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BASIC MECHANISMS OF OCULAR MOTILITY AND
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Opening Address

COMPARING SOME CONTROL MECHANISMS IN SKELETAL AND EYE MUSCLES

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FOR one who like myself has worked with the eye and with muscular afferents, but never with the two of them co-operating in extraocular muscles, it seems natural to discuss some points of contact between eye muscle and skeletal muscular control in the hope that this would be of some interest to an audience of specialists on eye movements.

There seems to prevail among many of those working on eye movements the misunderstanding that the stretch reflex is one only. Long ago I (1955) pointed out that there are three such reflexes or as many as there are types of stretch-sensitive endings. This has recently again been stressed by Matthews (1972). Of them the best known is the excitatory one of the primary spindle afferents which is both mono- and polysynaptic. This is the extensor stretch reflex of Liddell and Sherrington (1924). Another one from the muscle spindle's secondary endings is inhibitory on the leg extensors and thus opposes the former. It has excitatory effects in the flexors and in both places is wholly polysynaptic. The third stretch reflex derives from the Golgi tendon organs and so far, wherever seen, has been found to be inhibitory on its own muscle.

These statements refer to reflexes within the spinal cord but in addition all three sensory endings have cortical cerebral and cerebellar projections whose elaboration exceeds what one could anticipate a few years ago. It is not known what purposes they serve but, in view of the dominating alpha-gamma linkage in motor acts, it seems reasonable to expect the spindles to be coactivated in order to make possible feedback information about the resulting movement. My own favourite hypothesis is that their cerebral role is to check whether a demand has or has not been accomplished according to order. The recording of spindle activity in man, introduced by Hagbarth and Vallbo (1967) and perfected by Vallbo (1970, 1971) has shown voluntary movement to be carried out in alpha-gamma linkage and this, indeed, is a situation in which it is possible to vary demand and study accomplishment.

Considering that spindles mostly operate in alpha-gamma linkage, their role in eye muscles should be to accompany contraction. They would be feebly active in passive stretch as, for instance, in the particular motoneurons under reciprocal inhibition. If only the polysynaptic component were present in the extraocular muscular afferents—as we have reason to believe—the decisive factor would be the nature of the biasing activity. To pursue these problems the experimenter would need a preparation in which

there is a large number of extraocular spindles. The monkey can hardly be called such a preparation. It has only about six spindles in each eye muscle (Greene and Jampel, 1966) whereas man has about fifty (Cooper and Daniel, 1949, 1963) and the goat a still greater number (Cooper *et al.*, 1951). We have no definite explanation of why this should be so, only the basic conviction that evolution does not support a meaningless increase of afference on such a scale.

To give my attitude to spindle physiology in a nutshell, the emphasis should be on the fact that these are organs under control of the gamma loop and that hence the chance of being able to elucidate their role in oculomotor mechanisms is tied to the chance of finding from where and under what circumstances the loop can be shown to become operative. This, in the first instance, means finding central stations which excite or inhibit the discharge of spindle afferents. It is impossible to advance such problems without putting next on the list the need for finding out to what an extent there is alpha-gamma linkage also in the oculomotor system and, again, this would begin with a search for places from which the ocular gamma system can be activated. Its existence has already been demonstrated by Whitteridge (1959).

I find it pointless to delay the proceedings of this conference by theorizing extensively about the possible role of extraocular muscular afferents in the various types of eye movements known. But it may be worth while to draw the attention of this gathering to the fact that a substantial body of evidence supports the general conclusion that the gamma efferents are activated also in general arousal which of course is highly pertinent to the experimental analysis of eye movements.

There is an amusing parallel between the two fields of skeletal and eye muscle control respectively. I mean the fact that the number of central sites from which activation somehow correlated with eye movements can be obtained, just as is the case in the field of skeletal muscle control, appears to increase virtually in proportion to the number of experimenters devoting themselves to central stimulation and recording. This actuates three general problems: (i) the definition of prime movers and the study of interactions and constraints in their operations; (ii) separation from prime movers of places merely in need of information to the effect that eye muscles are being or have been activated including the problem of why these places should require such knowledge; (iii) the question of whether there are sites which are activated merely for the sake of being prepared to play a role should need for this arise.

While the first two points are obvious enough and also recognized in the literature on eye movements, the third may seem obscure. However, I have in mind an analogy with skeletal muscle control which may be relevant also in the field of oculomotor physiology. This is the fact that commands to certain limb motor units to execute a definite, restricted movement can be shown to elicit changes of membrane potential in motoneurons which are not called upon to participate in the movement ordered from above. The evidence is derived by the technique of monosynaptic testing which is a way of measuring the number of excited or inhibited motoneurons raised above or suppressed below threshold within the pool of one specific muscle or synergic muscle group. For instance, when the right soleus alone was given the command to act in response to a warning signal, the Achilles tendon reflex was enhanced on both sides during the preparatory period (Requin, 1969). A number of experiments of this general type have been published recently and some were mentioned by Zalkind at the recent Conference on motor control in Varna. I was reminded of this kind

of evidence for accompanying "ghost" motor activity not demanded for a specific act, when I found Westheimer and Blair (1972) stating, that "there is, physiologically speaking, no such thing as a single direction of pull of an extraocular muscle... In general, any saccadic movement involves all muscles". But in a wider context one might think of preparatory activity in, say, extraocular muscle nuclei, vestibular or mesencephalic reticular nuclei, neck muscle motoneurons and other sites when only one of them actually produces the given motor act.

Returning to the afferent side of control problems, it deserves to be emphasized that many inputs are relevant only in combination with others. There is, for instance, the recent experiment by Marsden *et al.* (1972) in which they studied the responses to loading and unloading of the flexor of the top joint of the thumb. When the hand was anaesthetized with the aid of a wrist cuff, the spindles and tendon organs in the muscle, whose tendon alone runs down to the top joint, could not by themselves produce the normal load compensation to a resistance. Seemingly redundant information proved to be non-redundant.

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