily explained by reference to the muscle spindles alone.

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The Action of Succinylcholine and Curare on the Muscle Spindles.

By

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Succinylcholin-iodide is a quarternary ammoniumbase which has a transient blocking effect on the neuromuscular transmission. Working with isolated muscle afferents we have found it to be a powerful activator of muscle spindles. This activation is quite selective and leaves the Golgi-organs intact.

The excitation of the spindles is favoured by placing the muscle under some tension but can be obtained at zero tension by injecting larger doses. After a previous blocking of both large and small fibre (gamma) motor endplates by curare it is still possible to activate the spindles by succinylcholine.

The results will be published in full in this Journal (1953).
