FUSIMOTOR STIMULATION AND THE DYNAMIC SENSITIVITY OF THE SECONDARY ENDING OF THE MUSCLE SPINDLE

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SUMMARY

The response of secondary endings of de-efferented muscle spindles in the soleus muscle of the anaesthetized cat was recorded during stretching of the muscle at velocities of 5–30 mm/sec. Stimulation of single fusimotor fibres, most and probably all of which were static fusimotor fibres, produced no appreciable change in the normally small dynamic sensitivity of these endings.

INTRODUCTION

It is now well established that the primary afferent ending of the muscle spindle of the cat is controlled by two functionally distinct groups of motor fibres, the static and the dynamic fusimotor fibres (Matthews, 1962). These may be distinguished by their action on the sensitivity of the ending to dynamic stimuli. Recently, Appelberg, Bessou & Laporte (1966) have shown that the secondary afferent ending of the spindle is acted upon by the static fibres alone. The primary ending is strongly excited by static fusimotor activity when the muscle is at a constant length, but its additional response to a dynamic stimulus tends to be reduced (Crowe & Matthews, 1964*a*, *b*). The present paper shows that the action of static fusimotor fibres on the secondary ending is largely similar, and that they do not alter the normally small dynamic response of this ending over a range of velocities of stretching. Appelberg *et al.* (1966) have already published a couple of records showing this effect on two endings in tenuissimus.

METHODS

The experiments were performed on six cats anaesthetized with pentobarbitone sodium. The endings studied all lay in the soleus muscle, which had been functionally isolated from the spinal cord by section of the appropriate spinal roots. The methods were the same as those previously employed and already fully described (Matthews, 1962; Matthews, 1963; Crowe & Matthews, 1964*a*). Indeed, three of the endings included in the present paper were studied in the course of an earlier series of experiments and the findings then very briefly mentioned (Crowe & Matthews, 1964*b*).

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The discharge of functionally single afferent fibres was recorded from the peripheral ends of thin dorsal root filaments. The afferent fibres were considered to supply muscle spindle endings because of the pause in their discharge on stimulating the muscle nerve. The endings were presumed to be secondary endings because all the afferent fibres studied had conduction velocities below 60 m/sec, and because they were rather insensitive to dynamic stimuli (Matthews, 1964). Functionally single fusimotor fibres were isolated in the peripheral ends of thin ventral root filaments. They were sought by repetitively stimulating a number of medium-sized ventral root filaments while observing the response of an individual secondary ending to stretching the muscle. Any filament with an excitatory effect on the ending was subdivided until a filament was obtained which contained only one motor fibre to soleus (i.e. only one spike recordable from the filament on stimulating the muscle nerve), and which still produced an excitatory effect. All fibres so isolated proved to be γ motor fibres with a conduction velocity of 25–40 m/sec, and on stimulation produced no detectable contraction of the muscle. The muscle was stretched with an electromagnetic puller (Matthews, 1962). All endings were studied with extensions of 4, 5 or 6 mm applied at velocities of 5–30 mm/sec. The final length of the muscle corresponded approximately to the maximal length it could take up in the body with its normal attachment. The discharge of the afferents was used to trigger a reciprocal pulse interval display which was photographed along with records of the length of the muscle and the tension in it.

RESULTS

Eleven secondary endings were studied during stimulation of single fusimotor fibres. Sixteen fusimotor fibres were studied, two of which each acted upon two endings. Thus, in all, eighteen combinations of a single fusimotor fibre with a secondary ending were studied. On the basis of the findings of Appelberg *et al.* (1966) the fusimotor fibres may be assumed to have been static fusimotor fibres, for these are the only ones which significantly excite the secondary ending. On eight occasions the fusimotor fibre studied was unequivocally shown to be a static fibre for it was possible to show that its stimulation influenced the behaviour of a single primary ending in the required manner. The primary ending is unlikely to have been in the same muscle spindle as the secondary ending, but this is immaterial for the above argument as an individual static fusimotor fibre produces a static effect on all the primary endings that it influences (cf. Brown & Matthews, 1966).

Figure 1 shows the typically small effect of static fusimotor stimulation on the response of a secondary ending to velocities of stretching of 5 and 30 mm/sec. In the absence of fusimotor stimulation the ending was firing about 20 impulses/sec at the initial length and about 40 impulses/sec at the final length; but at the beginning and end of the dynamic phase of stretching the frequency of discharge of the ending changed only slightly, thereby showing its comparative insensitivity to the velocity stimulus (Matthews, 1963). Stimulation of a single static fusimotor fibre at 100/sec increased the discharge of the ending at all lengths of the muscle by about 40 impulses/sec, but the alteration in its discharge at the beginning and end of the dynamic phase of stretching remained very small for both

velocities of stretching, showing that its dynamic sensitivity had not been increased by the fusimotor stimulation.

The effects of fusimotor stimulation on the dynamic sensitivity of all the endings studied were compared by means of the 'dynamic index' which provides a crude measure of the velocity sensitivity of an ending (Crowe & Matthews, 1964a; Matthews, 1963). This figure is defined as the difference in frequency between the discharge at the very end of the dynamic phase of stretching, while the velocity stimulus was still present,
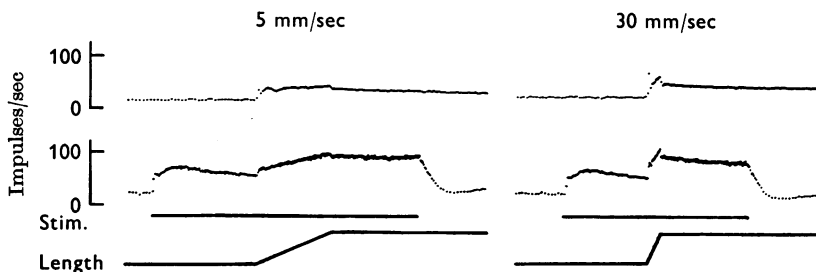

Fig. 1. The effect of static fusimotor stimulation on the response of a secondary ending to stretching. The scale shows the instantaneous frequency of discharge of the ending (reciprocal pulse interval display). The muscle was stretched 5 mm at 5 mm/sec, and at 30 mm/sec, both in the absence of stimulation (above), and during stimulation of a single fusimotor fibre at 100/sec (below). (The stimulus and length markers are diagrammatic. The time scale may be judged from the duration of the periods of dynamic stretching. The conduction velocity of both the afferent fibre and the fusimotor fibre was 39 m/sec. The fusimotor fibre was shown to be a static one by observing its action on a primary ending.)

and the discharge occurring 0·5 sec later when the muscle is at the final length and there is no velocity stimulus. In the absence of stimulation the dynamic index was always small ($<$ 15 impulses/sec for 5 mm/sec stretching, and $<$ 30 impulses/sec for 30 mm/sec stretching; cf. Matthews, 1963). During fusimotor stimulation at 100/sec (occasionally 70/sec or 130/sec used instead) the dynamic index was on average barely altered for any velocity of stretching (5, 10, 20, 30 mm/sec). Figure 2 shows the actual changes produced by fusimotor stimulation in the dynamic index on stretching at 5 and 30 mm/sec for each combination of a secondary ending and a fusimotor fibre. In some cases the dynamic index was slightly increased, but the largest increase was only 13 impulses/sec, which is far smaller than that produced by dynamic fusimotor stimulation on the response of the primary ending when the dynamic index may increase by up to 250 impulses/sec (see comparable illustrations in Crowe & Matthews, 1964b and Brown, Crowe & Matthews, 1965). Similar small increases in the dynamic index are sometimes seen when a static fibre is acting on a primary ending. It may be noted that because of the normally small

dynamic index of the secondary ending there is not as much scope for its reduction as there is for the normally larger one of the primary ending. A more important point is that the absolute value of the dynamic index of the secondary endings remained very low during fusimotor stimulation (mean dynamic index for 5 mm/sec stretching $7 \cdot 7 \pm 2 \cdot 3$ s.d. impulses/sec, and for 30 mm/sec $17 \cdot 9 \pm 8 \cdot 8$ s.d. impulses/sec). It was similar to or smaller than that of a primary ending during static fusimotor stimulation.
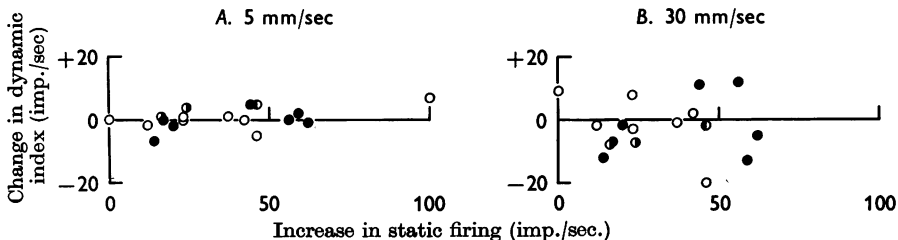

Fig. 2. Scatter diagrams relating the effect of stimulating single fusimotor fibres on the 'dynamic index' to their effect in exciting the same endings under static conditions. Each point represents one combination of a fusimotor fibre with a secondary ending. Ordinate, the difference between the dynamic index during fusimotor stimulation and that occurring in the absence of stimulation, *A*, for 5 mm/sec stretching, *B*, for 30 mm/sec stretching. Abscissa, the increase in the discharge of the ending produced by the fusimotor stimulation when the muscle was at the initial length. The frequency of stimulation was usually 100/sec (●, ○), but twice was 130/sec (◑), and once was 70/sec (◒); the open circles (○) show effects due to fusimotor fibres which were proved to be static ones by their action on a primary ending.

Figure 1 and 2 also demonstrate the rather considerable excitatory effect produced on secondary endings by fusimotor stimulation when the muscle was at a constant length. The mean figure for the increase in the discharge of secondary endings on fusimotor stimulation at 100/sec with the muscle at the initial length was 35 ± 14 s.d. impulses/sec (15 observations). This may be compared with the figure of 65 ± 29 s.d. impulses/sec (30 observations) given by Crowe & Matthews (1964a) for the action of static fusimotor fibres on primary endings with the muscle at the initial length (the stimulation frequency in the earlier experiments was also 100/sec, but this information was inadvertently omitted from the paper). For both primary and secondary endings the increase in discharge produced by fusimotor stimulation was usually slightly larger when the initial length was increased. Thus, within the limits of sampling errors and those involved in the comparison of different series of experiments, it may be concluded that in terms of impulses/sec the excitatory effect of static fusimotor fibres on secondary endings is about half as great as it is on primary endings.

DISCUSSION

These results show more systematically than any done before that, while fusimotor stimulation may powerfully excite the secondary ending, this ending nonetheless remains largely insensitive to velocity stimuli. The fibres stimulated in the present experiments were probably all static fusimotor fibres, and their action on the secondary ending is seen to be very similar to that on the primary ending. Appelberg *et al.* (1966) observed, on a single occasion, a secondary ending which was acted upon by a dynamic fusimotor fibre. The effect was to increase markedly the response of the ending to a dynamic stretch while only weakly exciting it at the initial length of the muscle. A. Crowe & P. B. C. Matthews (unpublished) also made a similar observation for one dynamic fusimotor fibre acting on two separate secondary endings (soleus of cat, afferent conduction velocities 39 and 27 m/sec, fusimotor conduction velocity 33 m/sec), but the effects were very much smaller than that illustrated by Appelberg *et al.* (1966). The main finding of Appelberg *et al.* was that in their seven other preparations dynamic fusimotor fibres produced no significant effect on the secondary ending, even though the fusimotor fibre had been shown to supply the muscle spindle in which the secondary ending lay. The method of selection of fusimotor fibres in the present experiments would probably not have led to the isolation of fibres with only a weak excitatory action.

The precise action of the fusimotor fibres within the spindle is obscure, but the present results would be adequately explained by supposing that static fusimotor fibres excite intrafusal muscle fibres which behave as if they have a relatively low 'viscosity' during their contraction (Brown & Matthews, 1966) and as if the secondary ending lay on a region of intrafusal fibre which did not contract as strongly as the rest of the fibre. It is tempting to attribute the present findings to such a contraction of the nuclear-chain intrafusal fibres, but any further discussion seems best deferred until the investigation of isolated muscle spindles has produced further results (Boyd, 1966; Diete-Spiff, 1966; Smith, 1966).

The secondary ending again emerges as functionally simpler than the primary ending. Its sensitivity to dynamic stimuli is rather low both in the presence and absence of fusimotor activity; and this is so whether that motor activity is produced by stimulation of single fibres (present experiments) or is that occurring 'spontaneously' in the decerebrate cat (Jansen & Matthews, 1962). The secondary ending seems to provide the simple 'misalignment signal' between the length of a muscle and its 'γ bias' (static) which is important for the postulated servo control of muscle (Hammond, Merton & Sutton, 1956). The primary ending provides a

misalignment signal which is so greatly influenced by local dynamic conditions in the muscle that, though useful for the reflex control of the muscle, it would be of little value to a higher centre which required to be informed whether its command had been successfully executed by the lower motor centres. The secondary ending would appear to provide such information, though whether any such use is made of it by the central nervous system is another matter.

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