

## RECRUITMENT ORDER OF HUMAN SPINDLE ENDINGS IN ISOMETRIC VOLUNTARY CONTRACTIONS

BY DAVID BURKE, KARL-ERIK HAGBARTH\*  
AND NEVELL F. SKUSE

*From the Unit of Clinical Neurophysiology, Division of Neurology,  
The Prince Henry Hospital and School of Medicine,  
University of New South Wales, Sydney, N.S.W. 2036, Australia*

(Received 8 May 1978)

### SUMMARY

1. The responses of twenty-two spindle endings in the anterior tibial and toe extensor muscles of human subjects were studied during isometric voluntary contractions of the receptor-bearing muscle with the ankle joint fixed in 25° plantar flexion.

2. The discharge of eighteen endings accelerated in voluntary contractions when the contraction strength exceeded a threshold level which differed for different endings but was reproducible for the same ending.

3. With contractions of slow onset the latency to spindle acceleration varied with the speed of onset of the contraction. Endings with a background discharge were often unloaded by contractions until the contraction strength exceeded the threshold for activation of the ending.

4. No correlation was found between the sensitivity of a spindle to external length changes and its ease of activation in a voluntary contraction. For two spindle endings with a background discharge there was no change in either discharge frequency or the regularity of spindle discharge during contractions which were below the threshold for activation of the endings. It is concluded that the threshold for activation of a spindle ending in an isometric voluntary contraction is determined by its fusimotor innervation, and that fusimotor neurones probably have a recruitment order, much as do skeletomotor neurones.

5. Once activated, the discharge of spindle endings fluctuated with changes in skeletomotor activity but the relationship for some endings contained non-linearities. Such non-linearities were not as apparent in multi-unit recordings from a number of spindle endings in the contracting muscle. It is concluded that the fusimotor drive to a muscle is proportional to the skeletomotor drive to the muscle, and that skeletomotor and fusimotor neurones are subjected to similar if not identical descending command signals. From the work of Evarts (1968), it seems likely that these command signals are related more to desired muscle force than to desired muscle length.

\* Permanent address: Department of Clinical Neurophysiology, Academic Hospital, Uppsala, Sweden.

## INTRODUCTION

The orderly recruitment of skeletomotor neurones in reflex and voluntary contractions has been demonstrated repeatedly for cat and man, respectively (Henneman, Somjen & Carpenter, 1965; Milner-Brown, Stein & Yemm, 1973; Freund, Büdingen & Dietz, 1975; Clamann & Henneman, 1976; Desmedt & Godaux, 1977). Voluntary contractions are also associated with an increased discharge from muscle spindle endings due to activation of fusimotor neurones (Vallbo, 1970, 1971, 1974; Burg, Szumski, Struppler & Velho, 1973; Hagbarth, Wallin & Löfstedt, 1975; Burke, Hagbarth & Löfstedt, 1978), but little is known of their pattern of recruitment.

In accordance with the 'size principle' (Henneman *et al.* 1965), findings in the decerebrate cat indicate that  $\gamma$  motoneurones have a lower threshold and tend to be recruited at an earlier stage than  $\alpha$  motoneurones when exposed to increasing synaptic drive (Granit & Kaada, 1952; Eldred & Hagbarth, 1954). On these grounds, one might expect the acceleration of spindle discharge accompanying a voluntary contraction to occur before the appearance of the electromyographic activity. However, recordings in man show that, in isometric voluntary contractions, the initial electromyographic potentials precede spindle acceleration, the minimum interval in fast contractions varying within the range 10–50 ms, depending on the initial length of the muscle (Vallbo, 1971; Hagbarth *et al.* 1975). This interval can be fully explained by the slow conduction velocity in  $\gamma$  motor fibres, by intrafusal mechanisms, and by the afferent conduction time to the recording site. The findings are consistent with simultaneous activation of fusimotor and skeletomotor neurones by descending commands, but they do not exclude the possibility that one type of neurone might have a slightly lower threshold than the other.

The question remains whether, in voluntary contractions of slowly increasing strength, fusimotor neurones are recruited in an orderly manner as are skeletomotor neurones so that individual spindle endings in the contracting muscle become activated at specific contraction strengths. The present study provides evidence that such an orderly recruitment of spindle endings does occur, and suggests that this depends on a corresponding recruitment order for the fusimotor neurones innervating the spindle endings. The results are considered to support the view that in voluntary contractions the skeletomotor and fusimotor neurones are recruited in parallel by descending commands in cortico-spinal tract neurones which signal desired force rather than desired muscle length (Evarts, 1968).

## METHODS

The experimental data are based on observations on twenty-two spindle endings made during twelve experiments on seven healthy adult volunteers, all of whom gave informed consent to the experimental procedure.

*Experimental procedures.* Afferent potentials from single spindle endings were recorded at the level of the fibular head from fascicles of the peroneal nerve innervating either tibialis anterior, extensor digitorum longus or extensor hallucis longus, using techniques described in full previously (Hagbarth *et al.* 1975; Burke, Hagbarth, Löfstedt & Wallin, 1976a). All afferent potentials were identified as of muscle spindle origin using electrically induced twitch contractions of the receptor-bearing muscle.

Subjects lay supine with the ankle joint fixed in 25° plantar flexion and the foot secured to

a foot-plate attached to a rigid metal bar. A four-arm strain gauge bridge was bonded to the bar to provide a measure of contraction strength. The electromyogram (e.m.g.) of the receptor-bearing muscle was recorded using surface electrodes orientated longitudinally along the muscle belly on either side of the receptor. All experimental data were monitored during the experiment and recorded on tape for subsequent analysis. Subjects were carefully instructed in how to contract predominantly and at will either the anterior tibial or toe extensor muscles. During the experiment contraction of the receptor-bearing muscle was checked by palpation of the muscle tendon, and, in most experiments, by needle e.m.g. electrodes.

*Data analysis.* The routine data analysis procedures have been described previously (Hagbarth *et al.* 1975; Burke *et al.* 1976a). In three experiments, potentials from two different spindle endings were recorded simultaneously. Separation of the activity of each ending was achieved by altering filter settings to maximize amplitude differences and then using a window discriminator (Ortec 730L Single Channel Analyzer). To determine the regularity of muscle spindle discharge, the afferent potentials were converted into pulses of standard amplitude using the 730L Single Channel Analyzer and then fed into a LAB 8E computer programmed to measure the interspike interval to the nearest 500  $\mu$ s. From these measurements, computations were made of the mean interval and its standard deviation, the coefficient of variation (= standard deviation divided by mean interval), and the mean discharge frequency for the analysed sequence. Full details of these procedures and of the experimental controls will be published separately (D. Burke, N. F. Skuse & D. G. Stuart, in preparation).

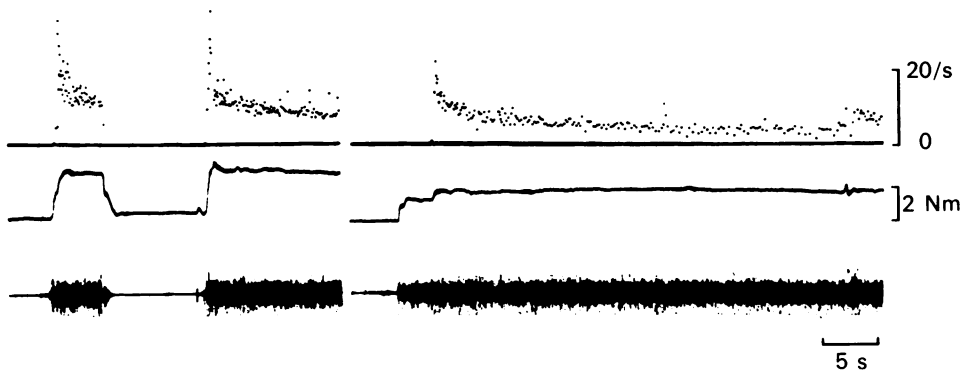


Fig. 1. Recording from a spindle ending in tibialis anterior during isometric voluntary contractions. Upper trace: instantaneous frequency plot; middle trace: contraction torque; lower trace: e.m.g. of tibialis anterior.

## RESULTS

For twenty-two spindle endings studied in detail, the discharge of eighteen accelerated in at least some voluntary contractions, provided that a full range of contraction strengths could be tested. With the remaining four endings, recording conditions deteriorated before testing was completed. However one of these endings could not be activated in contractions of up to 4 Nm.

### *Individual torque thresholds for different spindle endings*

Of the twenty-two spindle endings, ten had no background discharge at +25°. In voluntary contractions these endings could either remain silent or begin to discharge. The spindle discharge always followed the appearance of e.m.g. potentials in the receptor-bearing muscle. The latency between the appearance of e.m.g. activity and the onset of spindle discharge depended on both the strength of

contraction and the rise time of the contraction. In Fig. 1 (left) a spindle ending was activated at relatively short latency in response to relatively rapid increases in contraction torque to approximately 3 Nm. In Fig. 1 (right) the ending was not activated in an equally rapid but weaker contraction of 1–1.5 Nm, although it was so in a subsequent step increase in torque to 1.5–2.0 Nm. With contractions of slow rise time, the latency to spindle activation was variable; for the ending in Fig. 1 it



Fig. 2. Recording from a spindle ending in tibialis anterior during isometric voluntary contractions of different speeds of onset. Same unit as in Fig. 1. Traces as in Fig. 1. The interrupted horizontal line indicates the torque level at which the ending was activated.

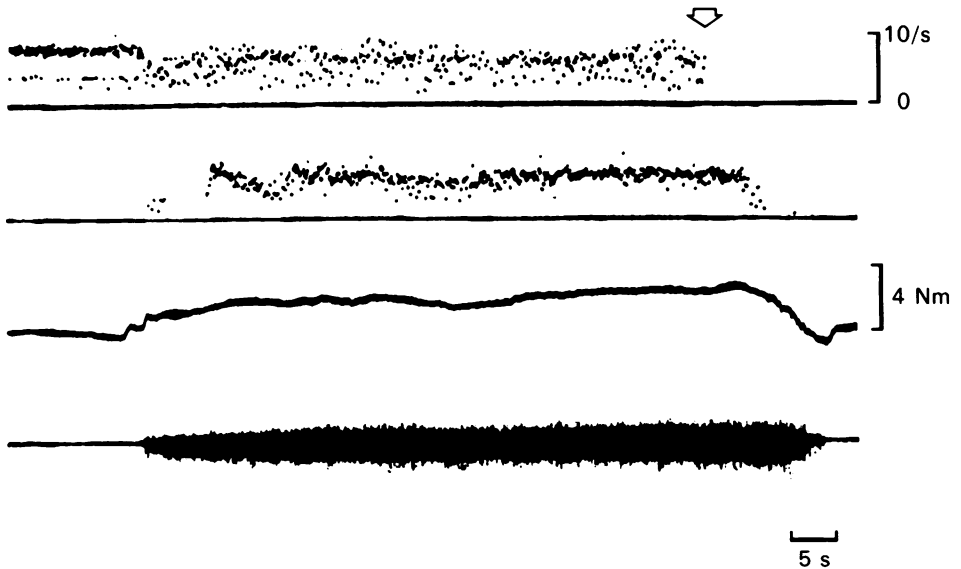


Fig. 3. Simultaneous recordings from two spindle endings in tibialis anterior during an isometric voluntary contraction. Upper trace: instantaneous frequency plot from an initially active ending; second trace: instantaneous frequency plot from an initially silent ending; third trace: contraction torque; fourth trace: e.m.g. of tibialis anterior. At the vertical arrow the recording conditions for the initially active ending deteriorated. The slight change in torque before the onset of e.m.g. activity was due to a postural adjustment in preparation for the contraction.

could be as long as 15 s (Fig. 2). From these Figures, it is clear that if contraction torque did not exceed 1.5 Nm the spindle ending would remain silent, but once activated it could be 'recruited' or 'de-recruited' at will by appropriate changes in contraction strength (Fig. 2).

With six of the twelve spindle endings which had a background discharge at  $+25^\circ$  it was possible to demonstrate that weak voluntary contractions decreased spindle discharge frequency (Fig. 3). For three of these six endings, spindle acceleration occurred in stronger contractions, once contraction torque had exceeded a threshold level. The frequency plots of Fig. 3 are from two different spindle endings, simultaneously recorded. The upper frequency plot shows the discharge of an

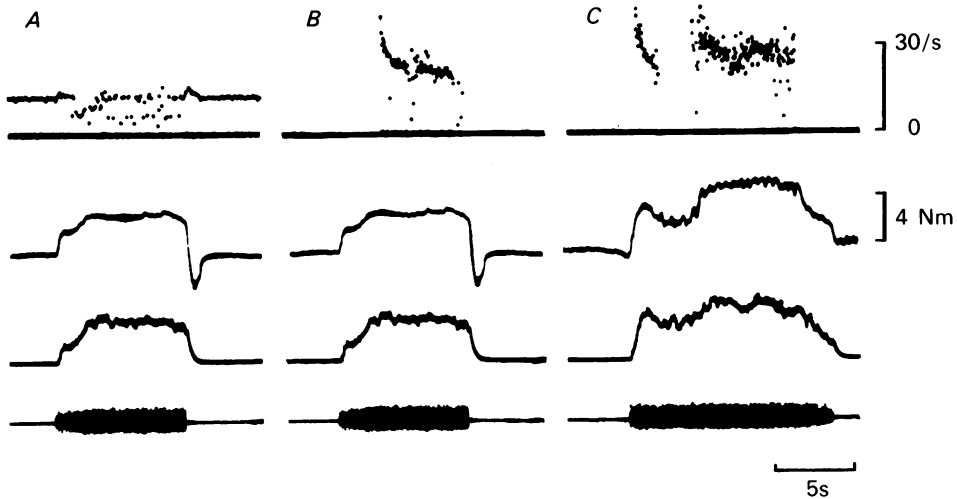


Fig. 4. Simultaneous recordings from two spindle endings in tibialis anterior. *A*, recording from an initially active ending during an isometric voluntary contraction below threshold for the ending. *B*, recording from an initially silent ending which was activated in the same contraction. *C*, a second isometric contraction, the initially silent ending being activated at the same torque level as in *B*. Traces are: instantaneous frequency plot; contraction torque; integrated e.m.g. of tibialis anterior (time constant 0.2 s); and e.m.g. of tibialis anterior.

initially active ending, which is unloaded by the contraction. Unfortunately, the recording conditions for this ending deteriorated abruptly at the vertical arrow. If only the record from this ending is considered, there is no evidence that the contracting muscle was subjected to increased fusimotor drive. However, in the second frequency plot, an initially silent spindle ending in the same muscle was activated during the same contraction, indicating that there was an increase in fusimotor outflow to the muscle even if it was not sufficient for or not directed to the initially active ending. Identical conclusions may be drawn from a second recording from two different spindle endings (Fig. 4*A, B*).

When expressed in terms of contraction torque, the threshold at which most spindle endings were activated was less than 2 Nm. The range for the eighteen endings was 0.5–3.5 Nm. Differences in the threshold for activation of different endings are illustrated in the sequences of Figs. 5 and 6, obtained from the third

recording from two spindle endings. In the record shown in Fig. 5 the first ending began to discharge at 1.5–2 Nm, 30 s before the second, which had a threshold of about 3 Nm; in the faster contraction of Fig. 6A the threshold for the second ending was reached much more quickly, but the first recruited ending was still activated at lower threshold, some 4 s before the second (cf. Fig. 6B).

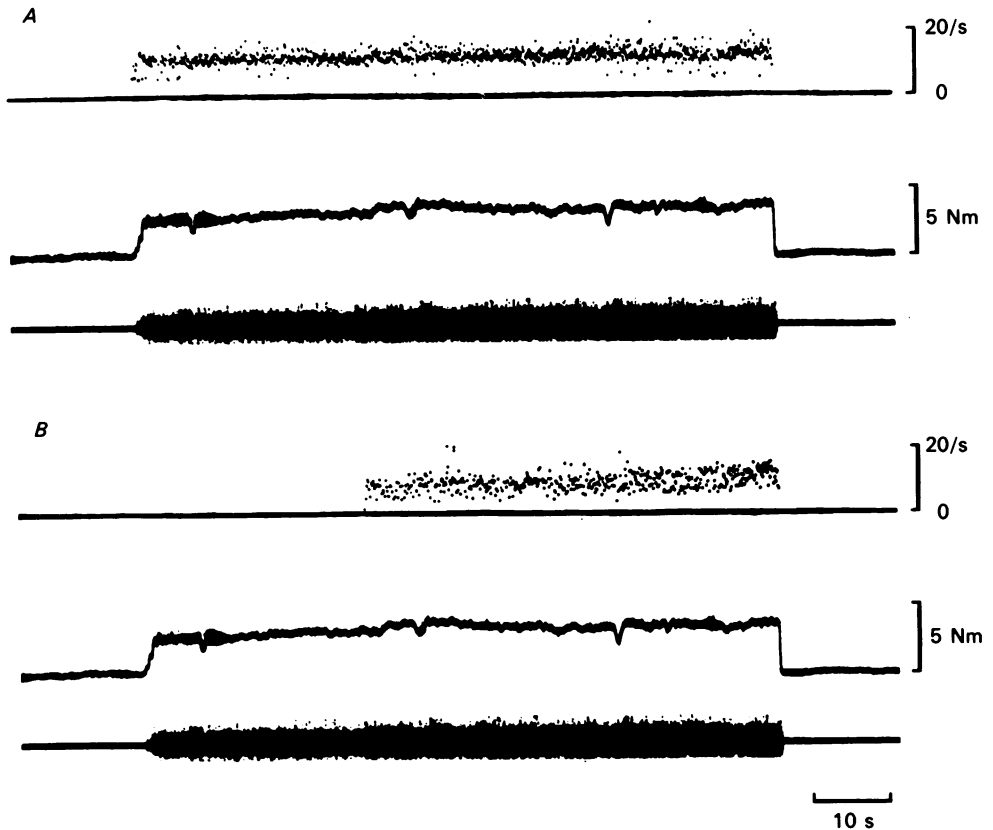


Fig. 5. Simultaneous recordings from two spindle endings in tibialis anterior during an isometric voluntary contraction. *A*, spindle ending activated early in the contraction; *B*, spindle ending activated late in the contraction. The traces in *A* and *B* are as in Fig. 1.

Within the range of contraction speeds used, the threshold for activation of a spindle ending remained constant, as seen in Figs. 2 and 4 and in the superimposed traces of Fig. 6C. However contraction torque always took 1–2 s to reach maximum. Fast contractions were not attempted in the present study because of the risk of dislodging the micro-electrode. It is probable that with fast contractions the torque level at which an ending is activated is lower, since, in earlier studies with very rapid phasic contractions, spindle endings discharged as early as 10–50 ms after the onset of e.m.g. activity, before or shortly after torque had begun to rise (Vallbo, 1971; Hagbarth *et al.* 1975).

*Orderly recruitment of fusimotor neurones?* Given that different spindle endings have different thresholds for activation in an isometric voluntary contraction, the failure

to activate an ending could result from either: (i) the contraction being subthreshold for the fusimotor neurones innervating the spindle; or (ii) the fusimotor effect on the spindle being insufficient to overcome the unloading effect of the skeletomotor activation. These alternatives are not mutually exclusive. The second alternative would require spindle endings to be sufficiently length-sensitive that they could detect the small internal length change that occurs in an isometric contraction. Unloading during a weak voluntary contraction could then be expected in the most length-sensitive endings. A correlation was sought between the responsiveness of spindle

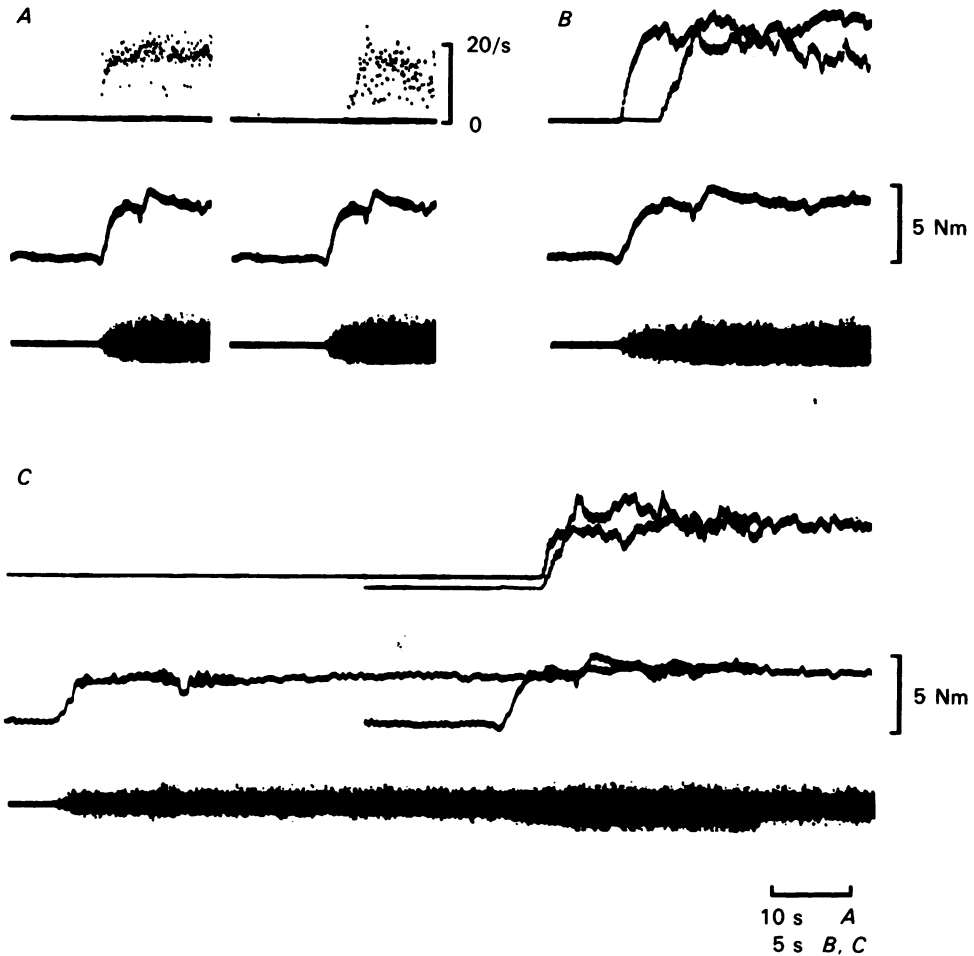


Fig. 6. Simultaneous recording from two spindle endings in tibialis anterior during isometric voluntary contraction. *A*, responses of the same two endings as in Fig. 5 during a faster contraction. Traces as in Fig. 5. *B*, same contraction as in *A*, with faster time base, and with the responses for the two units superimposed. The frequency plots are shown in analogue form obtained using an RC low pass filter (time constant 0.2 s). The higher threshold ending is activated some 4 s after the lower threshold ending. *C*, the responses of the higher threshold ending during the contractions of Fig. 5 and Fig. 6*A*, *B*. Records during the two contractions have been superimposed. Traces are instantaneous frequency plots (in analogue form, as in Fig. 6*B*); torque from the two contractions; e.m.g. of tibialis anterior from the two contractions. The torque level at which the ending is activated is similar in the two contractions.

endings to passive stretch and their ease of activation in a voluntary contraction, but no obvious correlation, positive or negative, was found. Similarly, no correlation was noted between the site of the spindle ending in the muscle and its ease of activation in a voluntary contraction.

Some support for the first alternative was found with two experiments on spindle endings whose discharge frequency did not alter in weak isometric contractions. Analysis of the variability of discharge of the two endings revealed that in contractions of 0.5–1.1 Nm there was no change in the coefficient of variation of the interspike intervals. Both endings could be activated in stronger contractions of 1.5–2.0 Nm. Thus, in the weaker contractions the only objective indicators of an

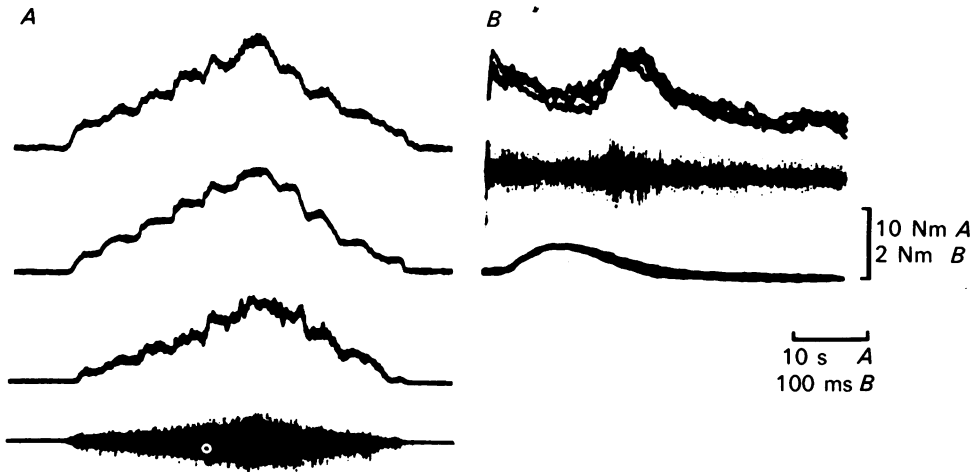


Fig. 7. Multi-unit spindle afferent responses from tibialis anterior. *A*, responses during an isometric voluntary contraction of tibialis anterior. Contraction force reached 60–70% maximum voluntary power. Upper trace: integrated multi-unit spindle activity (time constant 0.2 s); second trace: contraction torque; third trace: integrated e.m.g. of tibialis anterior (time constant 0.2 s); fourth trace: e.m.g. of tibialis anterior. *B*, responses during electrically-induced twitch contractions of tibialis anterior, showing characteristic spindle behaviour. Upper trace: integrated multi-unit spindle activity (time constant 0.02 s); second trace: original multi-unit spindle activity; third trace: twitch torque; three traces superimposed. The sequence in *B* was recorded from the same micro-electrode site, 7 min after the sequence in *A*.

increase in fusimotor activity, namely an increase in discharge frequency and an increase in the variability of discharge, were lacking (cf. Matthews & Stein, 1969; D. Burke, N. F. Skuse & D. G. Stuart, in preparation). It seems reasonable to conclude that there was probably no significant fusimotor activity destined for these two endings in the weaker contractions.

*Overall spindle inflow during contraction.* Under the conditions of the present study, the threshold for spindle activation could be expressed in terms of a measure of skeletomotor activity, and this proved quite accurate and reproducible for the same ending on different occasions (see Figs. 1 and 2; Fig. 4*B, C*; Fig. 6*C*). In addition, fluctuations in skeletomotor activity were generally accompanied by fluctuations in spindle discharge (cf. the disturbance near the end of the long contraction in Fig. 1; the graded change in spindle discharge frequency during step changes in contraction,



Fig. 2; the discharge pattern of the activated endings in Figs. 3 and 4C). However, spindle discharge did not parallel torque. There were non-linearities with individual endings, particularly at the onset of spindle activation (see Figs. 1, 2 and 4), and the threshold for spindle activation itself represents a non-linearity. Additionally, although spindle discharge frequency increased with contraction torque, it tended to reach a plateau with stronger contractions. Such individual non-linearities were not seen in multi-unit recordings of muscle spindle activity. Fluctuations in integrated multi-unit spindle activity correlated well with fluctuations in torque and integrated e.m.g. (Fig. 7), there being a linear relationship between spindle activity and contraction torque (Fig. 8).

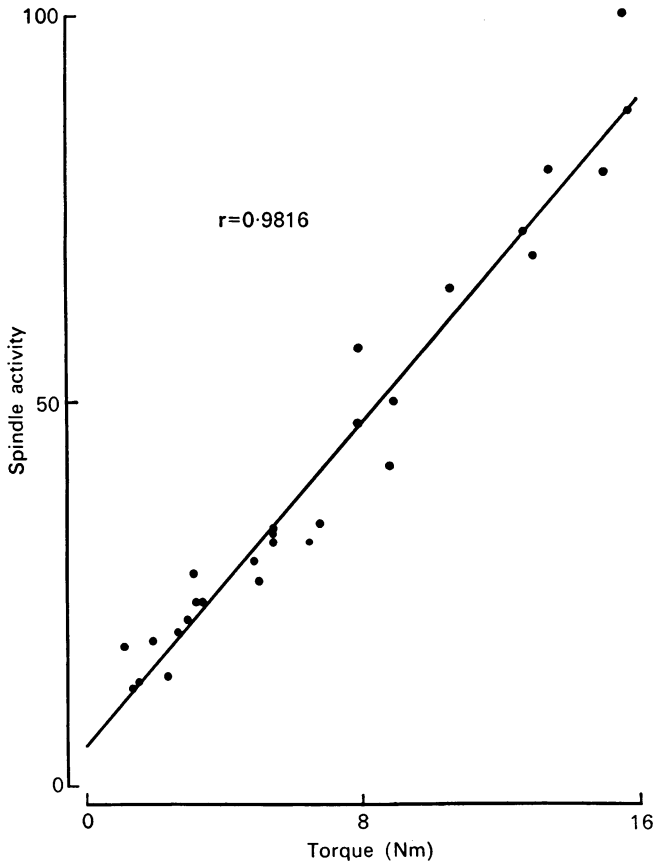


Fig. 8. Relationship between spindle afferent activity and strength of contraction in a series of isometric voluntary contractions. Same multi-unit recording site as in Fig. 7. Spindle activity is plotted in arbitrary units based on measurement of the amplitude of the integrated multi-unit neurogram (time constant 0.2 s). The relationship is linear (correlation coefficient 0.9816).

#### DISCUSSION

The present results indicate that in a voluntary contraction of slowly increasing strength spindle endings in the contracting muscle are activated in an orderly manner with different endings being recruited at widely different thresholds. The fact that

some endings have a high threshold for recruitment explains a number of previous observations which, on face value, seemed to oppose the view that voluntary motor acts are organized according to a fixed strategy of  $\alpha$ - $\gamma$  co-activation. Such findings are the failure to activate some spindle endings during voluntary contractions of the receptor-bearing muscle (Vallbo, 1970; Burg *et al.* 1973); the deceleration of spindle discharge that may occur at the onset of or for the duration of a voluntary contraction, even when unloading from neighbouring muscles is minimized or avoided (Vallbo, 1970, 1974; Burg *et al.* 1973; Burg, Szumski, Struppler & Velho, 1976; Hagbarth *et al.* 1975; Burke, Hagbarth, Löfstedt & Wallin, 1976*b*); and other examples of variable behaviour of different spindle endings during voluntary contractions (Prochazka, Westerman & Ziccone, 1976, 1977).

*Orderly recruitment of fusimotor neurones.* If internal length changes could be eliminated during an isometric contraction, the orderly recruitment of spindle endings as contraction strength increases could probably be attributed to orderly recruitment of the fusimotor neurones innervating the spindles. It is probable that the contractions of extrafusul muscle fibres anatomically close to a spindle ending modulate its discharge (Binder, Kroin, Moore, Stauffer & Stuart, 1976; Windhorst & Meyer-Lohmann, 1977; Binder & Stuart, 1978), but it is unlikely that such modulation would result in a reproducible threshold for activation for each spindle ending. Were the high threshold for some spindle endings solely the result of the shortening that occurs in an isometric contraction then an inverse correlation could be expected between the responsiveness to imposed length changes and the ease of activation in a voluntary contraction. No such correlation was seen. Furthermore, some evidence was found to support the view that if a spindle ending is not activated in an isometric voluntary contraction it may not yet be receiving a significant increase in fusimotor drive. Taken together, these findings provide suggestive evidence that the recruitment threshold of a spindle ending is determined by its fusimotor innervation and probably depends on a recruitment threshold for the fusimotor neurone(s) innervating that ending. By analogy with the well-documented recruitment order of skeletomotor neurones, such a conclusion seems eminently reasonable.

The present study was performed under isometric conditions and at a standard muscle length. It is probable that changes in muscle length would modify the ease with which a spindle ending was activated by its fusimotor innervation, thus altering the threshold for activation of the ending. During natural movements, the spindle discharge at any one time will be determined not only by the effort-related fusimotor drive on the ending but also by the extent and direction of the accompanying length change (Burke, Hagbarth & Löfstedt, 1978). It is also probable that if a shift in the  $\alpha$ - $\gamma$  balance were to occur in a different form of motor act the torque threshold for spindle activation would also change. However, with the exception of stretch reflex contractions (Burke *et al.* 1976*b*), there is, as yet, no definite evidence in man that such shifts occur.

*The nature of the command signal to the fusimotor neurones.* As shown in previous studies, especially that of Vallbo (1974), and confirmed in the present study, the spindle discharge induced in an isometric voluntary contraction is largely proportional to the skeletomotor outflow to the muscle, particularly if the ensemble input from a number of spindles in the muscle is considered. The possibility that

this relationship exists because the fusimotor-driven spindle input in turn drives the skeletomotor neurones has not withstood experimental testing; the close relationship between skeletomotor activity and fusimotor-driven spindle activity depends predominantly on co-activation of the skeletomotor and fusimotor neurones by central commands (Vallbo, Hagbarth, Wallin & Torebjörk, 1978). If, in addition, the recruitment threshold of fusimotor neurones can be expressed in terms of skeletomotor activity, it is likely that the supraspinal commands initiating the fusimotor activity are similarly related if not identical to those initiating the skeletomotor activity. Since it has been shown that desired muscle force rather than desired muscle length is the parameter signalled by corticospinal tract activity (Evarts, 1968), it is reasonable to conclude that the command signal to fusimotor neurones is not directly related to desired muscle length.

The tight coupling between skeletomotor activity and spindle discharge seen in human studies would be readily explicable if the responsible fusimotor fibres were of the  $\beta$  type, i.e. skeleto-fusimotor fibres. However, recent nerve block experiments in man using pressure indicate that the fusimotor effects are at least partly due to  $\gamma$  motoneurones, since muscle spindle endings can still be activated in an attempted voluntary contraction when the skeletomotor activity has been suppressed (Burke, Hagbarth, & Skuse, 1978).

This study was carried out under grants from the National Health & Medical Research Council of Australia and the Swedish Medical Research Council (Project Number B78-14X-02881-09A). The authors are grateful to Professor J. W. Lance and Dr A. K. Lethlean for their support.

#### REFERENCES

- BINDER, M. D., KROIN, J. S., MOORE, G. P., STAUFFER, E. K. & STUART, D. G. (1976). Correlation analysis of muscle spindle responses to single motor unit contractions. *J. Physiol.* **257**, 325-336.
- BINDER, M. D. & STUART, D. G. (1978). Motor unit-muscle receptor interactions: design features of the neuromuscular control system. In *Progress in Clinical Neurophysiology*. Vol. 8, *Motor Control in Man: Suprasegmental and Segmental Mechanisms*, ed. DESMEDT, J. E. Basel: Karger.
- BURG, D., SZUMSKI, A. J., STRUPPLER, A. & VELHO, F. (1973). Afferent and efferent activation of human muscle receptors involved in reflex and voluntary contraction. *Expl Neurol.* **41**, 754-768.
- BURG, D., SZUMSKI, A. J., STRUPPLER, A. & VELHO, F. (1976). Influence of a voluntary innervation on human muscle spindle sensitivity. In *The Motor System: Neurophysiology and Muscle Mechanisms*, ed. SHAHANI, M., pp. 95-110. Amsterdam: Elsevier.
- BURKE, D., HAGBARTH, K.-E. & LÖFSTEDT, L. (1978). Muscle spindle activity in man during shortening and lengthening contractions. *J. Physiol.* **277**, 131-142.
- BURKE, D., HAGBARTH, K.-E., LÖFSTEDT, L. & WALLIN, B. G. (1976a). The responses of human muscle spindle endings to vibration of non-contracting muscles. *J. Physiol.* **261**, 673-693.
- BURKE, D., HAGBARTH, K.-E., LÖFSTEDT, L. & WALLIN, B. G. (1976b). The responses of human muscle spindle endings to vibration during isometric contraction. *J. Physiol.* **261**, 695-711.
- BURKE, D., HAGBARTH, K.-E. & SKUSE, N. F. (1978). Voluntary activation of spindle endings in human muscles temporarily paralysed by nerve pressure. *J. Physiol.* (In the Press).
- CLAMANN, H. P. & HENNEMAN, E. (1976). Electrical measurement of axon diameter and its use in relating motoneuron size to critical firing level. *J. Neurophysiol.* **39**, 844-851.
- DESMEDT, J. E. & GODAUX, E. (1977). Ballistic contractions in man: Characteristic recruitment pattern of single motor units of the tibialis anterior muscle. *J. Physiol.* **264**, 673-693.
- ELDRED, E. & HAGBARTH, K.-E. (1954). Facilitation and inhibition of gamma efferents by stimulation of certain skin areas. *J. Neurophysiol.* **17**, 59-65.

- EVARTS, E. V. (1968). Relation of pyramidal tract activity to force exerted during voluntary movement. *J. Neurophysiol.* **31**, 14-27.
- FREUND, H.-J., BÜDINGEN, H. J. & DIETZ, V. (1975). Activity of single motor units from human forearm muscles during voluntary isometric contractions. *J. Neurophysiol.* **38**, 933-946.
- GRANT, R. & KAADA, B. R. (1952). Influence of stimulation of central nervous structures on muscle spindles in cat. *Acta physiol. scand.* **27**, 130-160.
- HAGBARTH, K.-E., WALLIN, G. & LÖFSTEDT, L. (1975). Muscle spindle activity in man during voluntary fast alternating movements. *J. Neurol. Neurosurg. Psychiat.* **38**, 625-635.
- HENNEMAN, E., SOMJEN, G. & CARPENTER, D. O. (1965). Functional significance of cell size in spinal motoneurons. *J. Neurophysiol.* **28**, 560-580.
- MATTHEWS, P. B. C. & STEIN, R. B. (1969). The regularity of primary and secondary muscle spindle afferent discharges. *J. Physiol.* **202**, 59-82.
- MILNER-BROWN, H. S., STEIN, R. B. & YEMM, R. (1973). The orderly recruitment of human motor units during voluntary isometric contractions. *J. Physiol.* **230**, 359-370.
- PROCHAZKA, A., WESTERMAN, R. A. & ZICCONI, S. P. (1976). Discharges of single hindlimb afferents in the freely moving cat. *J. Neurophysiol.* **39**, 1090-1104.
- PROCHAZKA, A., WESTERMAN, R. A. & ZICCONI, S. P. (1977). Ia afferent activity during a variety of voluntary movements in the cat. *J. Physiol.* **268**, 423-448.
- VALLBO, Å. B. (1970). Discharge patterns in human muscle spindle afferents during isometric voluntary contractions. *Acta physiol. scand.* **80**, 552-566.
- VALLBO, Å. B. (1971). Muscle spindle response at the onset of isometric voluntary contractions in man. Time difference between fusimotor and skeletomotor effects. *J. Physiol.* **218**, 405-431.
- VALLBO, Å. B. (1974). Human muscle spindle discharge during isometric voluntary contractions. Amplitude relations between spindle frequency and torque. *Acta physiol. scand.* **90**, 319-336.
- VALLBO, Å. B., HAGBARTH, K.-E., WALLIN, B. G. & TOREBJÖRK, H. E. (1978). Proprioceptive, somatosensory and sympathetic activity in human peripheral nerves. *Physiol. Rev.* (In the Press).
- WINDHORST, U. & MEYER-LOHMANN, J. (1977). The influence of extrafusal muscle activity on discharge patterns of primary muscle spindle endings. *Pflügers Arch.* **372**, 131-138.