MUSCLE SPINDLE RESPONSES IN MAN TO CHANGES IN LOAD DURING ACCURATE POSITION MAINTENANCE

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SUMMARY

1. Single unit and multi-unit recordings of muscle spindle activity were made from the peroneal nerves of human subjects. While the subjects attempted to maintain a constant ankle joint position, an external load on the receptor-bearing muscle was altered unexpectedly.

2. The spindle discharge produced by a sudden increase in load was of similar strength when the receptor-bearing muscle was relaxed as when it was contracting at the moment of the impact. A motor response at a latency consistent with a spinal reflex mechanism occurred only when the muscle was contracting. It is concluded that the potentiation of the reflex mechanism during contraction was not due primarily to a fusimotor action.

3. Sudden decrease in load produced a pause in spindle discharge followed by a pause in on-going e.m.g. activity at a latency consistent with spinal reflex mechanisms.

4. Slow changes in load produced parallel changes in e.m.g. and spindle discharge. It is suggested that the voluntary effort involved in maintaining joint position in the face of gradually changing loads results in corticospinal activity adjusted in strength to the opposing torque and operating on α and γ motoneurones in parallel.

INTRODUCTION

According to the servo assistance view of stretch reflex mechanisms a major functional role for muscle spindle endings activated in a voluntary contraction is to provide supportive excitation to the contracting muscle (Granit, 1970; Matthews, 1972). Thus, a change in load on a muscle is thought to induce corresponding changes in spindle feed-back and appropriate changes in motoneurone discharge. In those experiments on human subjects where torque motors have been used to produce a sudden increase in load, the compensatory response has been found to contain a mixture of voluntary and reflex activity, the latter composed of short and long latency reflex components (Marsden, Merton & Morton, 1971, 1976; Lee & Tatton, 1975). While much experimental work has been done in man on the motor responses to load changes, data on the spindle responses have been limited to those available from

animal experiments. The present investigation was undertaken to study some aspects of the muscle spindle responses accompanying changes in external load while subjects were attempting to maintain a constant joint position.

METHODS

Using micro-electrodes inserted percutaneously into the peroneal nerves of normal human volunteers, recordings were obtained from twelve muscle spindle afferents, the receptors of which were located in tibialis anterior (TA) or occasionally in extensor digitorum longus (EDL). In seven experiments, multi-unit recordings of muscle spindle afferent activity from the same muscles were also obtained. The experimental techniques were similar to those described previously (Hagbarth, Wallin & Löfstedt, 1975; Burke, Hagbarth, Löfstedt & Wallin, 1976). In each case, the single or multi-unit activity was demonstrated to be of muscle spindle origin using electrically induced muscle twitch contractions (cf. Wallin, Hongell & Hagbarth, 1973; Hagbarth et al. 1975). Strict subclassification of spindle endings as primary or secondary was not attempted, but nine endings behaved in a predominantly dynamic manner and three in a predominantly static manner in response to passive stretching movements.

Subjects reclined on one side on a bed, with foot fixed to the rotating plate of a hydraulically driven muscle stretcher (Löfstedt, 1977). For these studies the drive to the rotating plate was disconnected to allow friction-less movement. The torque and electromyogram (e.m.g.) produced by contraction of the receptor-bearing muscle and ankle joint position were recorded on tape with the neurogram. Subjects were requested to maintain, as accurately as possible, a constant ankle joint position, usually between 10 and 15° plantar flexion, while a dorsiflexion or plantar flexion load was applied unpredictably to the foot-plate. Changes in load were produced manually by varying the length of a rubber band attached to the foot-plate. In different trials, the responses induced by abrupt and gradual changes in load were studied. Instantaneous changes in load such as can be produced by a torque motor were not attempted, partly because such disturbances might jar the limb and jeopardize the neural recording site. It was also considered that the time course of the load change and of the afferent and efferent responses in the system used would reproduce more closely those of the physiological situation than would those produced by an artificially abrupt stimulus. Thus, in the present experiments, even with the most abrupt disturbances possible the spindle response built up over some 5–10 ms, so that the latencies of the motor responses do not represent the minimal conduction times for the responsible reflex arcs. Reflex latencies were estimated from multi-unit recordings because these sampled the activity of a number of spindle afferents and provided a more reliable basis for calculation.

RESULTS AND DISCUSSION

Responses to abrupt increases in external load. The latency of the motor response to an abrupt increase in external load depended on whether the receptor-bearing muscle was contracting or not when the load was applied. Throughout the traces in Fig. 1 the subject was attempting to maintain a constant ankle joint angle as accurately as possible. In the absence of pre-existing plantar flexion load (*A*), no background contraction of TA was required. The unexpected application of a load of 0·55 Nm at the vertical line produced a relatively large deviation of the foot, an afferent stretch response and a motor response at relatively long latency (175 ms) after the peak of the afferent response. In different experiments and with different degrees of prepared-ness latencies for the earliest motor responses of up to 300 ms were recorded. These long and variable latencies suggest that the responses were voluntary reactions rather than reflexes. In *B*, when the subject was already exerting a steady dorsiflexing force an increase in external load of 0·55 Nm at the vertical line produced a smaller stretch of the contracting muscle and an afferent response which was comparable to but

slightly smaller than that in *A*. The onset of the motor response occurred earlier, 40 ms after the peak of the stretch-induced afferent volley. In different trials and in different subjects latencies of 40–80 ms were recorded under these conditions. Allowing for the relatively slow time course of the load change, these latencies are quite consistent with spinal reflex mechanisms. It cannot be excluded, however, that supraspinal reflex loops may have contributed to the later components of the early response.
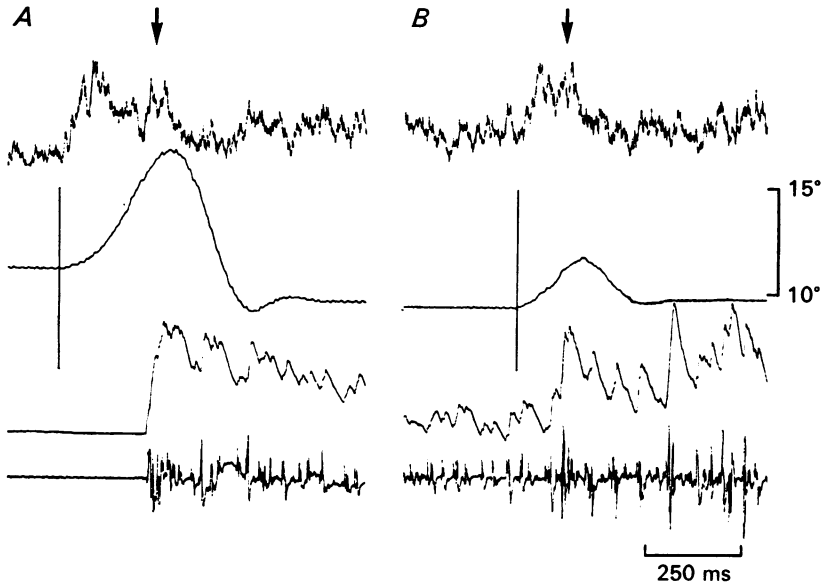

Fig. 1. The responses to an abrupt increase in external load of 0·55 Nm when TA was previously unloaded (*A*) and when already loaded with 0·55 Nm (*B*). Traces are, from above, integrated multi-unit afferent neural activity from TA (time constant 0·01 s); ankle joint angle; integrated e.m.g. of TA (time constant 0·05 s); e.m.g. of TA. The vertical lines indicate the timing of load application. The second bursts of neural activity (indicated by vertical arrows) are probably due to synchronized efferent responses.

As in Fig. 1, the initial multi-unit stretch response was sometimes followed by a second neural volley (arrowed), coinciding with the initial e.m.g. potentials. This second volley was not seen in single unit recordings, and may have been due to synchronized activity in motor fibres.

The reflex potentiation seen in *B* could not have been primarily the result of fusimotor action since the afferent response to stretch was not greater than in *A*. This conclusion is reminiscent of earlier studies of spindle responses during the Jendrassik manoeuvre (Hagbarth, Wallin, Burke & Löfstedt, 1975) and during voluntary suppression of the tonic vibration reflex (Burke *et al.* 1976), which studies demonstrated that there were mechanisms independent of the fusimotor system by which the gain of segmental stretch reflex pathways could be adjusted. It remains conjectural to what extent the reflex potentiation seen in Fig. 1*B* resulted from a change in reflex transmission within the spinal cord or from greater ease of activating an already discharging motoneurone pool. However, the phenomenon does appear to be central, and it may be analogous to the change in gain of the long latency (long loop)

reflex responses that occur with increasing background contraction level (Marsden *et al.* 1976). It therefore seems that when a muscle is contracting spinal reflex mechanisms are also 'primed' and more capable of generating a reflex response.

Responses to abrupt decreases in external load. The abrupt decrease or removal of a load on an active muscle produced the unloading reflex (cf. Merton, 1951; Angel, Eppler & Iannone, 1965; Struppler, Burg & Erbel, 1973). The reflex pause in e.m.g. activity was preceded by a pause in muscle spindle activity in both multi-unit (Fig. 2*A*) and single unit (Fig. 2*B*) recordings. In different trials and in different experiments, the latency between the onset of the decrease in afferent activity and the last e.m.g. potential was 35–70 ms, values which are again consistent with spinal reflex mechanisms. These findings may be interpreted as resulting from the withdrawal of
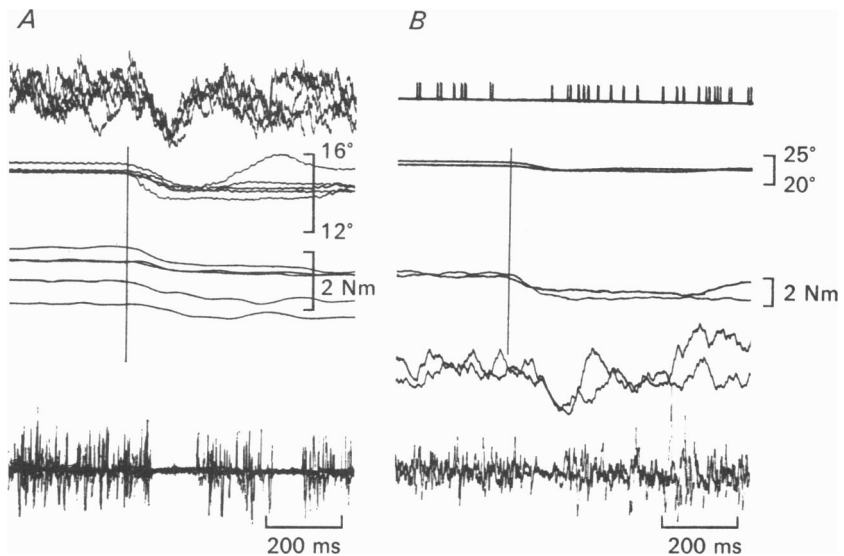

Fig. 2. The responses to abrupt removal of load seen in multi-unit spindle activity from TA (*A*) and the discharge of a 'static' spindle ending in TA (*B*). Load decreased at the vertical lines by 0·55 Nm in *A* and by 1·14 Nm in *B*. Five traces superimposed in *A*; 2 in *B*. Traces are, from above, neural activity (multi-unit activity integrated with time constant 0·01 s) in *A*; standardized spindle afferent potential in *B*; ankle joint angle; torque; integrated e.m.g. of TA in *B* only; e.m.g. of TA.

supportive excitation from muscle spindle endings in the contracting muscle. However, although the results demonstrate the existence of an excitatory drive, probably transmitted through spinal pathways, they do not allow a reliable estimation of its strength. The sudden withdrawal of a small excitatory synaptic input can significantly affect the timing of motor unit discharge even if the major synaptic input is mediated over other independent pathways (cf. Matthews, 1975).

Responses to gradual changes in external load. Fig. 3 shows the discharge of a 'static' spindle ending during an isometric voluntary contraction (*A*) and during attempts to maintain accurately a constant joint position in the face of a slowly changing external load (*B*). The attempts were quite successful since large changes in load of up to 4 Nm produced joint position changes of less than 2°. The spindle response waxed and

waned in parallel with the load and with the contraction strength. The relationship between spindle discharge rate and e.m.g. activity was similar whether joint position was maintained by external fixation (*A*) or by active load compensation (*B*). For all spindle endings studied, the discharge rates accompanying the load-bearing contractions exceeded those produced by comparable passive stretch when the receptor-bearing muscles were relaxed, indicating that such contractions are accompanied by a significant increase in fusimotor drive.
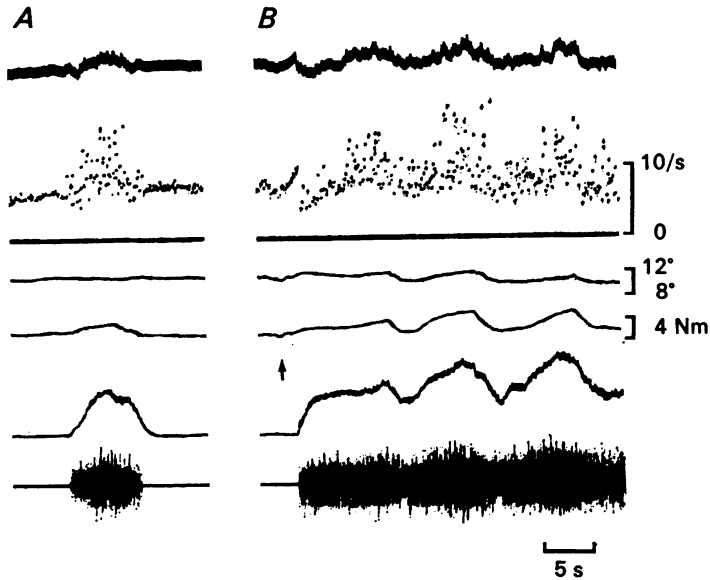

Fig. 3. The responses of a 'static' spindle ending in TA during an isometric contraction (*A*) and a load-bearing contraction (*B*). Traces are from above, smoothed instantaneous frequency plot (time constant 0·5 s); instantaneous frequency plot; ankle joint angle; torque; integrated e.m.g. of TA (time constant 0·5 s); e.m.g. of TA. In *B*, a load equivalent to 0·55 Nm was applied at the arrow and, while the subject attempted to maintain a constant joint position, this load was then varied, as seen in the torque record.

On indirect evidence obtained during recordings from cortical cells in conditioned monkeys, Tanji (1976) suggested that accurate maintenance of joint position involves a dissociation of the skeletomotor and fusimotor drives to the contracting muscles. The present results lend no support to this suggestion. Instead they indicate that slow load-compensating contractions are accompanied by significant fusimotor activation, much as occurs in isometric voluntary contractions, but unlike the situation in segmental stretch reflexes such as the tonic vibration reflex (Burke *et al.* 1976). Thus, although small changes in length of spindle endings may provide one of the inputs signalling variations in load, the segmental stretch reflex does not appear to be the main generator of the motor response. Effective load compensation is associated with adjustment of the strength of corticospinal commands to the opposing load (Evarts, 1973). The present results suggest that such commands operate on α and γ motoneurones in parallel. This does not exclude the possibility that during load-bearing contractions there may be changes in the α-γ balance depending on the

extent to which the segmental stretch reflex at any particular moment assists in the load-compensating task.

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