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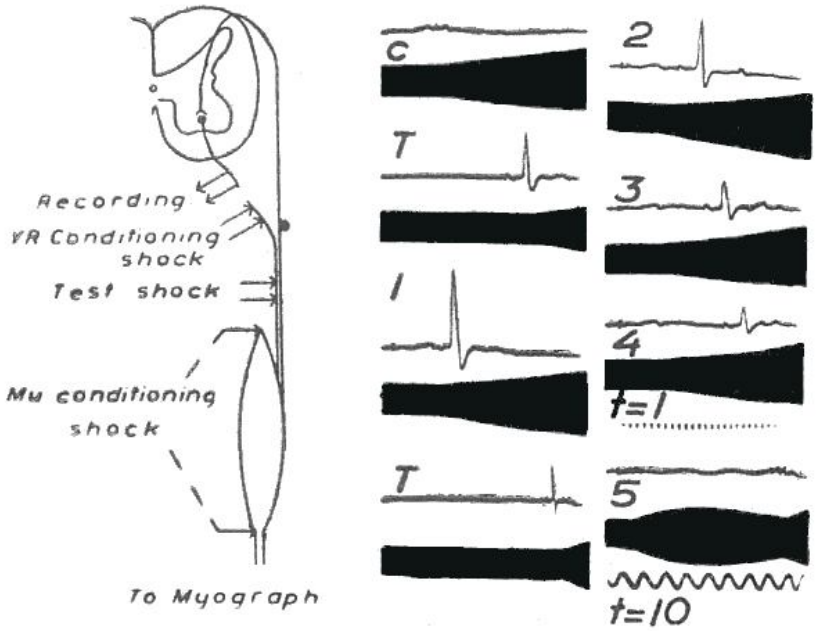
Self-Regulation of the Muscle Contraction by Facilitation and Inhibition from its Proprioceptors

In order to approach the question raised by the title of this communication, we need a method of testing the excitability of the motoneurones of one muscle, and of that muscle alone, while the muscle itself is contracting or passively stretched. To this end we make use of the properties of the monosynaptic arc analysed by Lloyd[1,2]. (i) A weak electrical test shock (see left half of diagram), set up through electrodes on the nerve of the ankle extensors (cat under 'Dial'), delivers a fast volley through the monosynaptic path in the spinal cord, faster than any other impulses, and this volley can be picked up at



Left half. Diagram of monosynaptic reflex circuit from the ankle flexor afferents to ventral root, which is divided into two portions. Stimulating electrodes on distal stump, recording electrodes on proximal stump. Electrodes for test shock on muscle nerve

Right half: The eight paired records all consist of response from 'recording' electrodes (above) and muscle tension on an isometric myograph (below). Initial tension in all records about 250 gm.; conditioning shock, alone in *C*, adds about 280 gm. *T* (upper), test shock alone. 1–4, both combined at different intervals, measurable on time-scale $t = 1$ (= 1 msec. between marks). *T* (lower) with time-scale ten times as big, $t = 10$. 5, on same scale shows long interval between conditioning shock and test shock

the point marked 'recording' on the central stump of the halved ventral root S_1. The other ventral roots from L_5 backwards have been severed and the leg denervated except for the nerve to the ankle extensors. (ii) The monosynaptic volley traverses

fibres which, on the afferent side, originate in, and, on the efferent side, return *to*, the muscle concerned, so that the test shock actually tests the excitability of its motoneurones alone.

This test shock sets up control response T on the fast record in the diagram (right half, T, upper) for which the speed of sweep of the cathode ray is found from the line $t = 1$ (= 1 msec. between dots). The volley is seen to have needed about 3 msec. from its preceding shock artefact to reach the recording electrodes. Below the response T is given a record of the beginning of the muscle contraction which, of course, succeeds T and thus cannot influence the testing of the motoneurones by T traversing the spinal cord. The muscle can, in addition, be made to contract by administering a preceding conditioning shock C, either to the distal stump of the cut ventral root (= *VR*-conditioning shock) or, alternatively, to the muscle itself (= *Mu*-conditioning shock). In the right half of the diagram, C shows the muscle contraction, again below the corresponding impulse record, initiated by the *VR*-conditioning shock alone. An *Mu*-conditioning shock would have given similar results. **Conditioning shocks must be weak.**

The muscle contraction, whether elicited in one way or the other, sets up impulses which modify the excitability of the motoneurones, tested by shock T, which in records 1, 2, 3 and 4 is shifted farther away from the conditioning shock that is always placed in the records as in C. In 1 there is strong facilitation of T. This diminishes in 2. In 3 the test shock is already depressed, and in 4 this depression is still greater. The speed of sweep of the cathode ray is then diminished to $t = 10$ (= 10 msec. between wave tops). A new test shock T (bottom record in first row) is first thrown in as control. It is somewhat smaller than the earlier one, and this amount of natural variation is nearly always present with monosynaptic volleys. Then, in record 5, the test shock is thrown in very late in the contraction set up by the conditioning shock, and is now found to be almost completely inhibited. This transient or phasic inhibition is less prominent with low initial tension of the muscle and becomes very much stronger when the contraction starts from a level of good tension. If the sweep is triggered by merely stretching the muscle quickly instead of stimulating it to contract, the phasic inhibition obtained can be just as complete as that set up by a contraction. **Part of the inhibition may be peripheral.**

The muscle is thus provided with nervous governors, first facilitating its contraction, then putting on the brakes. At least in some animals, *both* governors may be 'tonic', a fact of great interest

for spastic states and the phenomenon of decerebrate rigidity, which hitherto has been interpreted chiefly on the basis of afferent excitation, because adequate methods for the analysis of autogenetic afferent inhibition have not been available. A few references to early important work[3,4,5] may serve to indicate the background.

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