MUSCLE SPINDLE ACTIVITY IN MAN DURING SHORTENING AND LENGTHENING CONTRACTIONS

By DAVID BURKE*, KARL-ERIK HAGBARTH AND LARS LÖFSTEDT

*From the Department of Clinical Neurophysiology,
Academic Hospital, Uppsala, Sweden*

SUMMARY

1. The responses of forty-one muscle spindle endings, mostly in tibialis anterior, were studied in human subjects during voluntary movements of the ankle joint performed at various speeds against different external loads.

2. During slow shortening contractions, the discharge rates of spindle endings in the contracting muscle accelerated after the appearance of the first e.m.g. potentials but before sufficient force had been generated to move the limb. With some endings, the discharge rate decreased during the shortening movement while the e.m.g. activity was increasing, but it always remained higher than before the onset of contraction. If the speed of the movement was increased fewer spindle discharges were seen during muscle shortening. If the shortening contraction was opposed by an external load, so that greater effort was required to perform the same movement, more discharges were seen and the discharge pattern became less modulated by the change in muscle length.

3. These findings indicate that during shortening contractions the fusimotor system is activated together with the skeletomotor system. However, the fusimotor drive is generally insufficient to maintain a significant spindle discharge unless movement is slow or the muscle is shortening against an external load.

4. During lengthening contractions the spindle responses were greater than to passive stretch of similar amplitude and velocity, suggesting heightened fusimotor outflow.

5. During shortening and lengthening contractions small irregularities in the speed of movement occurred commonly. Unintended acceleration of a shortening movement caused a pause in spindle firing, and unintended acceleration of a lengthening movement caused an increased discharge from spindle endings. These spindle responses were associated with corresponding alterations in the discharge pattern of the voluntarily activated motor units at latencies consistent with the operation of spinal reflex mechanisms.

6. It is suggested that a functional role for the fusimotor activation during slow shortening contractions is to provide spindle endings with a background discharge so that they can detect irregularities in the movement and initiate the appropriate reflex correction.

INTRODUCTION

Considerable data have accumulated recently concerning co-activation of the skeletomotor and fusimotor systems in man during a voluntary contraction (Hagbarth & Vallbo, 1968; Vallbo, 1970b, 1971, 1973, 1974; Burg, Szumski, Struppler & Velho, 1973; Hagbarth, Wallin & Löfstedt, 1975; Burke, Hagbarth, Löfstedt & Wallin, 1976b). The contractions studied have been largely 'isometric', with minimal external changes in muscle length. In such contractions, the increase in fusimotor drive appears to be directed specifically to the contracting muscle, not to inactive synergists or other muscles, and both the time course and the intensity of the resultant spindle discharge have been shown to parallel those of the skeletomotor activity. Thus, in the isometric situation, there is a close association between the activity of α motoneurones and that of γ motoneurones, such that the skeletomotor and fusimotor drives to a muscle are related spatially, temporally and in intensity. Conversely, when a muscle is completely relaxed, spindle endings in that muscle behave as if deprived of fusimotor innervation.

Even in supposedly isometric contractions, a small change in muscle fibre length cannot be prevented, particularly in experiments on human subjects, and a pause in spindle firing has been demonstrated when the degree of stretch on the endings is decreased by contraction of neighbouring muscles or neighbouring portions of the same muscle (Vallbo, 1970b, 1974; Hagbarth et al. 1975; Burke et al. 1976b). During voluntary movements spindle endings will undergo greater changes in length. There is some controversy whether voluntary shortening movements ('shortening contractions') involve co-activation of α and γ motoneurones, as occurs in the isometric situation, and, if so, whether the fusimotor activation is capable of producing spindle firing in the face of decreasing muscle length (cf. Vallbo, 1973; Cody, Harrison & Taylor, 1975; Goodwin & Luschei, 1975; Prochazka, Westerman & Ziccone, 1976, 1977). The present study was designed to investigate these questions during normal voluntary movements of the human ankle. Particular attention was paid to the spindle and motor responses to unintentional irregularities in the execution of the movement.

METHODS

Data were obtained from fifteen experiments in twelve healthy subjects, aged 18–48 years, all of whom had given informed consent to the experimental procedure. Muscle afferent activity was recorded at the fibular head from fascicles of the peroneal nerve innervating preferably tibialis anterior but also occasionally extensor digitorum longus and extensor hallucis longus.

Identification of afferent activity. All single units included in this study were identified using electrically induced muscle twitch contractions (cf. Szumski, Burg, Struppler & Velho, 1974; Hagbarth et al. 1975; Burke, Hagbarth, Löfstedt & Wallin, 1976a) as muscle spindle endings or as Golgi tendon organs. Muscle spindle endings were further classified as 'dynamic' or 'static' on the basis of their responses to passive stretching movements of approximately sinusoidal wave form (5–10° of ankle joint angle at 0·25–0·5 Hz) generated manually by the experimenters. These subdivisions probably correspond reasonably closely to primary and secondary endings respectively, but the units studied were not subjected to the controlled passive stretching used in previous studies (Hagbarth et al. 1975; Burke et al. 1976a). In multi-unit recordings, the neural discharge was demonstrated to be dominated by muscle spindle activity by the characteristic spindle response to electrically evoked muscle twitch contractions. These were elicited while the subject maintained an increased background of neural activity by contracting the receptor-bearing muscle voluntarily (Wallin, Hongell & Hagbarth, 1973).

Recording techniques. Details of electrodes, equipment and recording procedures have been given in full previously (Hagbarth, Hongell, Hallin & Torebjörk, 1970; Vallbo, 1970a, 1971; Hagbarth *et al.* 1975; Burke *et al.* 1976a). The subjects lay on one side on a comfortable bed with knee extended and foot fixed to the plate of a hydraulic device, used for generating controlled passive movements of the ankle joint (Hagbarth *et al.* 1975; Burke *et al.* 1976a; Löfstedt, 1977). For the present studies, the shaft of the rotating plate was disconnected from the drive so that free rotation of the plate, and therefore of the ankle joint, could occur. The ankle joint was aligned over the axis of rotation of the plate and the position of 90° at the joint was taken as the reference (zero) position for each muscle. *Ankle joint position, torque* produced by contraction of muscles acting at the ankle joint, and the *electromyographic activity* (e.m.g.) of the muscle in which the receptor was located (the 'receptor-bearing muscle') and, occasionally, of other muscles were recorded, in addition to the neural discharge. The e.m.g. recordings were obtained with a pair of needle electrodes inserted close to the receptor. When a more representative measure of total muscle activity was required additional surface e.m.g. recordings were made. In order to define minor irregularities in the performance of a movement, an Endevco 2222A *accelerometer* was attached to the foot-plate. The experimental variables were recorded on a Precision Instruments PI-6200 or a Sangamo Sabre VI tape-recorder for subsequent analysis.

Experimental procedures. With the assistance of visual feed-back of the signal of ankle joint position, subjects were requested to reproduce, as smoothly as possible, the amplitude and velocity of earlier passive movements of the ankle joint. A range of velocities of movement was studied, and between test sequences different loads were applied in a plantar flexion direction to the foot-plate. In no instance were rapid movements used. The profile of the integrated e.m.g. showed that the contraction force of the receptor-bearing muscle increased gradually as the shortening movement proceeded, in contrast to the situation in rapid voluntary contractions in which e.m.g. and (often spindle discharge) may finish before movement has begun (Vallbo, 1971; Hagbarth *et al.* 1975).

The plantar flexion load was produced by the elastic recoil of a rubber band which passed through reversing pulleys and was attached at one end to the foot-plate and at the other to the experimental table. The load was altered by changing the length of the rubber band. Three standard loads were used, equivalent to 0·55, 1·14 and 1·74 Nm with the foot in 15° plantar flexion. Movements of the ankle joint altered the effective torque at each level of load, due partly to elasticity of the rubber band, but mainly to changes in the direction of the plantar flexion vector. For example, ankle rotation from 15° plantar flexion to the zero position resulted in an increase in external load of about 0·6 Nm. Thus shortening contractions were performed against either no external load (the 'isotonic' situation) or a progressively increasing external load. Controlled elongation of a muscle contracting against an external load (a form of 'lengthening contraction') was performed against a progressively decreasing external load. Sudden changes in load were produced manually by rapid stretching or shortening of the rubber band.

Analysis. The experimental variables were monitored continuously during the experiment, but all analyses were performed subsequently, using procedures described previously (Hagbarth *et al.* 1970, 1975; Burke *et al.* 1976a). To illustrate clearly the relationship between spindle discharge and changing muscle length, the recorded afferent potentials were transformed into pulses of standard amplitude and superimposed on the joint position signal (cf. Fig. 2). The discharge frequency of single units was obtained using an 'instantaneous' frequency meter (Hagbarth *et al.* 1975). An analogue representation of the instantaneous frequency was obtained by 'integrating' the standard pulses using an R-C low pass filter of time constant 0·2 or 0·5 s. Multi-unit recordings of afferent activity were 'integrated' using an R-C low pass filter of time constant 0·01 or 0·05 s.

RESULTS

Single unit recordings were made from afferent nerve fibres innervating forty-six muscle stretch receptors. Forty-one units were classified as of muscle spindle origin, and of these thirty-one were classified as 'dynamic' and ten as 'static'. However, no evidence was found that the 'static' endings behaved in a qualitatively different manner in the various test contractions, and, unless otherwise stated, the spindle

endings referred to in the following were of the 'dynamic' type. Five single units were classified as of Golgi tendon organ origin. In seven of the fifteen experiments multi-unit recordings of muscle spindle activity were also studied.

The effect of varying the speed of movement. For ten spindle endings the responses during very slow voluntary movements of 0·25–0·5°/sec were compared with those
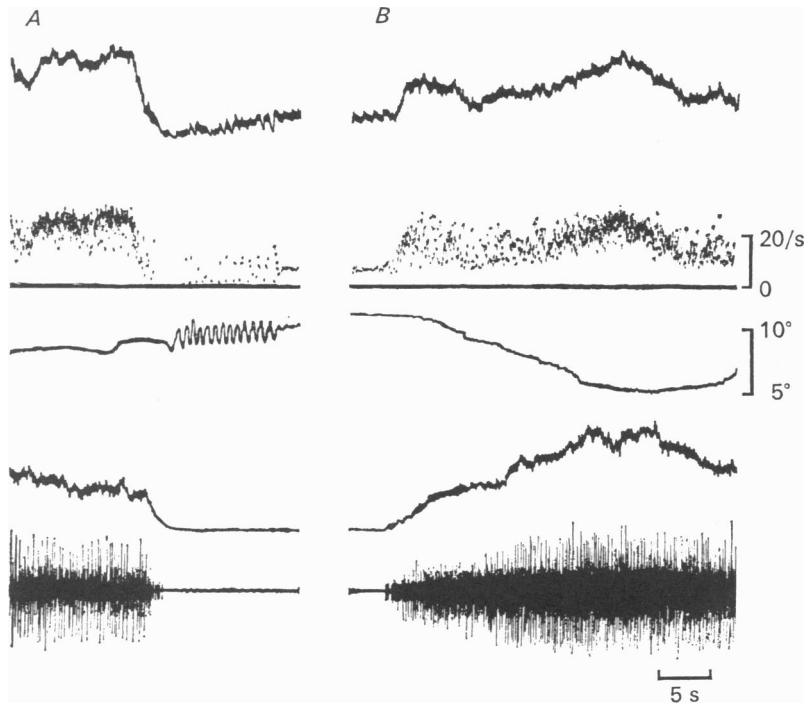

Fig. 1. The responses of a dynamic spindle ending in the tibialis anterior (TA) during an isometric contraction (*A*) and a shortening contraction (*B*). Traces are, from above, smoothed instantaneous frequency plot (time constant 0·5 sec); instantaneous frequency plot; ankle joint angle; integrated e.m.g. of TA (time constant 0·5 sec); e.m.g. of TA. The trace in *A* begins half-way through the isometric contraction, following which there is a sequence of passive stretching movements. The shortening contraction in *B* was performed against an external load equivalent to 0·55 Nm. As in subsequent Figures, muscle shortening is indicated by a downward deflexion of the angle record.

obtained in isometric contractions, the strength of which increased equally slowly. Each ending was clearly activated in the isometric contractions, which produced torques of up to 4 Nm. The shortening contractions involved comparable voluntary effort and produced comparable integrated e.m.g. profiles. In the shortening contractions, the discharge of all ten endings accelerated after the appearance of the first e.m.g. potentials but before the limb had actually commenced moving. During the shortening movement the discharge did not increase in parallel with the e.m.g. activity as occurred in the control isometric contractions. Six endings showed a firing pattern of the type illustrated in Fig. 1*B*, namely an increase in discharge during the initial isometric phase before movement had started, a period of deceleration during movement, and a further increase as movement slowed down. The

firing frequencies of the remaining four endings were maintained relatively unaltered or even increased slightly during the shortening movements, but the increases were always smaller than in isometric contractions which produced an equivalent level of integrated e.m.g. activity.
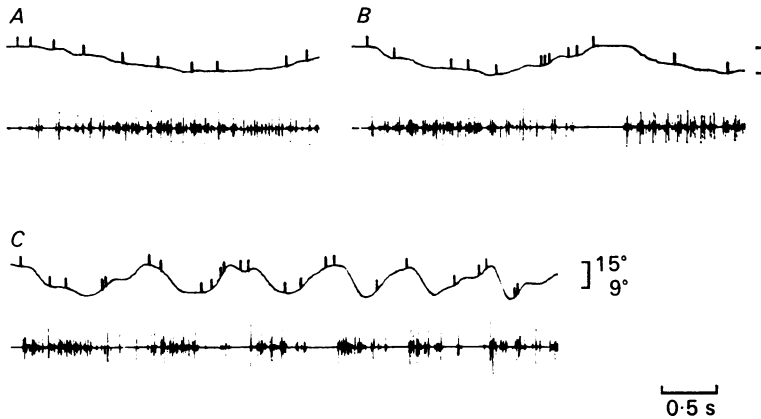

Fig. 2. The responses of a dynamic spindle ending in the tibialis anterior (TA) during voluntary shortening movements of increasing speed, *A*, *B* and *C*. In the upper traces, the afferent potential was converted into a pulse of standard amplitude and super-imposed on the ankle joint angle signal. Lower trace: e.m.g. of TA. The sequences were performed against an external load equivalent to 0·55 Nm.
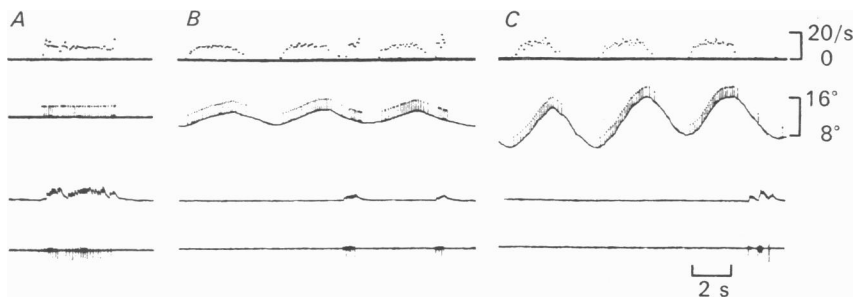

Fig. 3. The responses of a dynamic spindle ending in the tibialis anterior (TA) during weak isometric voluntary contraction (*A*) and during passive stretching movements (*B* and *C*). Traces are, from above, instantaneous frequency plot; afferent potential superimposed on ankle joint angle (as in Fig. 2); integrated e.m.g. of TA (time constant 0·1 sec); e.m.g. of TA. The unintentional contractions of TA during some of the passive shortening movements (the shortening reaction, or Westphal phenomenon) are asso-ciated with spindle activation, particularly in *B*, but this is not as prominent in *C*, where the speed of shortening is greater.

   The degree of spindle deceleration during shortening contractions was found to be critically dependent on the speed of movement. When the speed was increased as in Fig. 2, the decrease in the spindle response during shortening became more apparent. Fig. 2 also shows that the discharges which occurred during the shortening movements were not distributed evenly throughout the movement. Spindle firing tended to be suppressed when the speed of movement momentarily increased. Spindle

discharge became related to the irregularities in the movement, being confined largely
to the plateaux of the irregularities (cf. also Fig. 4 A).

The effect of altering the external plantar flexion load. For twenty-six spindle endings
it was possible to compare the responses obtained with control passive movements
of 5–10° at 0·25–0·5 Hz to those obtained when the subjects performed similar
movements against different loads. When the receptor-bearing muscle was relaxed,
passive stretching and shortening movements produced firing of dynamic spindle
endings only during the stretching phases (cf. Fig. 3 B and C). This modulation of
spindle discharge by the change in muscle length became blurred when the subject
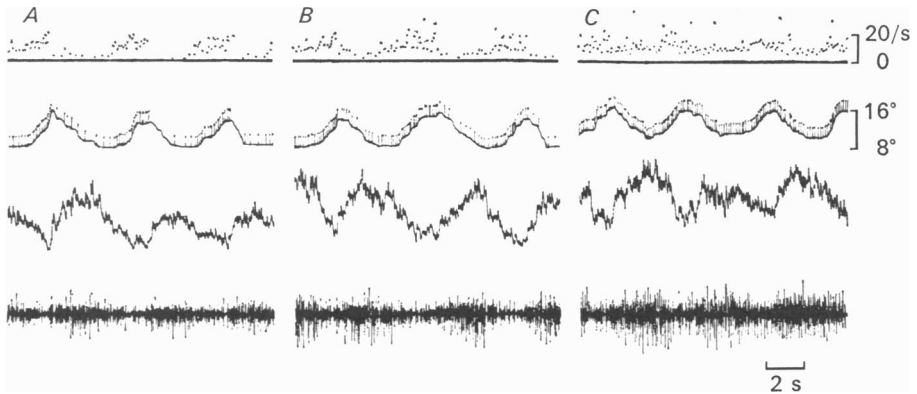

Fig. 4. The responses of a dynamic spindle ending in the tibialis anterior (TA) during
voluntary movements, against no external load (A), against 0·55 Nm (B), and against
1·14 Nm (C). Same unit as in Fig. 3. Traces as in Fig. 3. The e.m.g. activity persists into
the stretching phase even in A when no external load was applied to TA.

attempted to reproduce the same movements, particularly if the receptor-bearing
muscle had to act against an external load. The greater the external load, the more
closely spindle discharge tended to follow the variations in contraction strength
rather than muscle length. With the ending illustrated in Fig. 3, a few scattered
discharges were seen during isotonic shortening against no external load (Fig. 4 A).
When greater effort was required to perform the same movement due to an external
load, the spindle ending discharged throughout the shortening movement (Fig. 4 B).
In Fig. 4 C, the discharge rate during shortening was similar to that recorded during
the stretching phases. The effect of the external load on the spindle discharge was to
decrease the contrast between the spindle responses to the shortening and lengthen-
ing movements.

When the receptor-bearing muscle was contracting against an external load, the
stretching phases of a sequence of voluntary stretching and shortening movements
were controlled by gradually yielding contractions of the receptor-bearing muscle.
The discharge frequency of spindle endings in the resultant lengthening contraction
exceeded that recorded in control passive stretching movements. Fig. 5 shows the
extent to which the mean discharge rate increased with increasing load during both
active shortening and active lengthening contractions. In isotonic shortening con-
tractions against no external load, the e.m.g. activity of the receptor-bearing muscle

was commonly confined to the shortening phases. In such cases, the spindle responses during the stretching phases did not differ significantly from those recorded during the control passive movements, provided that allowance was made for the irregularities in the voluntary movements.

Four spindle endings had an even greater tendency than the unit illustrated in Figs. 4 and 5 to follow the integrated e.m.g. envelope rather than the length change.
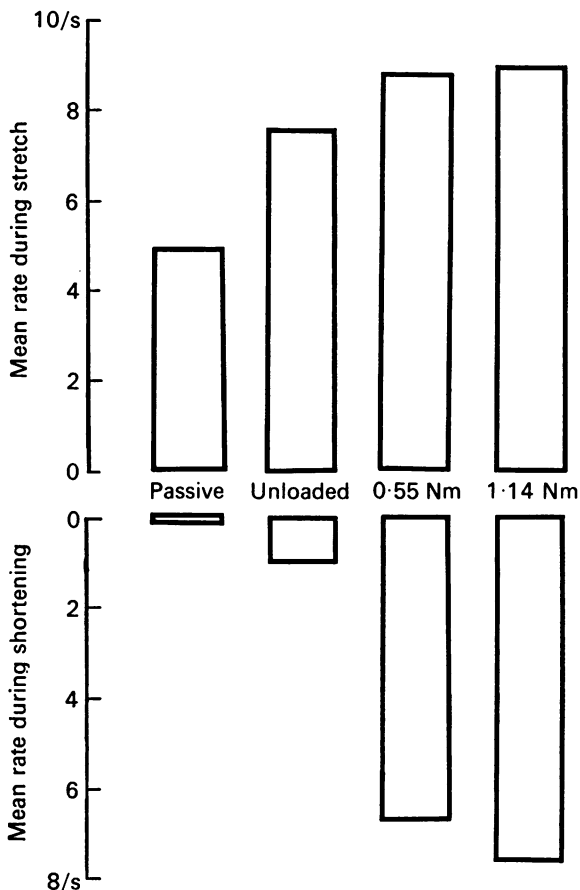

Fig. 5. The mean rates of discharge of a dynamic spindle ending in the tibialis anterior (TA) during passive movements and during voluntary movement. Same unit as in Figs. 3 and 4. Each histogram plot represents the mean data from at least four stretching or shortening sequences. The chosen sequences had the same average rate of change of length in order to eliminate effects due to variability in the speed of movement. The column to the left represents the values obtained with passive movements of relaxed TA. The three columns to the right are based on voluntary movements, with TA subject to no external load or to external loads of 0·55 Nm and 1·14 Nm.

With the external loads the responses of these endings were maximal at the shortest position where e.m.g. was maximal. In the control tests, the discharge frequencies of these four endings had been influenced only slightly by passive movements of the ankle joint, but each had responded vigorously during isometric voluntary contractions. Other endings appeared relatively more sensitive to changes in muscle length

than to voluntary effort, but the modulation of spindle discharge by changes in length still became progressively less apparent when voluntary movements were performed against greater external loads.

Tendon organ responses. The five tendon organs studied responded readily to isometric voluntary contractions, but all were unresponsive to passive stretching movements of 5–10° at 0·25–1·0 Hz, unless the receptor-bearing muscle was contracting slightly. Four tendon organs discharged readily during shortening contractions, even in the absence of an external load, the discharge increasing throughout the movement as e.m.g. built up. The fifth tendon organ could be activated during shortening contractions only by the application of relatively large external loads (greater than 2 Nm), but then its discharge increased and decreased during the movement with the intensity of e.m.g. activity. Thus, during shortening contractions, the patterns of discharge of tendon organs and spindle endings can be quite similar, particularly if the receptor-bearing muscle is contracting against a large external load.
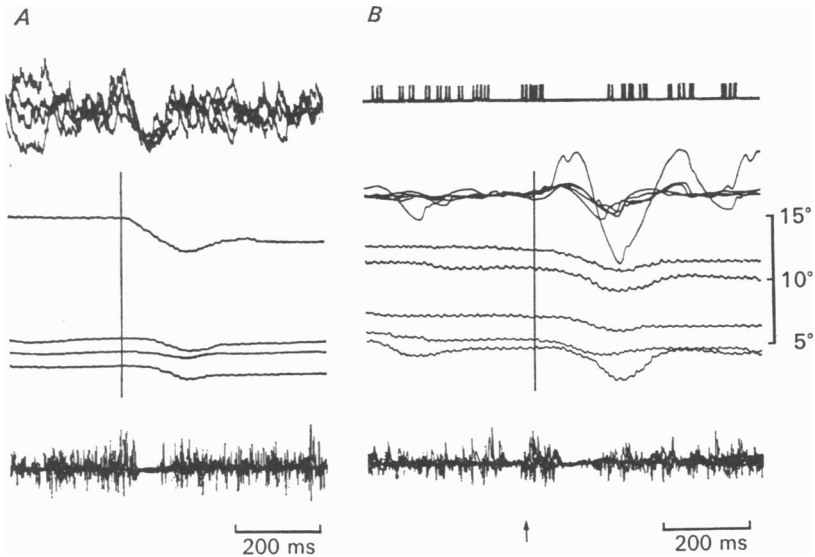

Fig. 6. Unloading responses resulting from naturally occurring irregularities in a voluntary shortening movement. *A*, spindle-dominated multi-unit recording from the tibialis anterior (TA). Four traces superimposed. *B*, responses of a dynamic spindle ending in TA, five traces superimposed. Traces are, from above, neural activity (integrated neurogram, time constant 0·01 sec in *A*; standardized spindle afferent potential in *B*); output of accelerometer (in *B* only); ankle joint angle; e.m.g. of TA. In *B* the event initiating the irregularity appears to be a grouping of e.m.g. potentials (indicated by the arrow). This burst of e.m.g. activity is accompanied by a burst of spindle activity (i.e. there is evidence of $\alpha - \gamma$ co-activation in the neural activity that appears to be responsible for the irregularity). Vertical lines indicate approximate start of acceleration.

Responses to irregularities in the speed of voluntary movements. None of the subjects was able to generate a completely smooth movement of the ankle joint. As seen in Figs. 2 and 4, the speed of movement varied randomly within the movement. During shortening contractions an unintended acceleration of movement produced a transient reduction in the spindle discharge and a pause in the voluntary e.m.g. activity. Such unloading responses recorded during the course of a slow *shortening contraction* against an external load of 0·55 Nm have been superimposed in Fig. 6*B* for a single

unit recording and in Fig. 6*A* for a multi-unit recording. The latency between the onset of the decrease in afferent activity and the onset of the pause in e.m.g. activity was more reliably measured in multi-unit recordings because they sampled the activity of a number of spindle afferent fibres. The latency was 35–70 ms in all experiments in which the spontaneously occurring irregularities were sufficiently large to produce unloading effects. In different trials the precise latency value depended on the abruptness of the irregularity. Similar pauses in spindle discharge and e.m.g. activity with similar latencies were produced in other experiments if the experimenters removed or decreased the external load unexpectedly in an attempt to mimic the spontaneous irregularities.
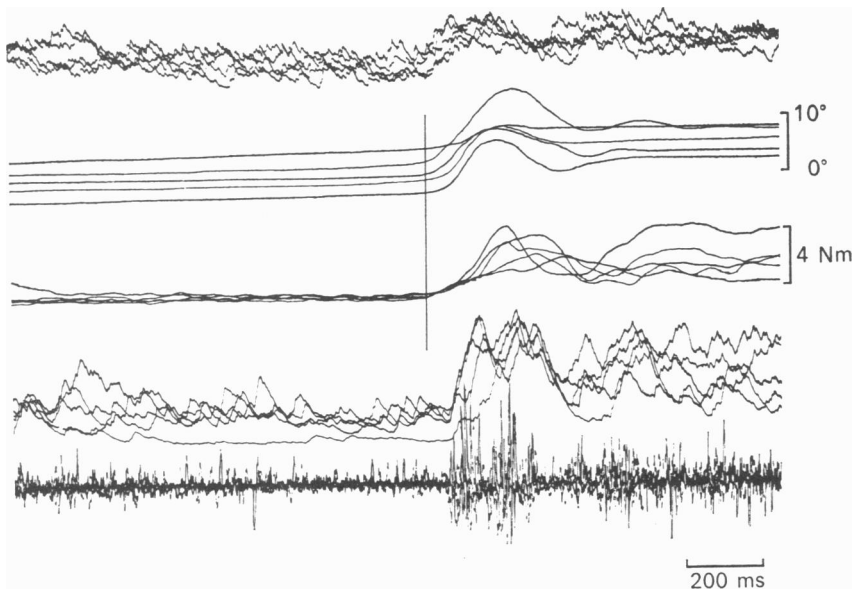

Fig. 7. The responses to a sudden increase in load during a lengthening contraction of the tibialis anterior (TA). TA was contracting against a load of 1·14 Nm, slow elongation being brought about by gradual relaxation. At the vertical line the load was abruptly increased, increasing the speed of elongation. Responses obtained in five separate sequences are superimposed. Traces are, from above, spindle-dominated multi-unit neural activity (time constant 0·05 sec); ankle joint angle; torque; integrated e.m.g. of TA (time constant 0·05 sec); e.m.g. of TA.

The converse phenomenon could be demonstrated when a muscle contracting against an external load was allowed to relax slowly so that the gradual yield produced a *lengthening contraction*. An unexpected increase in the external load then produced a sudden acceleration of movement. As shown in the superimposed records of Fig. 7 an externally induced acceleration of movement produced an afferent stretch response, followed approximately 50 ms later by a synchronized burst of e.m.g. potentials. In some trials the e.m.g. response was double-peaked, as in Fig. 7, the second peak occurring 80–100 ms after the first. Similarly, a sudden acceleration of movement occurring spontaneously during the course of lengthening contraction produced an increase in spindle discharge followed by a transient increase in e.m.g. activity.

<center>DISCUSSION</center>

The present findings indicate that the fusimotor system is activated with the skeletomotor system during voluntary movement, much as it is in the isometric state. The results are therefore quite consistent with the view that in man voluntary contraction is associated with a fixed strategy of $\alpha - \gamma$ co-activation. However, during *shortening contractions*, the change in muscle length did prove to have a potent modifying influence on spindle behaviour, and it cannot be maintained that the fusimotor activation would constitute an effective stimulus for spindle endings under all conditions. The reflex support available during a shortening movement is likely to be significant only with relatively slow movements or when the muscle is contracting against an external load.

These conclusions are basically similar to those of Goodwin & Luschei (1975), who studied natural jaw movements in the monkey, but differ from those reached by Cody *et al.* (1975) and Prochazka *et al.* (1976, 1977), who studied feline jaw movements and hind limb movements, respectively. The failure of presumed primary endings in the jaw-closing muscles of unanaes-thetized cats to maintain a discharge during voluntary jaw closure (Cody *et al.* 1975) does not necessarily indicate a lack of fusimotor drive to the endings. Fusimotor drive may well have been present but ineffective in the face of a fast shortening movement. The interpretation of results obtained from natural movements is critically dependent on the extent to which neigh-bouring synergistic muscles participate in the execution of the movement, since the contraction of a muscle can unload spindle endings in less active synergists (Vallbo, 1970*b*; Hagbarth *et al.* 1975; Burke *et al.* 1976*b*). Such considerations are of particular importance in freely behaving animals which, unlike human subjects, cannot be requested to modify the motor act to suit experimental convenience. Similar reservations may be expressed about the conclusion drawn by Prochazka *et al.* that $\alpha - \gamma$ linkage may be quite variable, even absent, in some voluntary movements. Indeed, in these studies, the precise localization of a spindle ending within a muscle group was not possible, and e.m.g. activity was monitored by chronically implanted electrodes in standard sites not necessarily appropriate to the ending under study. In view of the complex effects that can occur between and within synergistic muscles and the possibility that fusimotor neurones have a recruitment order (D. Burke, K.-E. Hagbarth & L. Löfstedt, unpublished observations), the demonstration of a dissociation of e.m.g. and the discharge of an individual spindle ending cannot be accepted as unequivocal evidence of a dissociation of the skeletomotor and fusimotor drives to the muscle.

The tendency for spindle firing rate to follow increasing force rather than de-creasing length when a shortening contraction was performed against an external load raises questions about the ability of spindle endings to provide an unambiguous signal about muscle length during movement. Some spindle endings even reached higher discharge frequencies when shortened than when stretched. In general terms, it seems that, under these conditions, spindle endings behave less like length-transducing receptors and more like tension-transducing organs. It can be argued that it is not beyond higher centres to compute a meaningful length signal, given knowledge of the degree of fusimotor drive, but such computations seem too complex for segmental reflex mechanisms. Whatever sensory messages individual spindle endings may signal, the combined inflow from primary and secondary endings during a voluntary contraction probably has an overall autogenetic excitatory effect at spinal level. From the motor control viewpoint it may be advantageous if the reflex support to the contraction increases with voluntary effort rather than with muscle length.

During gradual *lengthening contractions*, the spindle discharge rate was higher than

when the relaxed muscle was subjected to passive stretching movements of similar amplitude and velocity. The simplest explanation for this finding seems to be that, in the lengthening contractions of this study, spindle endings were subjected to the additional stimulus of fusimotor activity, occurring in parallel with the declining skeletomotor activity.

The irregularities in voluntary movement. It has been questioned recently whether segmental stretch and unloading reflexes are capable of compensating for large changes in external load or whether they should be regarded as compensating for small internal disturbances during movement (Evarts & Bizzi, 1976). At least in the cat, spindle endings and the stretch reflex are much more sensitive to small perturbations than to large (Matthews, 1969, 1972; Matthews & Stein, 1969). The present results indicate that, in man, segmental stretch and unloading reflexes may play an important role during movement. As suggested by Vallbo (1973), these reflexes may operate as speed-controlling mechanisms, compensating for unintentional irregularities in the speed of movement. The changes in spindle discharge induced by the irregularities seem capable of altering the discharge pattern of voluntarily activated motor units through segmental reflex pathways, thus generating fast compensatory responses capable of smoothing the movement. It seems likely that one of the roles for the fusimotor activation during a slow or a loaded shortening contraction is to give spindle endings in the contracting muscle the background discharge necessary to encode the unloading that occurs when the speed of movement suddenly increases.

The primary origin of the irregularities in movement seen in the present study may have been central or peripheral. In some instances (cf. Fig. 6B), the mechanical events were preceded by a tendency for grouping of e.m.g. potentials, suggesting that the initial event was of neural origin, possibly due to an 'irregularity' in the motor command signals. In other instances e.m.g. built up smoothly, the initial evidence of a disturbance being seen in the mechanical records (goniometer, torque or accelerometer), suggesting a peripheral cause, such as the inertia and friction of the components of the moving limb. The compensatory responses may be considered speed-controlling (Vallbo, 1973) when the irregularities are of central origin. With irregularities of primarily peripheral origin the responses may also be considered 'load-compensating', but such a distinction may well be merely semantic.

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