J. Physiol. (1982), **329**, *pp*. 509–526
With 6 *text-figures*
Printed in Great Britain

EFFECT OF FUSIMOTOR STIMULATION ON Ia DISCHARGE DURING SHORTENING OF CAT SOLEUS MUSCLE AT DIFFERENT SPEEDS

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(*Received 14 January 1982*)

SUMMARY

1. In barbiturate-anaesthetized cats, the L7 and S1 dorsal and ventral roots were dissected to isolate functionally single afferents identified as primary endings of soleus muscle spindles, and motor filaments which exerted a fusimotor action on the afferents with limited action on extrafusal muscle. Up to seven filaments, with an action on a given primary ending, could be isolated and each was classified as exerting either a predominantly dynamic or static action.

2. Combined stimulation of these filaments, at rates up to 200 impulses/s could maintain afferent firing during muscle shortenings at speeds up to 200 mm/s.

3. Fusimotor stimulation could also maintain afferent firing at a target frequency of 100 impulses/s during muscle shortenings up to 200 mm/s. The timing, in relation to the onset of shortening, and the rates of fusimotor stimulation were found to be critical in achieving the target frequency.

4. Sinusoidal modulation of the frequency of fusimotor stimulation was used to study the conditions required to achieve constant afferent firing in the face of imposed sinusoidal length changes.

5. For given depths of modulation, the phase advance of fusimotor stimulation needed to produce minimum modulation of afferent firing (best compensation) increased with increasing frequency of the sinusoids. The compensation deteriorated with an increase in the frequency of the sinusoids and a change in the mean muscle lengths, although in some cases it could be restored by adjustments to the depth of modulation of fusimotor rate. This suggests that for movements of varying speeds and amplitudes, settings which are appropriate for shortening at a given velocity and mean muscle length, do not apply if either of these two variables are altered.

6. These findings demonstrate that the fusimotor system is potentially capable of eliciting constant afferent firing as envisaged in the 'servo-assistance' hypothesis (Matthews, 1964, 1972; Stein, 1974). This, and the fact that constant afferent firing is not seen during normal unobstructed shortenings at velocities greater than 0·2 resting length/s (Prochazka, 1981), are used to argue that it is by choice rather than

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necessity that 'servo-assistance' (as defined above) is not employed during normal movements. However, servo-assistance of a different form (involving modulated spindle afferent feed-back from both agonists and antagonists) remains a viable alternative.

INTRODUCTION

Debate on the role of muscle spindle afferents during movements was dominated for some years by Merton's 'follow-up length servo' hypothesis (1953). This was gradually replaced by the 'servo-assistance' hypothesis (Matthews, 1964, 1972, 1980; Stein, 1974). It is well known that, in the absence of fusimotor action, spindle primary afferents are readily silenced by muscle shortening, and an important prerequisite of both hypotheses is that natural movements should be accompanied by sufficient fusimotor action to at least maintain a constant rate of discharge of spindle primary afferents during muscle shortening.

Hunt (1951) stated that fusimotor action would be 'effective in this regard only when the muscle shortening (velocity) was not great'. Eldred, Granit & Merton (1953), however, disagreed and provided anecdotal evidence for acceleration of spindle afferent discharge during isotonic muscle shortening of unspecified speed. These authors concluded that 'the γ system is therefore sufficiently powerful to drive the muscle under all conditions'. Surprisingly enough, this point has only been verified experimentally for speeds of shortening up to about 0·2 resting length/s (Lennerstrand & Thoden, 1968), representing at most 10% of the range of shortening velocities observed during voluntary movements for the muscles in question.

In recordings from presumed spindle primary afferents in man, a common observation has been that firing increases during voluntary muscle contraction (Hagbarth, 1981*a*; Vallbo, 1981*a*). However, the movements studied have usually been isometric or have involved velocities of shortening of less than 0·1 resting length/s (reviewed by Prochazka, 1981). The highest velocity of shortening so far studied in man was estimated at about 0·3 resting length/s (Burke, Hagbarth & Löfstedt, 1978, Fig. 2*C*) and in this instance the afferent fell silent during the shortening. Chronic animal recordings, in which a wider range of muscle shortening velocities have been studied, have often shown spindle primary afferents to decrease their firing rate or even to be silenced during active muscle shortening (Cody, Harrison & Taylor, 1975; Goodwin & Luschei, 1975; Prochazka, Westerman & Ziccone, 1975, 1976). A generalization recently proposed to account for the above observations is that the tendency for afferent discharge to decrease with decreases in muscle length becomes more prominent at velocities of shortening greater than 0·2 resting length/s (Prochazka, Stephens & Wand, 1979).

Two possible interpretations, both of relevance to the general applicability of the servo-assistance hypothesis, can be made of the above observations. The first is that the fusimotor system is inherently incapable of preventing spindle-afferent silencing during more rapid movements and therefore that servo-assistance (as currently envisaged) would be impossible in such cases. The second is that the fusimotor system, although capable of maintaining spindle-afferent discharge during rapid shortening movements, is not normally used to this end (i.e. it is choice rather than necessity which determines whether the conditions required for servo-assistance are met (Prochazka & Hulliger, 1982)). The present study was designed to distinguish between these two possibilities by determining whether combined stimulation of the fusimotor supply to a spindle could prevent silencing of the afferent discharge at rapid velocities of muscle shortening (up to 2 resting length/s). The term fusimotor is used throughout this report in its originally defined sense, namely 'with reference to neurones that are motor to the muscle spindle' (Hunt & Paintal, 1958). This definition draws no distinction between the separate actions of dynamic and static γ-fibres and 'β' ('skeletofusimotor') fibres on spindle afferents.

The results obtained indicate that the fusimotor system is indeed capable of preventing spindle-afferent silencing at even the highest natural velocities of shortening for the muscle studied. Furthermore, fusimotor stimulation can be timed to achieve a set afferent target frequency (arbitrarily set at 100 impulses/s in our trials) during such shortenings. An abstract of some of these findings has been presented to the Physiological Society (Appenteng, Prochazka, Proske & Wand, 1982).

METHODS

Five cats in the weight range 2·6–2·8 kg were initially anaesthetized with pentobarbitone (40 mg/kg, I.P.) and supplementary doses (12 mg/ml, I.V.) were administered when necessary to sustain a deep level of anaesthesia. Tracheal and venous catheters were inserted and rectal temperature was monitored and maintained around 37 °C.

The method for the preparation of the soleus muscle and nerve were similar to those described by Lewis & Proske (1972). All other hind-limb nerves were cut and the gastrocnemius and plantaris muscles removed. The tendon of the isolated soleus muscle was attached to a servo-controlled vibrator (Pye-Ling, V50) which was used to apply stretches of up to 10 mm amplitude at velocities of up to 200 mm/s, length being monitored by a compliant strain-gauge transducer. A force gauge was attached to the vibrator arm for measurement of muscle tension. A laminectomy was performed to expose the L7 and S1 dorsal and ventral roots which were then cut at their entry into the spinal cord. All exposed tissues were covered with pools of oxygenated mineral oil maintained at 36–38 °C.

Single soleus muscle afferents ($n = 7$) were isolated in dorsal root filaments and classified as spindle primaries if they were silenced during the rising phase of a maximal muscle twitch and had a conduction velocity exceeding 75 m/s. The L7 and S1 ventral roots were then dissected into small filaments, each of which was tested, using electrical stimulation, to see if it exerted a fusimotor effect on the afferent when electrically stimulated (brief 200 impulses/s tetani applied at 5 or 10 s intervals). As we were not concerned with the isolation of single fusimotor fibres, a degree of skeletomotor contamination was accepted (see Results). Up to seven filaments, each of which contained at least one fusimotor fibre, could be isolated for a given afferent. Individual filaments were classified as exerting either a predominantly dynamic or static fusimotor action according to the effect exerted on the afferent discharge during the rising phase of a ramp stretch. A further subclassification of the individual responses into the six categories of fusimotor action described by Emonet-Dénand, Laporte, Matthews & Petit (1977) was not attempted as we had no way of determining the exact admixture of fusimotor fibres in each filament.

Two modes of synchronous electrical stimulation were employed when studying afferent discharge during muscle shortening. One was to stimulate the filaments at a given constant rate and the other was to modulate sinusoidally the stimulation rate about a chosen centre frequency. Sinusoidal modulation was achieved by driving the stimulator with a voltage-controlled oscillator.

Muscle resting length. The definition of resting length used in this report is the distance between the origin and insertion of soleus, when the ankle is plantar-flexed up to the point at which the passive muscle just becomes slack. For the cats used in this study, we estimated this to be 100 ± 5 mm. The proportion of this length taken up by muscle fascicles was about 0·6, the remainder comprising tendon. Strictly speaking, the average resting length of the muscles proper was therefore

60 mm. However, since we wished to refer velocities of muscle shortening to those observable in chronic animal recordings (where length measurements are made between bony reference points), we have adhered to the definition above. It should be mentioned that during normal movements, the relative compliance of muscle and tendon varies depending upon the degree of active contraction of the muscle (Walmsley & Proske, 1981) and this may slightly affect comparisons made between the present results and observations in freely moving animals.

RESULTS

Classification of efferent filaments

The aim of this study was to examine the effect of combined stimulation of the efferent supply to soleus spindle primaries during variations in muscle length. In order to make this feasible, each of the naturally occurring L7 and S1 ventral root filaments was stimulated in turn, to establish whether it had a fusimotor action on the selected spindle primary. Such filaments usually gave rise to some concomitant extrafusal contraction since they presumably contained soleus α-motor fibres as well. However, a degree of skeletomotor 'contamination' was acceptable, and indeed even desirable, to ensure that the muscle would follow the rapid imposed shortenings used in these experiments. Thus, it was arbitrarily decided to accept filaments with a fusimotor action and eliciting less than 2 N extrafusal tension. Filaments developing high tensions were further subdivided, until acceptable levels were obtained. Inevitably, this led to the occasional loss of the fusimotor component in the filament.

Individual filaments were functionally classified as exerting either a predominantly dynamic or static fusimotor action by their effect on the discharge of a spindle primary afferent during the rising phase of a ramp stretch (Matthews, 1962). Stretches of 5 mm amplitude, starting from about 5 mm below maximal physiological length were employed. Fig. 1 illustrates the classification of the action of seven filaments, all influencing the same spindle primary. In the absence of efferent stimulation, the afferent displayed a marked phasic sensitivity to stretch (Fig. 1*A*). The filaments stimulated in Fig. 1*B* and *C* both produced prominent enhancements of the dynamic index and so were classified as predominantly dynamic fusimotor in action (Matthews, 1962). Stimulation of the other five filaments in Fig. 1*D–H* resulted in a decrease of the dynamic index and so these were classified as predominantly static fusimotor in action. It is evident that the responses in Fig. 1 range from clear dynamic (e.g. Fig. 1*B*) and static (e.g. Fig. 1*E* and *F*) to combinations of the two (see Emonet-Dénand *et al.* 1977). Since some of the filaments may have contained more than one fusimotor fibre, seven is the *minimal* estimate of the number of fusimotor fibres with an action on this spindle. In single-unit studies where attempts have been made to isolate as many fusimotor fibres to a spindle as possible, the numbers of γ fibres have ranged from five to ten (Hunt & Kuffler, 1951; Emonet-Dénand & Laporte, 1975; Emonet-Dénand *et al.* 1977, reviewed by Prochazka & Hulliger, 1982). The number of β fibres innervating a spindle has not been determined precisely but present evidence suggests this may be limited to one or two fibres per spindle (e.g. see Emonet-Dénand & Laporte, 1975). It is therefore reasonable to assume that an appreciable fraction of the whole fusimotor supply to the spindle of Fig. 1 was available for stimulation. For the other six spindle primaries studied, between one and seven fusimotor filaments were isolated (see Table 1, columns 1 and 2).

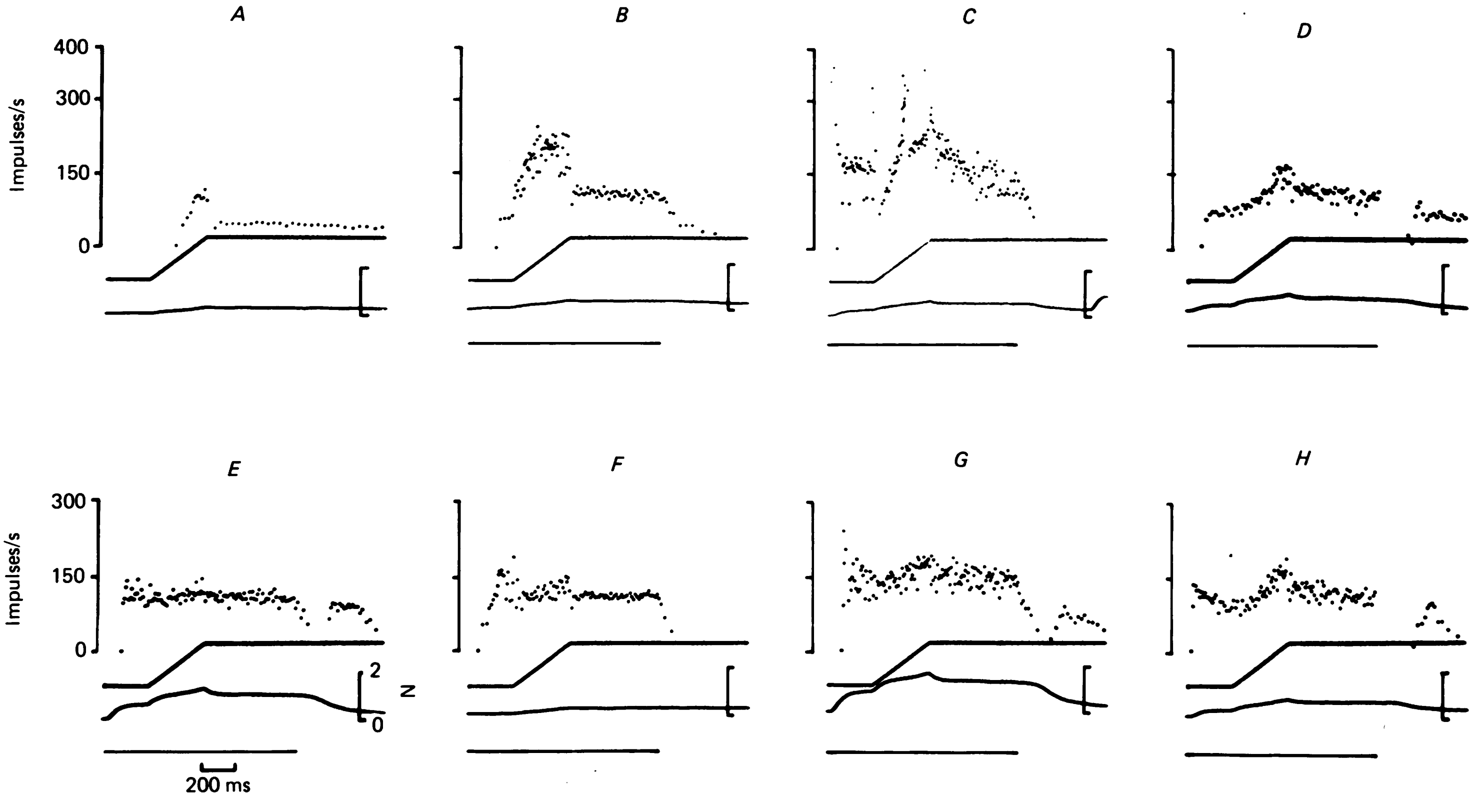

Fig. 1. Classification of the action of seven separate fusimotor filaments upon a single spindle primary afferent. In each case, traces show *top*: afferent firing rate; *middle*: ramp-and-hold muscle stretches (5 mm, 14 mm/s); *bottom*: force measured at tendon. *A*: response of the afferent in the absence of fusimotor stimulation. *B* and *C*: responses of the afferent during 200 impulses/s stimulation of the filaments having predominantly dynamic action. *D*, *E*, *F*, *G*, and *H*: responses of the afferent during 200 impulses/s stimulation of the filaments having predominantly static action. Period of stimulation in *B*–*H* indicated by horizontal lines. *Afferent 4.*

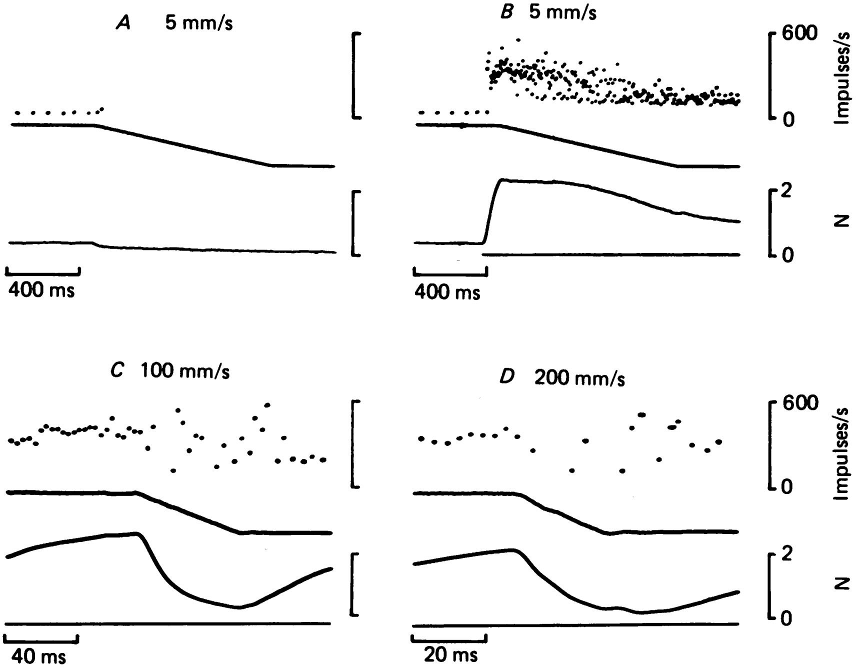

Fig. 2. Maintaining spindle afferent discharge during 5 mm shortening at increasing speeds with 200 impulses/s fusimotor stimulation. Traces as in Fig. 1. *A*: 5 mm/s shortening, no fusimotor stimulation. *B*: 5 mm/s shortening during 200 impulses/s stimulation of all seven fusimotor filaments. Period of stimulation shown by continuous horizontal line. *C*: same at 100 mm/s (stimulation throughout). *D*: same at 200 mm/s (stimulation throughout). *Afferent 4*.

TABLE 1

Afferent no.	No. of fusimotor filaments	Type 'Predominantly static'	 'Predominantly dynamic'	Max. shortening speed (resting length/s) for which *Ia* discharge present
1	2	1	1	1·0
2	1	1	—	0·3
3	4	3	1	1·0
4	7	5	2	2·0
5	3	1	2	2·0
6	1	—	1	1·0
7	7	5	2	2·0

Variations in velocity of shortening

The effect of combined stimulation of all of the available filaments acting on a given afferent was examined during the application of imposed ramp shortenings. It was found that the tension recorded at the tendon dropped to zero for shortening velocities in excess of 200 mm s^{-1}. In view of this, and the fact that 200 mm s^{-1}

(2 resting lengths/s) appears to be close to the limit of shortening velocities observed for soleus during rapid movements in normal cats (Goslow, Reinking & Stuart, 1973; Smith, Betts, Edgerton & Zernicke, 1980; and personal observations), we chose this as the upper limit in the present study. Shown in Fig. 2 are the responses of the same afferent illustrated in Fig. 1, during combined stimulation of the seven fusimotor filaments at 200 impulses/s. Stimulation commenced about 100 msec prior to the onset of shortening and was maintained throughout the movement. In the absence of stimulation (Fig. 2*A*), the afferent was silenced during shortening. Fusimotor stimulation elicited an increase in firing prior to shortening (Fig. 2*B*). During shortening (5 mm/s: velocity = 0·05 resting length/s) firing became irregular and showed a gradual decrease in mean rate with decrease in muscle length. In Fig. 2*C* the velocity of shortening was increased to 1 resting length/s (100 mm/s). Firing showed an initial decrease in rate but then recovered after 1·6 mm shortening to a value close to that seen prior to shortening. There then followed a gradual decrease in firing with further shortening which, as in Fig. 2*B*, was associated with some irregularity of discharge. At a velocity of shortening of 2 resting lengths/s (200 mm/s: Fig. 2 *D*), the firing frequency decreased smoothly with decreasing muscle length. Note in Fig. 2*B–D* that at no time during the movement did the force during shortening fall to zero, which indicates that the muscle was in fact following the imposed shortenings.

The observations of Fig. 2 indicate that the fusimotor system is capable of maintaining spindle primary afferent firing for shortening velocities of up to 2 resting lengths/s. For all but one of the other afferents studied, firing was maintained during shortenings at velocities up to 1 resting length/s (see Table 1). In two cases, firing was present during shortenings up to 2 resting lengths/s (afferents 5 and 7, Table 1). Note that the maximum velocities of shortening at which firing is observed is not well related to the number of filaments available for stimulation. For example, the one predominantly static filament isolated to afferent 2 could only maintain firing during shortening at a velocity of 0·3 resting length/s. In contrast, the single predominantly dynamic filament to afferent 6 maintained firing up to a velocity of 1 resting length/s.

The ability to attain a target afferent firing rate during shortening

A feature of the responses in Fig. 2 is that the afferent discharge, although maintained, decreased during muscle shortening from the high rates evoked by fusimotor action prior to shortening. In a discussion of the servo-assistance hypothesis, Matthews (1964, 1972) suggested that the relative level of skeletomotor and fusimotor activity might be adjusted so as to 'prevent any decrease in spindle discharge occurring during the contraction'. We were, therefore, interested to see whether, by carefully adjusting the timing and frequency of fusimotor stimulation, we could achieve a target frequency of spindle afferent firing (arbitrarily chosen as 100 impulses/s) at different velocities of shortening. Initially, we modulated the rate of fusimotor stimulation with the inverse of the length signal (so that during ramp shortening, there was a ramp increase in stimulation rate). However, although different depths of modulation of the stimulation rate were tried, the resulting afferent discharge was disappointingly uneven, particularly at the onset of shortening

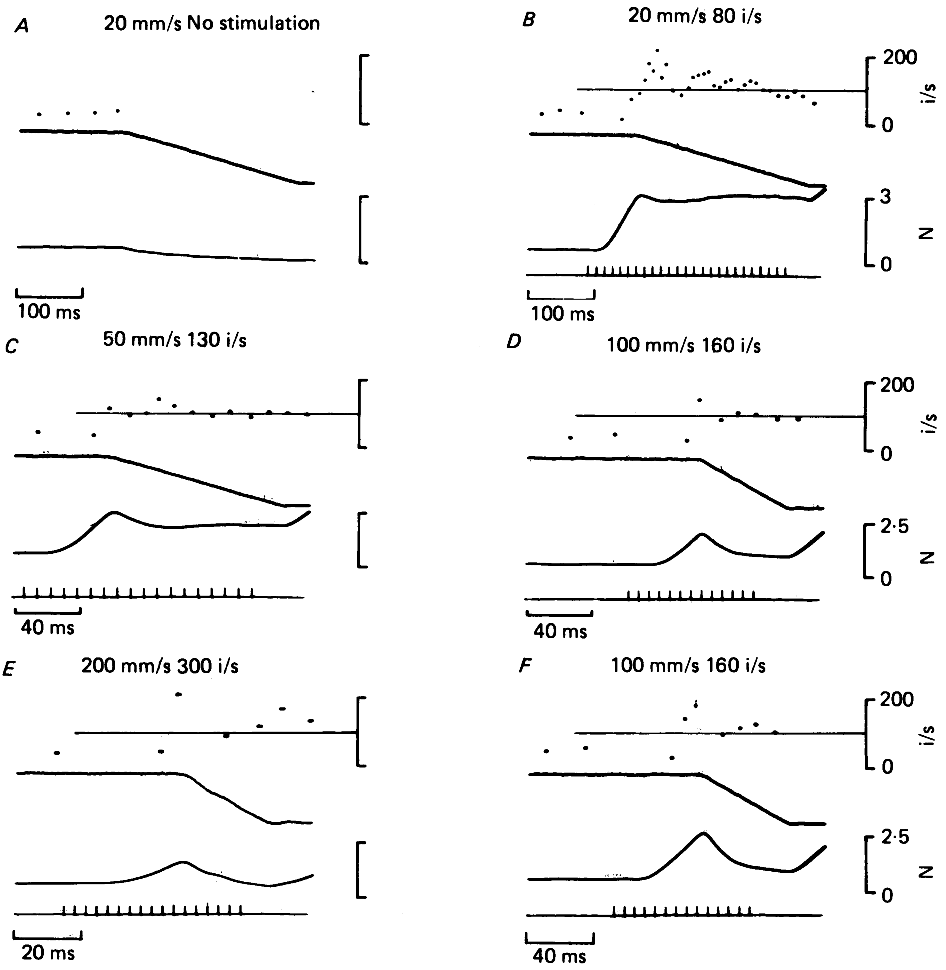

Fig. 3. Optimization of timing and frequency of fusimotor stimulation needed to produce afferent firing at a target frequency of 100 impulses/s (i/s) during shortening at different velocities. In each case, traces show from top to bottom: afferent firing rate, muscle length, force, fusimotor stimulus train (combined stimulation of five static and two dynamic fusimotor filaments). *A*: no fusimotor stimulation. *B–E*: Target frequency (100 impulses/s, indicated by horizontal line) reached for shortening velocities up to the maximum (200 mm/s). *F*: trial similar to *D*, except that fusimotor stimulation started 10 ms earlier. This resulted in afferent firing in excess of target frequency prior to onset of shortening. *Afferent 7*.

and at the higher shortening velocities. It was not possible technically to phase advance the fusimotor stimulus ramp with respect to the shortening ramp, and so we restricted ourselves to studying the effects of timed bursts of constant-rate fusimotor stimulation.

Fig. 3 shows the results of one such experiment. It was possible to attain afferent firing close to 100 impulses/s, during shortening velocities up to 1 resting length/s

(*B*, *C* and *D*), but at 2 resting lengths/s, although the target frequency was reached, the firing rate was uneven (Fig. 3*E*). The timing and impulse rates of the fusimotor bursts were critical in achieving the desired responses. Inappropriate timing is illustrated in Fig. 3*F*, where the fusimotor stimulation started 10 ms earlier than in Fig. 3*D*, and this led to a marked overshoot of the target frequency at the onset of shortening. It may be seen from Fig. 3 that the required rates of fusimotor stimulation ranged from 80 impulses/s at 0·2 resting length/s to 300 impulses/s at 2 resting lengths/s. The effect on afferent firing of varying the fusimotor stimulation rate at a given velocity of shortening (0·2 resting length/s) is shown in Fig. 4. The target frequency was again set at 100 impulses/s and the fusimotor stimulation commenced about 75 ms prior to the onset of shortening. Fusimotor stimulation at 30 impulses/s (Fig. 4*A*) elicited no firing during shortening but at 40 impulses/s (Fig. 4*B*) the afferent target frequency was reached late in shortening. With progressive 10 impulses/s increases in the stimulus rate the target frequency was reached progressively earlier during shortening (Fig. 4*C–F*). At stimulations of 90 and 100 impulses/s there was an initial marked overshoot of the target frequency prior to shortening. Note that the target frequency could be reached at some point during shortening when stimulating at 40 impulses/s, but to overcome the early unloading response of the afferent the stimulus frequency had to be increased.

Sinusoidal modulation of fusimotor stimulation and muscle length

(*a*) *Timing.* It could be argued that a ramp change in muscle length is not a good approximation to the length changes occurring during cyclical movements such as walking. This section describes the use of sinusoidal wave forms, which permitted a systematic investigation of the timing and depth of modulation of fusimotor stimulation needed to produce constant afferent firing in the face of variations in muscle length.

The outputs of two independent oscillators, set to slightly different frequencies, show progressive shifts in phase relative to one another with time. In this experiment, muscle length and fusimotor stimulation rate were modulated by separate sinusoids, the frequencies of which differed from each other by about 5 %. The result was that over a period of about 20 cycles, a full 360° phase shift occurred between the two signals (*ca.* 18° per cycle). The effects of such phase shifts on afferent firing are shown in Fig. 5*A*, where the sinusoidal modulation of fusimotor stimulation rate was at 1 Hz and that of length was at 1·05 Hz. In this case, only the five static fusimotor filaments were simultaneously stimulated. The most prominent depth of modulation of afferent firing was seen when the two sinusoids were approximately in phase. With progressive advancements in phase of the fusimotor stimulation with respect to muscle length (Fig. 5*B*), this depth of modulation gradually decreased and reached a minimum when the stimulation rate was phase-advanced by 36° (*minimum* of the stimulation sinusoid with respect to the *maximum* of the length sinusoid. 36° = 100 ms at 1 Hz). For convenience, we will refer to this as the point of *best compensation* (by the fusimotor stimulation of the afferent responses to the length variations).

When the frequencies of the modulating sinusoids were increased (modulation *depth* constant), the phase advance of the fusimotor wave form required to achieve the best

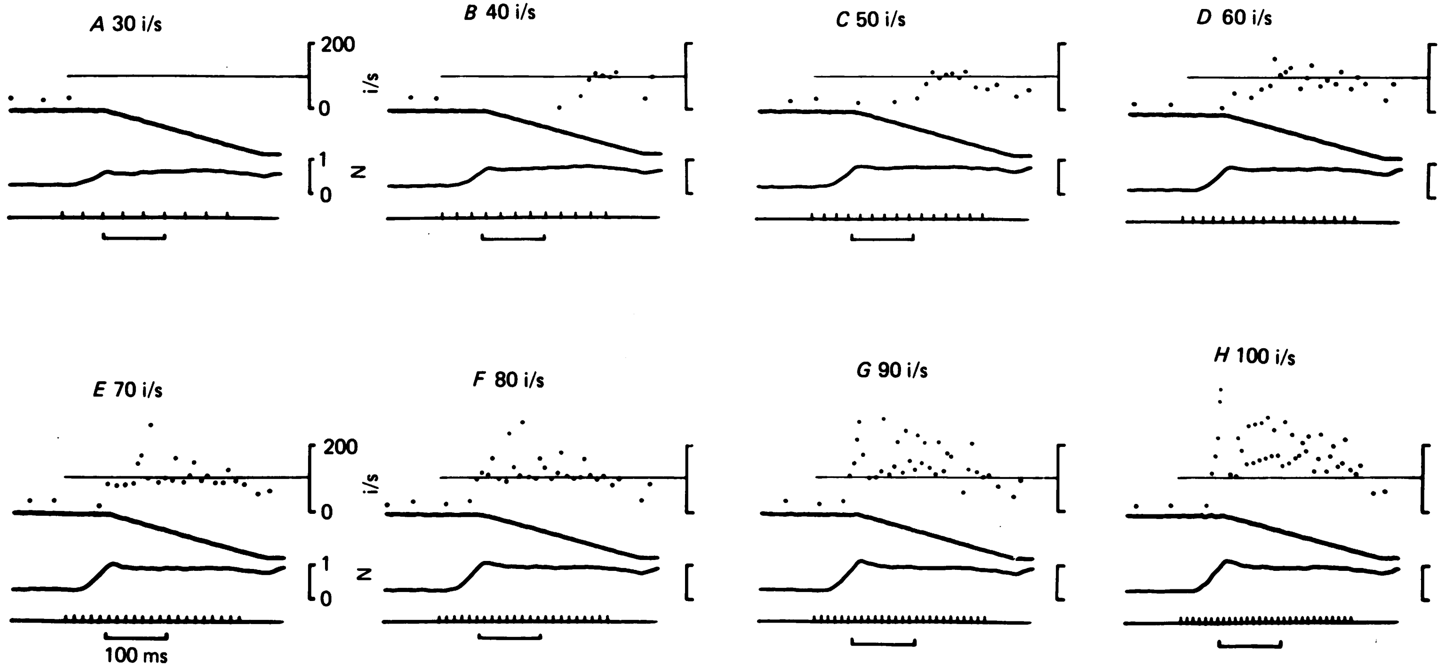

Fig. 4. Effect of increasing fusimotor stimulus frequency on the afferent response to 5 mm shortening at 20 mm/s. In each case, five static fusimotor filaments were simultaneously stimulated at the rates indicated. Traces as in Fig. 3, same time scale throughout. Target afferent firing rate (100 i/s) reached late in shortening in *B*, progressively earlier in *C*, *D* and *E*, exceeding for most of shortening in *F*, *G* and *H*. *Afferent 4*.

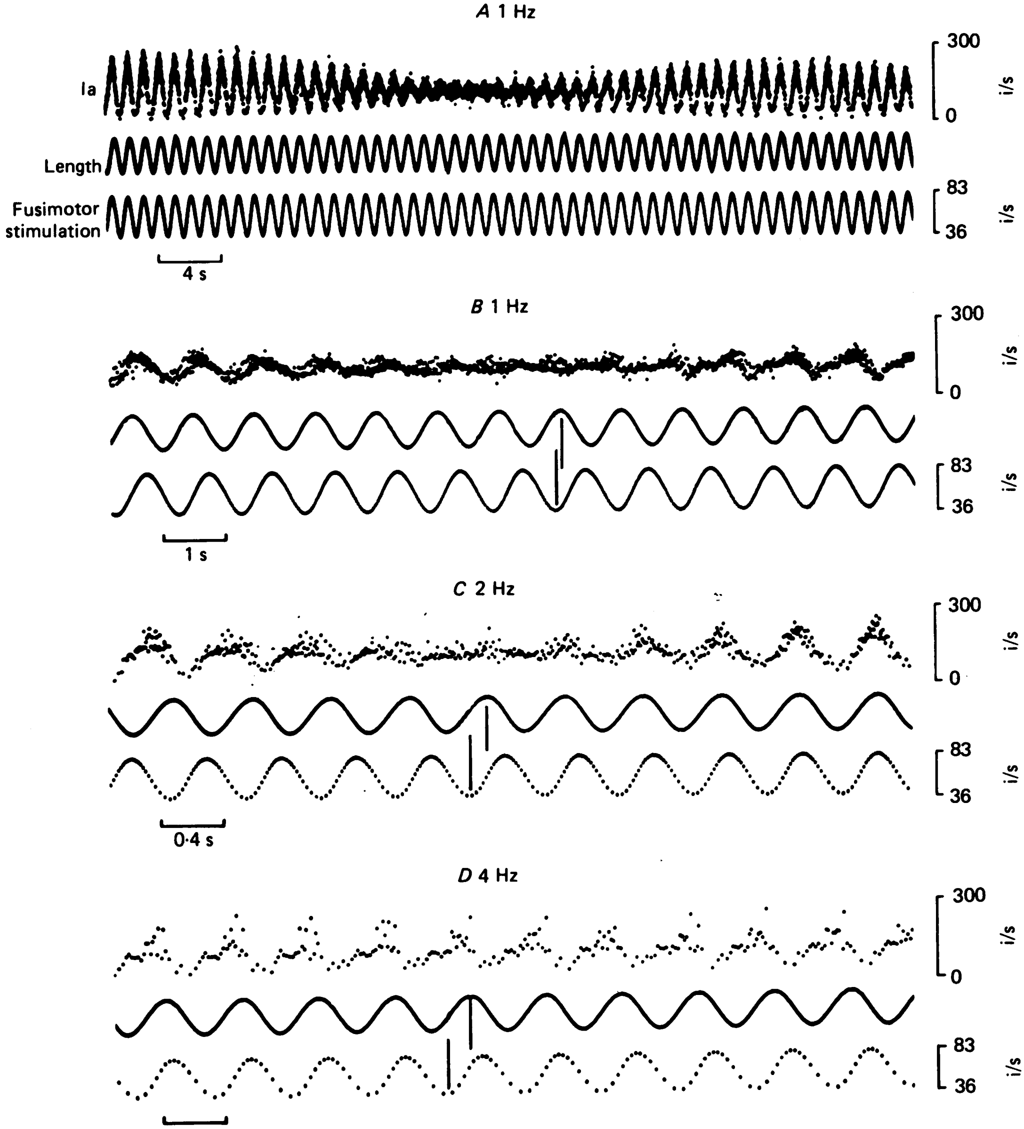

Fig. 5. Modulation of fusimotor stimulation to produce constant afferent firing in the face of sinusoidal length changes. Simultaneous, but independent, sinusoidal modulation of muscle length and rate of fusimotor stimulation with gradual change in relative phase. Traces: spindle primary afferent firing rate (top), muscle length, 5 mm peak-to-peak (middle), instantaneous rate of fusimotor stimulation (combined stimulation of five static filaments). *A*: full beat (360° phase shift between 1·05 Hz length sinusoid and 1·00 Hz sinusoid modulating fusimotor stimulation). 'Best compensation' of afferent responses to the length changes achieved by fusimotor stimulation at centre of record. *B*: central part of record in *A* on expanded time scale. Vertical lines indicate phase difference between fusimotor and length sinusoids at the cycle of 'best compensation': 36°. *C*: length sinusoid 2·00 Hz, fusimotor sinusoid 2·06 Hz. 'Best compensation' for phase difference of 72°. *D*: length sinusoid: 4·20 Hz, fusimotor sinusoid 4·10 Hz. 'Best compensation' for phase difference of 101°. *Afferent 7*.

compensation also increased (72° (100 ms) at 2 Hz: Fig. 5*C*; 101° (70 ms) at 4 Hz: Fig. 5*D*). At the higher frequencies, compensation became progressively less complete (i.e. the afferent firing rate showed a greater depth of modulation, e.g. Fig. 5*D* (cf. Fig. 5*B*)). The inclusion of the two dynamic fusimotor filaments changed the phase advance required for best compensation (54° (150 ms) at 1 Hz, cf. 36° (100 ms) for statics only, not shown in Fig. 5), and also resulted in a deterioration in compensation.

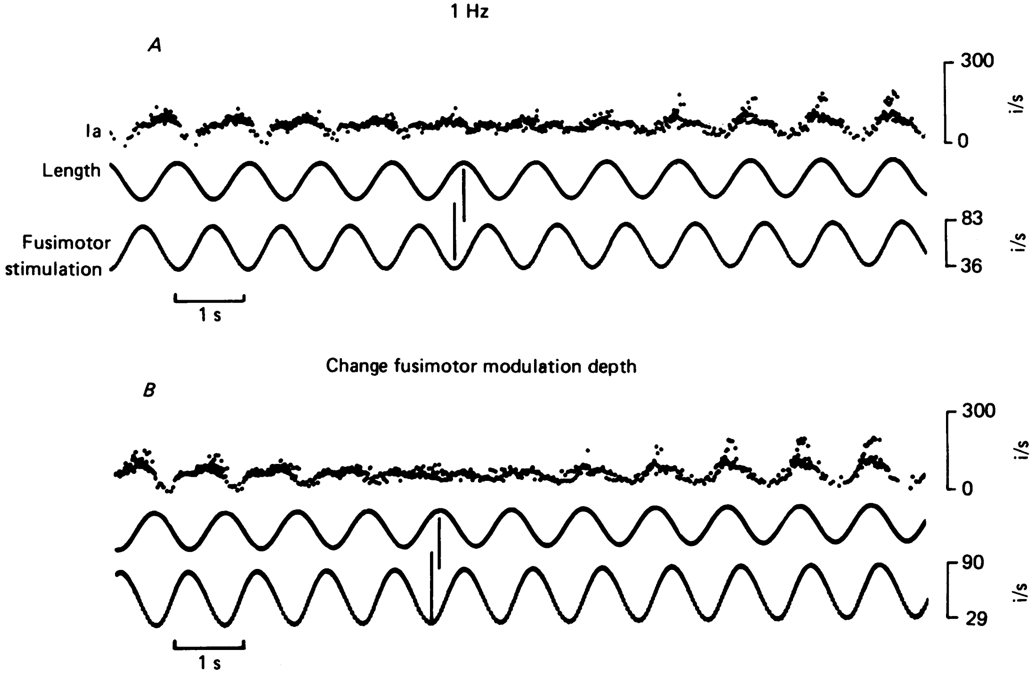

Fig. 6. Effect of change in mean muscle length and depth of fusimotor stimulus rate on compensation. *A*: conditions similar to Fig. 5*B*, except for a 5 mm reduction in mean muscle length. 'Best compensation' for phase difference of 54° (cf. 36° in Fig. 5*B*). *B*: depth of modulation of fusimotor stimulation rate increased to optimize 'best compensation', which now occurred for phase difference of 38°. Fusimotor sinusoid 1·00 Hz, length sinusoid 0·96 Hz in both bases. *Afferent 7*.

(*b*) *Effect of muscle length.* The timing and depth of modulation of static fusimotor stimulation found necessary to produce best compensation were very sensitive to alterations in the mean muscle length. Fig. 6*A* shows the effect of decreasing the mean muscle length by about 5 mm from that used for the response illustrated in Fig. 5*B*, but without changing the depth of modulation of length or stimulation rate. The phase advance for best compensation was now 54° (150 ms, cf. 36°, 100 ms). However, the best compensation was not as good as that at the longer muscle length, and an adjustment to the depth of modulation of stimulus rate was required to restore it to its optimal value (Fig. 6*B*; phase advance at best compensation: 38°, 106 ms).

To summarize, in order to produce best compensation at different mean muscle lengths, either the phase advance or the modulation depth of fusimotor stimulation had to be altered. Similarly, best compensation at different modulation frequencies required different phase advances.

DISCUSSION

The technique normally used to examine the effect of fusimotor action on spindle discharge involves the functional isolation and stimulation of single fusimotor fibres (Kuffler, Hunt & Quilliam, 1951). While this has yielded fundamental information on the action of individual fusimotor neurones, it has provided only limited insight into the effects to be expected from the activation of the whole fusimotor supply to a spindle. Combined stimulation of several fusimotor fibres acting on a given spindle has on occasion been performed (Hunt & Kuffler, 1951; Brown, Lawrence & Matthews, 1969), but the effect of such stimulation on the responses of spindle primary endings to controlled muscle shortening has only been studied for two fusimotor fibres at a time (Lennerstrand & Thoden, 1968; Hulliger, Matthews & Noth, 1977). As the effects elicited by individual fusimotor fibres vary, and may sum non-linearly (Hulliger *et al.* 1977), it has been difficult to assess the full potency of the entire efferent supply to a spindle, which may comprise in excess of ten γ fibres (see Fig. 15: Emonet-Dénand *et al.* 1977) and one or two β fibres (see Emonet-Dénand, Jami & Laporte, 1975). In the present study, we have tried to assess the action of an appreciable part of the fusimotor supply to a given spindle during muscle shortening at different speeds. Unlike Hunt & Kuffler (1951), however, we have arranged for the onset of fusimotor stimulation to precede the onset of the test ramp of muscle shortening. If fusimotor stimulation is not initiated until the onset of the movement, its capacity to maintain spindle firing is likely to be underestimated, as indeed it evidently was by Hunt & Kuffler (1951).

The results obtained have a direct bearing on whether the fusimotor system is powerful enough to fulfil its role in 'servo-assistance', namely to 'suit the expected trajectory of the planned movement, and so maintain the spindle firing approximately constant throughout', (Matthews, 1980). Before this is discussed, however, a comment on the use of the term 'servo-assistance' seems appropriate. According to Matthews (1972, p. 572), this was meant as a colloquial rather than an analytical description, of how the motor control system might work. It seems to have evolved from the idea that central nervous inputs via fusimotor neurones were inputs to the 'movement servo', while inputs directly to α-motoneurones would be passed on without the benefit of peripheral feed-back control. The latter would only hold, of course, if feed-back from spindles ceased as a result of muscle shortening (Matthews, 1964, p. 277), and the discharge of spindles in antagonist muscles undergoing lengthening were inaccessible to the control loop. Otherwise, the input to α-motoneurones would be perfectly consistent with normal servo function (Taylor, 1972), and rather than being advantageous, the input via γ-motoneurones would merely introduce additional delays and unwanted non-linearities. The apparent low gain of the segmental control loop, coupled with the ability of the motor system to execute very accurate movements, does however, suggest that other mechanisms, probably involving higher-order control loops and prediction, must be involved. Consequently, the term 'servo-assistance' would therefore best be used to describe the operation of such a low-gain control loop enclosed within successive higher-order control loops.

Our results show that combined stimulation of up to seven fusimotor filaments can prevent spindle primaries from being silenced during muscle shortening at speeds covering almost the full physiological range (0–3 resting lengths/s, Goslow *et al.* 1973; Smith *et al.* 1980). Furthermore, fusimotor stimulation can be timed so as to produce spindle afferent firing at a high target frequency (100 impulses/s) during these shortenings. Clearly, the fusimotor system is sufficiently powerful to elicit high levels of afferent discharge during even very rapid muscle shortening. This answers recent speculations (Hagbarth, 1981*b*; Prochazka & Hulliger, 1982) about whether there is a limiting velocity above which fusimotor action could not possibly keep spindle afferents firing.

It has been accepted since the work of Lennerstrand & Thoden (1968) that static fusimotor action is more capable than dynamic fusimotor action of maintaining the firing of spindle primary endings during muscle shortening. Superficially, some of our results seem to contradict this idea, as 'predominantly dynamic' filaments were in some cases better at maintaining firing than predominantly static filaments (e.g. afferent no. 2 compared with afferent no. 6 in Table 1). However, an important drawback of our technique is that in order to maximize the fusimotor action available for a given afferent, filaments were not subdivided to the point of containing demonstrably single fusimotor fibres. Thus, 'predominantly dynamic' filaments could conceivably have contained fibres with appreciable static fusimotor action.

With reference to the servo-assistance hypothesis, our findings demonstrate that it is within the capabilities of fusimotor neurones to maintain the constant level of afferent discharge envisaged for servo-assistance during unobstructed shortenings. However, whether this justifies the notion that the fusimotor system could potentially be used to this end during normal movements depends upon whether the stimulation frequencies employed were within the physiological range of fusimotor firing. Although it is true that only direct recordings of fusimotor activity during natural unobstructed movements will finally resolve this issue, there is some evidence presently available (from studies on anaesthetized animals) which suggests that discharge rates of at least 100 impulses/s may normally occur. Thus, Sears (1964) observed peak discharge frequencies ranging from 20 to 100 impulses/s of intercostal γ-motoneurones during quiet breathing in anaesthetized cats. Sjöström & Zangger (1975) reported peak γ-firing rates of about 100 impulses/s during fictive locomotion in spinal cats treated with DOPA. Appenteng, Morimoto & Taylor (1980) observed rates of up to 120 impulses/s in presumed fusimotor fibres to the jaw elevator muscles in lightly anaesthetized cats performing reflex jaw movements. In awake monkeys, performing an isometric biting task, Lund, Smith, Sessle & Murakami (1979) reported rates of up to 200 impulses/s but the criteria reported for recognition of fusimotor fibres were not fully verified.

As the range of muscle lengths and velocities in the present study was undoubtedly physiological, our results indicate that servo-assistance is potentially a strategy which could be employed by the central nervous system in the control of even the fastest movements. However, certain important requirements would have to be met. First, fusimotor discharge would have to be modulated during movements. Secondly, this discharge would have to be appropriately phase-advanced with respect to the onset of shortening. Thirdly, the profile of modulation of fusimotor discharge frequency would have to be accurately chosen. From our results, settings which were successful during shortening at a given velocity were unsuccessful if the velocity, or for that matter, the initial muscle length, were altered. Minute discrepancies in the timing of fusimotor activation led to large, unwanted modulations prior to the onset of shortening, particularly at the higher velocities (Fig. 3*F*). These effects were also apparent in the cyclical movements of Fig. 5. Here, compensation could deteriorate rapidly for small increments in the phase advance of fusimotor stimulation (e.g. Fig. 5*C*). When the frequency (and therefore the peak velocities) of the cyclical movements was increased it was also necessary to change the required phase advance of fusimotor stimulation for best compensation. Furthermore, the inadequacy of the best compensation at higher frequencies (4 Hz, Fig. 5*D*) suggested that optimal compensation would require a much greater depth of modulation of the rate of fusimotor stimulation (as predicted by M. Hulliger: Prochazka & Hulliger, 1982), or indeed that the modulating wave form should be of a non-sinusoidal form. Our observations of spindle-afferent responses to concomitant triangular or trapezoidal modulation of both muscle length and fusimotor stimulation (briefly alluded to above) also indicated that the use of the same signal for length and stimulus rate does not usually result in optimal compensation.

As pointed out previously, in our experiments the stimulation was applied to both fusimotor and skeletomotor fibres. It is conceivable that the extrafusal contractions might have contributed small 'internal' length changes to the muscle spindles additional to the externally imposed movements. If these experiments were repeated with different levels of extrafusal 'contamination', it is to be expected that the particular requirements for best compensation might vary slightly, but that the same general trends would hold. Since combined skeletomotor–fusimotor activation underlies the servo-assistance hypothesis, our mode of stimulation can be viewed as a reasonable approximation to this.

In emphasizing the complexities involved in maintaining spindle afferent firing constant during length variations, we do not wish to imply a judgement of whether the C.N.S. would or would not be able to cope with this task. On the other hand, there has been a tendency in the published theories of fusimotor control to disregard, or at least to omit, considerations of these complexities.

The question of whether servo-assistance (of the sort involving an approximately constant rate of spindle-afferent firing) actually occurs in normal voluntary movements, can to some extent be answered by examining the published data on spindle afferent discharge recorded in awake mammals. As mentioned earlier, a generalization which is consistent with most of these data states that 'in normal unobstructed movements in which muscle velocities exceed 0·2 resting lengths/s, increases in muscle length will cause increases in spindle discharge, and decreases in muscle length will cause decreases in spindle discharge' (Prochazka *et al.* 1979; cf. Loeb & Hoffer, 1981; reassessment by Prochazka & Hulliger, 1982). For muscle shortening at speeds lower than 0·2 resting lengths/s, examples have been published of spindle afferent discharge increasing (e.g. Hulliger & Vallbo, 1979; Schieber & Thach, 1980), remaining approximately constant (e.g. Vallbo & Hulliger, 1981; Prochazka, 1981) or decreasing (e.g. Burke *et al.* 1978; Burg, Szumski, Struppler & Velho, 1976), and indeed Vallbo (1981*b*, Fig. 3) showed all three types of behaviour in one and the same spindle afferent.

Thus, it would seem, on current evidence, that the basis for servo-assistance is present in some slow movements, but not generally in the faster movements. Taken together with the present results this leads us to conclude that during unobstructed, voluntary movements the fusimotor system is potentially powerful enough to ensure servo-assistance (of the sort discussed above) for movements of any speed, but in fact is used to this end only in some, and even then not all, relatively slow movements (it is 'choice' rather than 'necessity' which determines the mode of control). It seems appropriate to reiterate that servo-assistance of a different type (involving spindle afferent feed-back from both agonists and antagonists, modulated dynamically according to variations in muscle length) remains a consistent alternative.

The project was supported by the M.R.C. and the St Thomas's Hospital Endowments Fund. P. Wand was supported by the Deutsche Forschungsgemeinschaft SFB33.

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