

## VOLUNTARY ACTIVATION OF SPINDLE ENDINGS IN HUMAN MUSCLES TEMPORARILY PARALYSED BY NERVE PRESSURE

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### SUMMARY

1. In normal human subjects, the afferent activity from muscle spindle endings in the pretibial muscles was recorded while a pressure block was applied to the peroneal nerve proximally in the popliteal fossa.

2. In five of ten blocks, spindle activity increased in attempted isometric voluntary contractions when the receptor-bearing muscles were completely paralysed. In the remaining five blocks, voluntary effort still increased spindle activity when maximum voluntary power was reduced by more than 90 %, but the ability to activate spindles voluntarily was lost with or slightly before block of the last motor units. When the ability to activate spindle endings in an attempted voluntary contraction was lost sympathetic efferent fibres remained unblocked.

3. It is concluded that the fusimotor effects seen during a voluntary contraction are mediated by myelinated fibres of small calibre which probably innervate intra-fusal structures exclusively ( $\gamma$  fusimotor fibres). There is no necessity to postulate that skeleto-fusimotor ( $\beta$ ) fibres are responsible for the tight ' $\alpha$ - $\gamma$  co-activation' seen in man during voluntary contractions.

### INTRODUCTION

In man, when a muscle is contracted voluntarily, the fusimotor system to that muscle is activated such that spindle discharge is usually maintained or accelerated (cf. Vallbo, 1974*b*). These findings support animal data that natural or near-natural movements such as respiration, locomotion and jaw movements are associated with co-activation of the skeletomotor and fusimotor systems, at least during certain phases of movement (cf. Sears, 1964; Euler, 1966; Severin, 1970; Cody, Harrison & Taylor, 1975; Goodwin & Luschei, 1975; Prochazka, Westerman & Ziccone, 1976). In human studies, co-activation of the skeletomotor and fusimotor drives has been found in voluntary contractions whether they are deliberate or unintentional (Vallbo, 1971, 1974*b*; Hagbarth, Wallin, Burke & Löfstedt, 1975*a*; Burke, Hagbarth & Löfstedt, 1978*b*), whether they are fast or slow (Vallbo, 1971; Hagbarth, Wallin & Löfstedt, 1975*b*), and whether they are isometric, involve changes in muscle length,

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or are intended to compensate for changes in load (Burke, Hagbarth & Löfstedt, 1978*a, b*). The fusimotor activity appears to be proportional to the skeletomotor activity in intensity (Vallbo, 1974*b*), and to be directed specifically to the contracting muscle (Vallbo, 1974*b*; Hagbarth *et al.* 1975*b*; Burke, Hagbarth, Löfstedt & Wallin, 1976). Fusimotor neurones seem to be recruited in a reproducible order, much as are skeletomotor neurones (Burke, Hagbarth & Skuse, 1978). Conversely, when a muscle is not contracting, the available evidence suggests that there is no significant background fusimotor activity to that muscle (cf. Vallbo, 1974*a*; Burke *et al.* 1976). Thus, human studies indicate that, during a voluntary contraction, there is a very tight, possibly even 'hard-wired' linkage between the skeletomotor and fusimotor drives. The term ' $\alpha$ - $\gamma$  co-activation' has been used freely for this linkage, on the reasonable assumption that the fusimotor effects are mediated by  $\gamma$  fusimotor fibres.

Skeleto-fusimotor ( $\beta$ ) fibres, once considered an evolutionary relic, are now being demonstrated with increasing frequency in cat (cf. Emonet-Dénand & Laporte, 1975; McWilliam, 1975; Barker, Emonet-Dénand, Harker, Jami & Laporte, 1977). These fibres are of smallish size, their conduction velocities fall in the slow  $\alpha$  range, and their fusimotor effects are predominantly dynamic. More recently, Harker, Jami, Laporte & Petit (1977) have presented evidence of innervation of nuclear chain fibres by  $\beta$  axons of larger calibre and of conduction velocity within the fast  $\alpha$  range, suggesting that static as well as dynamic fusimotor effects can result from the activation of  $\beta$  fibres.

The tight coupling between spindle discharge and skeletomotor activity seen in man would be readily explicable if a proportion of the motor fibres to a muscle innervates both intrafusal and extrafusal muscle, if they were the ones activated in a voluntary contraction, and if the resulting fusimotor effect was predominantly static. Some indirect arguments against this possibility have been presented (Burke *et al.* 1976), but so far there is no unequivocal evidence that the fusimotor effects seen in a voluntary contraction can be attributed to motor fibres innervating intrafusal structures exclusively. In the present study experiments analogous to those performed by Leksell (1945) have been carried out in an attempt to demonstrate that the fusimotor effects seen during a voluntary contraction are mediated by fibres which do not also innervate extrafusal muscle.

#### METHODS

The experiments were performed on the authors because they involved subjecting a nerve to two invasive procedures at the same time: the recording of muscle spindle activity with a micro-electrode; pressure block of the motor nerve to and beyond the stage of complete paralysis. In two preliminary experiments the median nerve was blocked by a sphygmomanometer cuff inflated to 300 mmHg above the elbow, while recordings of muscle spindle activity were made at elbow level from flexor digitorum longus. In these blocks, evidence of progressive receptor dysfunction, presumably the result of ischaemia, was seen in addition to the effects of the nerve block. This form of nerve block was therefore abandoned, although the results were qualitatively similar to those to be presented using direct pressure applied to the nerve trunk.

In six subsequent experiments recordings of muscle spindle activity were made during pressure block of the peroneal nerve proximal to the recording site. All data were obtained from fascicles innervating tibialis anterior or extensor digitorum longus. The recording techniques have been described in full previously (Vallbo, 1971; Hagbarth *et al.* 1975*b*). Pressure was applied to the nerve in the popliteal fossa by a smooth wooden oval of 2.5 × 5 cm which was secured to one

wing of a G-clamp, the other wing of which was stabilized on the femur medial to the patella. The foot was secured in 25° plantar flexion in an isometric myograph so that the torque produced by contraction of the appropriate muscle could be recorded. The electromyogram (e.m.g.) of the receptor-bearing muscle was recorded using pairs of surface or needle electrodes.

The progress of each block was titrated as a percentage of maximum voluntary power, which was measured before each block and after complete recovery. No attempt was made to monitor the progress of the nerve blocks by stimulating electrically above the block, for a number of reasons: firstly, the block was applied to the nerve as proximally as possible in order to minimize mechanical disturbances to the recording site; secondly, a maximal twitch contraction would jeopardize the recording; and, thirdly, a partially blocked nerve fibre may still be able to transmit a single impulse although unable to maintain a physiologically meaningful train of impulses.

Ten pressure blocks were performed on the peroneal nerve during five single unit and five multi-unit recordings of spindle afferent activity. In all cases the afferent activity was demonstrated to be of muscle spindle origin by the typical response to an electrically induced twitch contraction of the receptor-bearing muscle, as illustrated for a multi-unit recording in Fig. 2C (cf. Hagbarth *et al.* 1975b).

### RESULTS

In all nerve blocks severe paresis of the receptor-bearing muscle was produced, with maximum voluntary power reduced to less than 10% control value, before the ability to activate spindle receptors was abolished. However, once detectable weakness and cutaneous sensory loss had begun to occur the time to complete paralysis was a matter of only 5 min at most. At the stage of complete paralysis of the receptor-bearing muscle the ability to activate spindle endings in an attempted voluntary contraction was retained with two single unit recordings (Fig. 1) and three multi-unit recordings (Fig. 2), but was lost with the other recordings. With further progression of the blocks the subjects invariably lost the ability to influence the spindle discharge. In single unit recordings this loss occurred suddenly, initially with inability to maintain a steady spindle discharge so that the frequency of discharge gradually decreased despite maintained effort. Within a few seconds the endings could be activated only in brief bursts at the onset of or sporadically during a maintained maximal effort to contract the muscle. For most endings the background discharge frequencies and the responses to tendon percussion remained unaltered when the endings could not be activated through efferent mechanisms. With release of the pressure, restoration of function occurred rapidly, with complete recovery usually within 2–3 min. During recovery, the neural recordings commonly contained increased spontaneous activity, and bizarre high frequency discharges in afferent fibres were recorded. These discharges were accompanied by intense paraesthesiae which subsided in parallel with the spontaneous discharges.

With the recording illustrated in Fig. 1 the nerve block had already progressed inadvertently to marked weakness (5% maximum voluntary power) when a stable single unit recording was obtained. A maximum voluntary effort activated the ending, but produced only a weak contraction, as seen in the torque and e.m.g. records (Fig. 1A). Ninety seconds later paralysis was complete, but the spindle ending still accelerated in an attempted maximum voluntary contraction (Fig. 1C). An example of the e.m.g. activity produced by a maximum voluntary contraction following recovery from the block is shown in Fig. 1D. With the other single unit studied during a selective block, the acceleration of discharge followed the onset of

e.m.g. activity in all control voluntary contractions, but during the development of the block the ending could be activated in attempted weak contractions without producing evidence of skeletomotor activity. With strong effort just before the

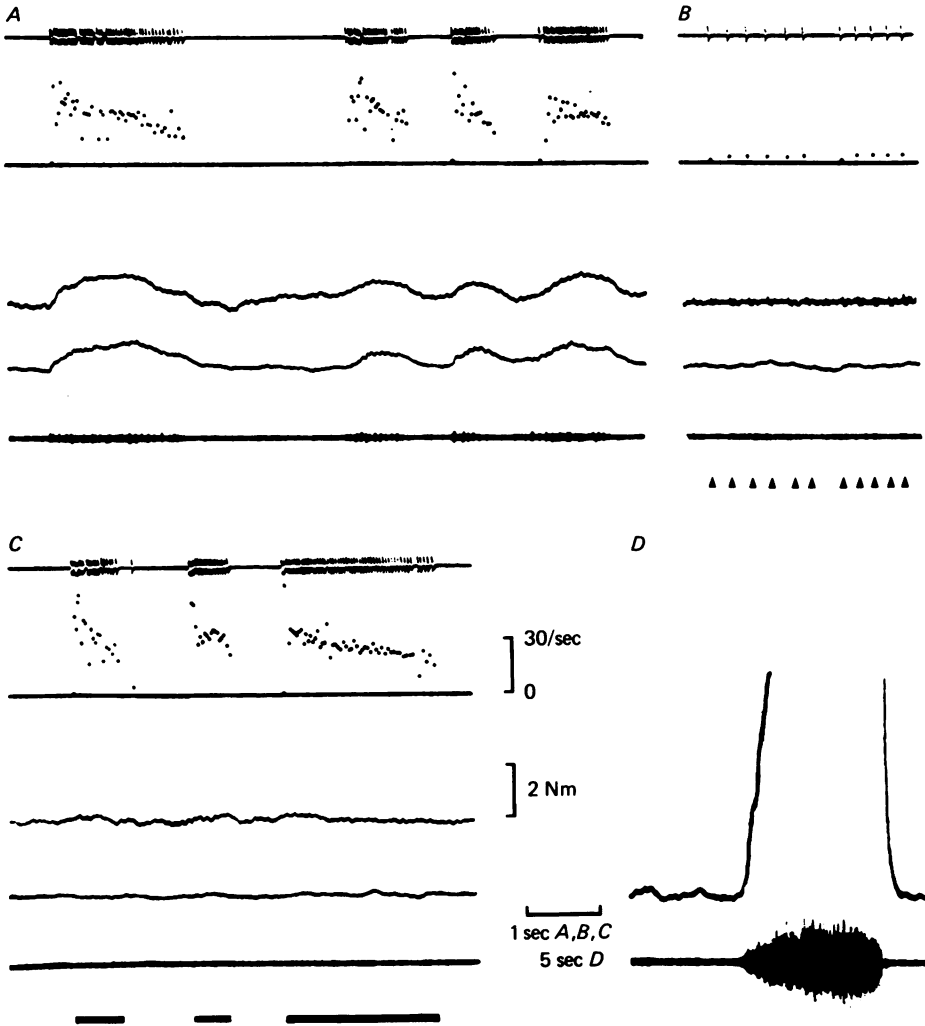


Fig. 1. Recording from a spindle ending in extensor digitorum longus during selective block of skeletomotor activity. The ending had no background discharge with the ankle fixed in 25° plantar flexion. *A*, activation of the ending in four voluntary contractions, using maximal effort. The block had already progressed to severe weakness, there is little e.m.g. activity, and the contraction torque is 4–5% maximum voluntary power. *B*, responses to tendon taps (indicated by arrows) at the stage of complete skeletomotor block. *C*, spindle activation during maximal efforts to contract extensor digitorum longus (indicated by horizontal bars) at the stage of complete skeletomotor block. *D*, e.m.g. activity at same gains in a maximal effort following recovery from the block. Traces in *A–C* are, from above, pulse representing spindle afferent potential; instantaneous frequency of discharge of the ending (calibration in *C*); torque produced by contraction (calibration in *C*); integrated e.m.g. of extensor digitorum longus (time constant 0.2 sec); and e.m.g. of extensor digitorum longus.

skeletomotor activity was completely blocked the ending fired at higher discharge frequencies than before the block. When the receptor-bearing muscle was completely paralysed the ending could still be activated voluntarily by maximal effort in an attempt to contract the muscle. A similar dissociation of skeletomotor activity and spindle acceleration was seen at the height of pressure blocks with three multi-unit recordings of spindle afferent activity (Fig. 2). In those recordings in which the subject lost the ability to activate spindle endings as the receptor-bearing muscle

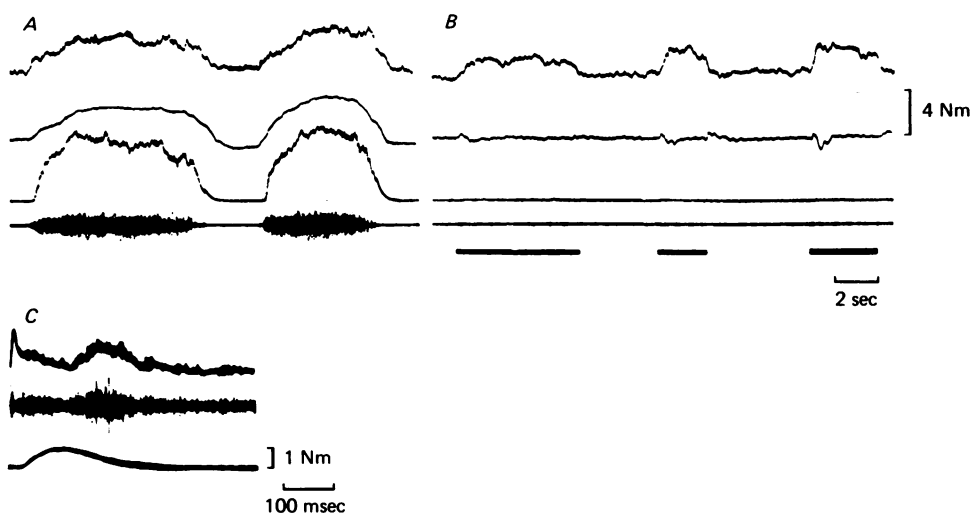


Fig. 2. Multi-unit recording of spindle afferent activity from extensor digitorum longus during a selective block of skeletomotor activity. *A*, control voluntary contractions before any sensory or motor deficit had developed. *B*, responses to maximal efforts to contract extensor digitorum longus (indicated by horizontal bars) at the stage of complete skeletomotor block. The transients in the torque trace resulted from passive displacement of the body and from contraction of unblocked triceps surae muscles, and could not be avoided if the effort to contract extensor digitorum longus was maximal. Traces in *A* and *B* are: integrated multi-unit spindle activity (time constant 0.2 sec); torque; integrated e.m.g. of extensor digitorum longus (time constant 0.2 sec); and e.m.g. of extensor digitorum longus. *C*, responses to electrically induced twitch contractions of extensor digitorum longus, confirming that the recording site was dominated by spindle afferent activity. Three sweeps superimposed. Traces are: integrated neural activity (time constant 0.01 sec); 'raw' record of neural activity; and twitch torque.

became completely paralysed, a greater effect on skeletomotor function than on fusimotor function could be demonstrated during the development of the block: the progressive reduction in contraction force was associated either with no change or with an increase in the amount of spindle activity accompanying a strong effort to contract the muscle (Fig. 3).

In most recordings pulsatile bursts of activity in unmyelinated sympathetic efferent fibres contributed to the background noise. The sympathetic bursts became more prominent with the progression of the blocks and remained so when the ability to activate spindle endings by voluntary effort had been abolished. These findings

indicate that the pressure blocks were not affecting unmyelinated fibres, and that the fusimotor effects occurring during a voluntary contraction cannot be attributed to these fibres.

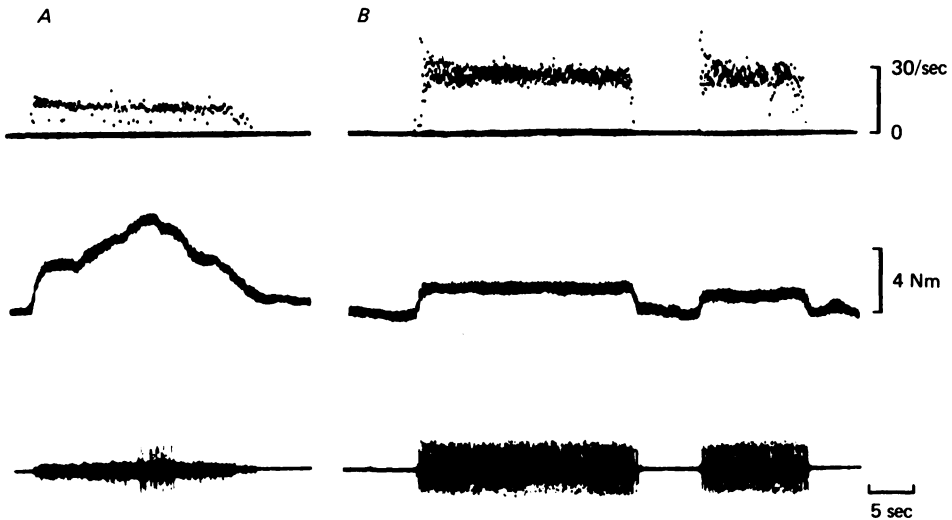


Fig. 3. Responses of a spindle ending in tibialis anterior during a preferential block of skeletomotor activity. *A*, control voluntary contraction of approximately 25% maximum voluntary power, before block. Note the recruitment of a large motor unit potential with strong contraction. *B*, maximal effort to contract tibialis anterior when skeletomotor activity almost fully blocked, and strength reduced to 6% maximum. E.m.g. pattern is dominated by the motor unit previously recruited only in moderately strong contractions. Despite the obvious skeletomotor paresis, there is no obvious deficit of fusimotor function, the spindle ending reaching higher frequencies than before the block. Traces are: instantaneous frequency of discharge of the ending; torque; e.m.g. of tibialis anterior.

#### DISCUSSION

It is apparent that the clear dissociation of skeletomotor and fusimotor activity described by Leksell (1945) for the cat is difficult to achieve in intact man. This is perhaps not surprising since human experiments require a less direct application of pressure to the nerve and since the size of the nerve trunk in man will result in a less even distribution of pressure over the cross-sectional area of the nerve. It should be noted that Leksell's blocks were not completely selective, there being a residual contraction of 1–2% maximum strength in a 'fairly selective' block. Viewed in this light the present results compare favourably with those in the cat.

From the present experiments, it is reasonable to attribute the spindle acceleration accompanying a voluntary contraction to myelinated fusimotor fibres of small calibre. In five of the ten nerve blocks, the fusimotor effects were mediated by efferent fibres which did not activate extrafusal muscle fibres, presumably  $\gamma$  fusimotor fibres. In the other instances, the fusimotor effects could have resulted from activation of either  $\gamma$  fusimotor fibres, the pressure blocks not being completely selective, or  $\beta$  fibres of small calibre. From cat experiments (Emonet-Dénand & Laporte, 1975; Harker *et al.* 1977) such  $\beta$  fibres should have a dynamic fusimotor effect, rather than

the static effect required to explain the human findings (Vallbo, 1974*b*; Burke *et al.* 1976). It is therefore not necessary to invoke  $\beta$  fibres to explain any of the present experimental findings. However, it is possible, even probable, that  $\beta$  fibres contribute to the activation of spindle endings that occurs during a voluntary contraction in man, but if so they are not responsible for all the fusimotor influences. It may be concluded that  $\gamma$  fusimotor fibres are co-activated in a voluntary contraction and that they are responsible for much of the effect on spindle discharge.

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