

THE PROBABLE ROLE OF MUSCLE SPINDLES
AND TENDON ORGANS IN EYE MOVEMENT CONTROL

RAGNAR GRANIT

It is not possible in this context to cover the information we possess on the role of muscle spindles, the gamma-loop and the tendon organs in posture and locomotion. The author has reviewed our knowledge and hypotheses in a book in course of publication (Granit, 1970) entitled, *The Basis of Motor Control*, and to this the reader is referred for the evidence behind the brief statements to be given below.

Eye muscles provided with muscle spindles are regularly found only in primates and ungulates. For these species the extrinsic eye muscles are stated to be the spindle richest in the body competing in this respect with the neck muscles. They are innervated by fusimotor gamma fibres of the static type (definitely shown) and the dynamic type (suggested by indirect evidence). It is not known whether fusimotor alpha innervation is present. The slope of curves illustrating impulse frequency in the afferent nerve fibres from spindle primaries plotted against muscle length increases a great deal, up to sevenfold, under fusimotor gamma stimulation, implying that the static sensitivity to stretch increases under pull. Impulses have never been recorded from the afferents of spindle secondaries in eye muscles, but since these are provided with a static fusimotor innervation, their impulse frequency-length curves are likely to follow those of the primaries.

The statements to the effect that stretch reflexes are absent in extrinsic eye muscles need not be taken too seriously. Stretch reflexes are absent also in the skeletal musculature of normal subjects, unless the fusimotor neurons are specifically activated and the alpha motoneurons (of the extrafusal musculature) in an active state, i.e., sufficiently depolarized. Normally only the brief stretch reflexes known as "tendon jerks" can be elicited. Good stretch reflexes are obtained in normal subjects by activating muscle spindles by rapid vibrations applied at the tendons. All the evidence at present available shows that the stretch reflex is an adjunct to contraction and that alpha and gamma motoneurons are activated together in working muscles. This is the concept of alpha-gamma linkage. Thus, for instance, in respiration gamma activated spindles fire in the contraction phase of intercostal muscles; in volitional activation of muscles of the extremities the spindles likewise fire during contraction, as shown by recent successful attempts to record spindle impulses in man. Many other examples could be mentioned. Essentially, the gamma-activated spindle mechanism may be regarded as a governor of

muscular performance both in tone and locomotion. As long as we do not possess as precise information of spindle and tendon organ functions in the normal operations of eye muscles as we have for muscles of the extremities and the ribs, the best one can do in order to understand the role of these organs in eye movements is to apply the principles derived from the other fields of study to the case in hand.

One of the best known tasks of the gamma-assisted stretch reflex is to provide a stable length-setting at any desirable length of the muscle. This is determined by the amount of gamma-bias applied. If the contracting muscle is stretched by a load, the spindles produce automatic *load compensation*; if it is contracted in excess of the applied gamma bias, the silent period *unloads* the spindles thereby preventing excitation of the muscle's alpha motoneurons. It seems more than probable that settings of the gaze are servo-assisted in this manner. The reason for this conclusion is that these two operations will all be automatic as soon as the spindles are under fusimotor influence.

Good evidence for feedback control of the eye muscles is provided by Dr. Carter Collins at this Symposium (Chapter 10). He and his co-workers have shown that in man the tension-extension curves of an extrinsic eye muscle in man are parallel at whatever angle of gaze stretching is begun. The experience from experimental work with the muscle-nerve preparation or with so-called alpha rigidities of cats tells us that in pure alpha activity stretch should produce a set of curves of different slopes depending on the number and firing rate of the alpha fibres. Parallel curves are a definite sign of proprioceptive control, probably executed jointly by spindles and tendon organs on the alpha motoneurons, the former excitatory, the latter inhibitory.

When two antagonist forces are active, as in non-reciprocal eye movements, the consequent variations of loading will automatically activate the muscle spindles and then fusimotor "settings" across the gamma-loop will determine the sensitivity of the muscle to changes of length. In reciprocal action the opposing force will be the elastic pull on bulbar tissue and this, too, will contribute to determining the static sensitivity in relation to angle of gaze.

Eyes without spindles can provide but a crude imitation of the mechanism of the gamma-controlled stretch reflex. This reflex at any one length (angle of gaze) lacks the automatic control that the gamma-spindle mechanism provides for this particular task.

The unvolitional saccadic movements in the eye of the cat are far less prominent and of much lower frequency than in man. Even though these movements are centrally induced and symmetrical in the two eyes, they are likely to make use of the built-in spindle control of the muscular acts which then would operate on binocular alpha-gamma linkage controlled from the same central station. The higher the sensitivity of the fusimotor setting, the greater would be the frequency of the saccades.

There has been no work specifically on muscle spindles in extrinsic eye muscles as involved in the actual process of controlling eye movements. But

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it is known from work on ungulates (goat) that the static sensitivity, also called the position sensitivity, may increase up to seven times under the influence of fusimotor gamma activity. A powerful augmentation of this order of magnitude can hardly be negligible for the motoneurons controlling the extrinsic muscles, unless the spindle input differs fundamentally from its central distribution elsewhere in the body where spindle projections go to the motoneurons of their own muscle. Regrettably we have no precise information on this important issue and the suggestions given above presuppose that spindle afferents project on the motoneurons of the eye muscles in which these organs are situated. They likewise presuppose that spindle primaries are excitatory and tendon organs inhibitory in the stretch reflex, as these organs are elsewhere in the body. As long as it has not been shown that in this respect these proprioceptors possess central projections differently organized from what they are elsewhere, it is necessary to assume that they are similar, that is, both mono- and polysynaptic.

Finally, it should be pointed out that dynamic fusimotor fibres sensitize the spindle primaries to velocity of stretch. As to the spindle secondaries, which only possess static sensitivity, some doubt may be entertained about their role in eye muscle control. These organs have been found to be excitatory on flexor muscles and inhibitory on extensor muscles. For this there is no obvious parallel in the organization of eye movements.

REFERENCE

GRANIT, R. (1970) *The Basis of Motor Control*. Academic Press, London.