Fusimotor Effects on Position and Velocity Sensitivity of Muscle Spindles

For the elaboration of a mathematical model of muscle spindle dynamics, more physiological data on the properties of primary and secondary spindle endings were considered necessary. With this in mind the response to stretch and release of the muscle along symmetrical ramp or parabolic length-time courses was studied both in the absence of any fusimotor bias as well as during steady stimulation of single fusimotor fibres of either the 'static' or the 'dynamic' type[1-3]. The following preliminary report concerns results obtained mainly with ramp movements. A full report will be published on a later occasion.

Methods. Muscle spindles of the soleus and lateral gastrocnemius muscles were studied in 43 cats anaesthetized with pentobarbital (Nembutal, 'Abbott', 35 mg/kg injected i.p.). The left hind leg was partially denervated. Laminectomy was performed to give access to dorsal and ventral roots of L7 and S1, both for recording from single spindle afferents and for stimulating single fusimotor fibres in ventral root filaments[2-5]. For dynamic analysis of impulse frequency (f)-muscle length (ΔL) relations, periodically recurring muscle length changes of triangular length-time courses were used; the increment and decrement of length were of equal duration with no pause in between. These movements were derived from an appropriately shaped cam driven by an electrical motor over a gear box. The periodicity was varied between $^1/_{512}$ c/sec and 2 c/sec in steps of one octave. The amplitude was mostly kept at 8 mm, yielding velocities varying between 0.03 mm/sec to 32 mm/sec. The length changes (ΔL) were monitored by a differential transformer and registered on the X-axis of a C.R.O. The impulse frequency (f) of the spindle afferents was recorded by means of an 'instantaneous frequency meter'[6]; the signal from the meter was displayed on the Y-axis of the same beam of the C.R.O. In this way, impulse frequency-muscle length diagrams, to be denoted as f-ΔL diagrams, were obtained.

Steady state f-ΔL diagrams were obtained from measurements of average discharge rate about 30 sec after each of a series of step changes of length. The slope of the steady state f-ΔL diagram has been regarded as an expression of the 'position sensitivity' of the ending. Test stimuli of parabolic ΔL-time relations did not reveal any specific sensitivity to accelerations. Therefore the difference between the dynamic and the steady state f-ΔL diagrams at the same extension has been regarded as an expression of the responsiveness to rate of change of position, i.e. 'velocity sensitivity'.

Results. (1) Without fusimotor activation. Primary endings. The response of primary endings to a step change from constant negative velocity to constant positive velocity could be subdivided into 2 parts of quite different time courses. The 'quick' part of the velocity response consisted of a rapidly rising step-increase of firing rate as compared with the steady state values. The amplitude of the 'quick' part of the response was found to be linearly related to the magnitude of the step-increase in velocity. The 'slow' response appeared as an increased slope of the rising phase of the f-ΔL diagram on top of the 'quick' response. It increased in magnitude up to velocities of 0.5 mm/sec, but, in the absence of fusimotor activation, no further increase of the slope was observed as the velocity increased above 0.5 mm/sec. It should be recalled that CROWE and MATTHEWS[3] observed 2 different time courses in the decay of discharge on completion of stretching.

In the relaxation phase, the rate of firing very rapidly dropped to zero at velocities of higher numerical values than 0.5 mm/sec (see Figure 1 A). Even at velocities as low as 0.03 mm/sec there was a greater difference in slope between the steady state diagram and the falling phase of the dynamic f-ΔL diagram than was found between the rising phase of the dynamic and the steady state diagrams.

Secondary endings, in contrast to primary endings, showed the same slope of the f-ΔL diagram during both release and stretch of the muscle. The slopes increased slightly with increasing velocity. A 'slow' part of the velocity response of the secondary endings thus existed. The release part of the diagram was shifted slightly downwards as compared with the phase of length increment (Figure 2 C). This indicates the existence of a 'quick' velocity response, which was of the same amplitude both during stretch and release of stretch.

(2) Dynamic fusimotor activation. Earlier work has shown that dynamic fusimotor fibres, on stimulation, increase the response of the primary ending to muscle stretch[2-4]. It is also generally agreed that the dynamic fibres predominantly exert their action on primary endings[3-5] and only very rarely influence secondary endings[5]. In the present study it was found that the position sensitivity of the primary ending was not changed by dynamic fusimotor activation. The increase in velocity sensitivity was predominantly caused by the 'slow' part of the velocity response. This is illustrated in Figure 1, where A is the unstimulated control diagram and B the

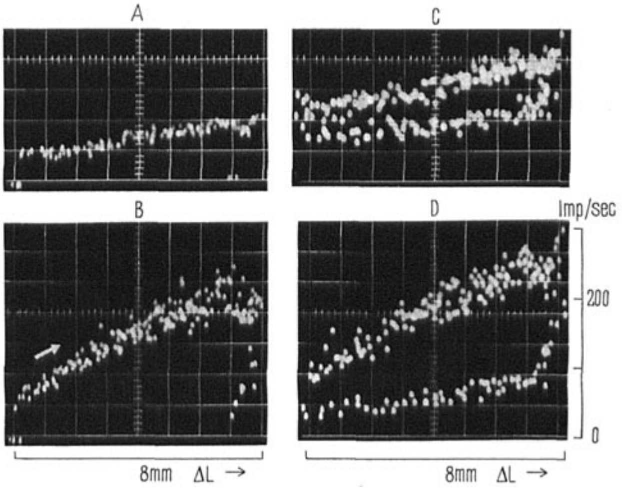

Fig. 1. f-ΔL diagrams of a primary ending during 8 mm/sec muscle stretch and relaxation in the absence and presence of fusimotor stimulation. The upper part of each diagram represents the phase of stretch. Extension (ΔL) increases to the right in the pictures. The arrow in B shows the point movement in time in the diagram. Impulses/sec calibration is the same in all diagrams. A, The ending without stimulation. In B a dynamic fusimotor fibre is stimulated at the rate of 70/sec. In C a static fibre (type I) is activated at the rate of 70/sec. D, the response to stimulation of the dynamic and the static fibre simultaneously at the rate of 70/sec.

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[6] P. B. C. MATTHEWS, J. Physiol., Lond. *169*, 58P (1963).

response to dynamic fibre stimulation. Since the position sensitivity remained uninfluenced by dynamic fibre stimulation, the increase in slope of the f-ΔL diagram was due to an increase in magnitude of the 'slow' component. During dynamic fusimotor activation, the 'slow' velocity response appeared to be logarithmically related to the velocity. In the dynamically activated ending, the 'slow' velocity response increased with increasing velocity values over a much larger velocity range than in the unbiased conditions.

The 'quick' part of the velocity response was also increased, but to a much less extent than the 'slow' response. The amplitude of the former part became more exponentially related to the velocity during dynamic fusimotor activation.

It was never found possible to compensate for the great reduction in firing during release of stretch by stimulation of a single dynamic fibre. The fall in frequency did not occur as rapidly, however, as without stimulation, so that the 'quick' part of the velocity response during relaxation could sometimes be recognized.

On activation of primary endings by stimulation of one of their dynamic fibres at high rates of stimulation, 'saturation' of the response was often observed. The level of saturation of frequency increased with increasing stimulus rate and increasing rate of change of length. The amount of extension at which the saturation first appeared mainly depended on the rate of fusimotor stimulation and occurred at shorter lengths in the upper range of stimulus rate.

(3) Static fusimotor activation. It is generally agreed that static fusimotor fibres on stimulation either do not influence the response of the spindle ending to rapid muscle stretch, or, sometimes, even lower the response[2-4]. It is also known that the responses of both primary and secondary endings can be influenced by static fibres[2-5]. The static fusimotor fibres controlling primary endings could be divided into 2 functional groups. On stimulation, members of the first group, or type I static fibres, increased the resting discharge of the ending but did not influence their sensitivity to both position and velocity. An example of this type of effect is given in Figure 1 C. In response to stimulation of fibres belonging to the second group, type II, both the resting discharge and the position sensitivity of the ending was augmented whereas the 'velocity response' remained unchanged. Examples of type II effects are given in Figure 2 A and B.

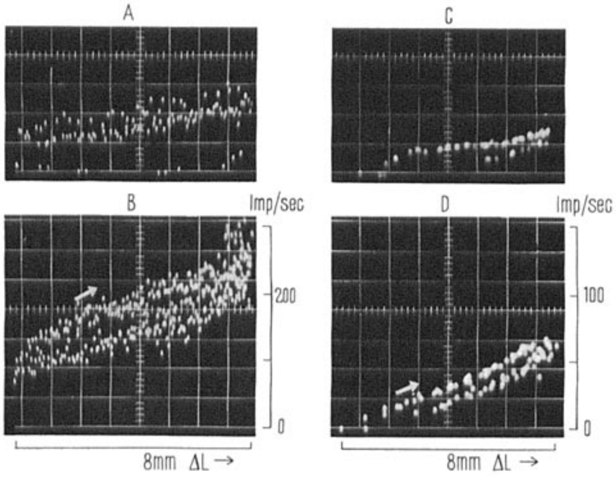

Fig. 2. f-ΔL diagrams showing the effect of static fusimotor type II activation of a primary and a secondary ending respectively. The velocity of movement is 8 mm/sec in A and B and 16 mm/sec in C and D. Extension (ΔL) increases to the right in the pictures. The arrows in B and D show the point movement in time in the diagrams. Impulses/sec calibration is the same for A and B, and for C and D. A, Response of primary ending in absence of stimulation; B, in the presence of stimulation of a static fibre at the rate of 70/sec. C, Response of a secondary ending without fusimotor stimulation; and D, with stimulation at the rate of 70/sec of a static fibre other than the one used in B.

The static fibres acting on the secondary endings could similarly be divided into 2 corresponding groups. The effects of the 2 types of fibres could be described in the same terms as used above for primary endings. The effect of a type II static fibre on a secondary ending is illustrated in Figure 2 C and D.

These 2 types of static fusimotor fibres were not equally distributed to primary and secondary endings. In the extensor muscles of the ankle, primary endings were more commonly activated by type I fibres, while the majority of the secondary endings were under the control of type II.

(4) Activation of 2 fusimotor fibres. Stimulation of 2 fusimotor fibres converging onto the same ending were made in several cases. A complete summation of the 2 individual responses was not seen. On simultaneous stimulation of one dynamic and one static fibre, the very characteristic effect illustrated in Figure 1 D was consistently obtained. During the phase of length increment the summated f-ΔL diagram corresponded to that of stimulation of the dynamic fibre alone, whereas the effect of static fusimotor stimulation dominated the response during the phase of release.

Conclusion. The dynamic analysis of muscle spindles reported have given the following new results: (1) Dynamic fusimotor activation had a different influence on the 'quick' and the 'slow' velocity response of the primary ending. The range of the 'slow' velocity sensitivity was greatly extended by dynamic fusimotor stimulation. (2) 2 types of static fusimotor effects acting on both primary and secondary endings occurred. Type I did not influence the position sensitivity, which was enhanced only by type II[7].

Zusammenfassung. Primäre und sekundäre Muskelspindelendigungen der Katze wurden mit sowie ohne statische und dynamische γ-Aktivierung, bei periodischer Dehnung und Entspannung über einen weiten Geschwindigkeitsbereich untersucht. Es wurde die Lage- und Geschwindigkeitsempfindlichkeit bestimmt; dabei wurden 2 Typen statischer γ-Effekte bei den primären wie auch sekundären Endigungen beobachtet.

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