

Fusimotor reflexes in relaxed forearm muscles produced by cutaneous afferents from the human hand

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1. This study was designed to determine whether cutaneous receptors in the hand exert reflex effects on fusimotor neurones innervating relaxed muscles. Recordings were made from fifty-four muscle spindle afferents in the radial nerve while the arm was held relaxed in a supporting frame. Cutaneous afferents were activated by trains of stimuli at non-noxious levels to the superficial radial nerve or to the palmar surface of the fingers.
2. For the population of muscle spindle afferents, the mean discharge rate was 7.1 ± 6.4 Hz (range 0–24 Hz). Thirty-three per cent had no background discharge, and this occurred significantly more often in finger extensors than wrist extensors.
3. Trains of cutaneous stimuli produced no change in the discharge rates of the majority of spindle endings irrespective of whether the spindle afferent had a background discharge or was given one by muscle stretch. However, with two of forty afferents, the stimuli produced an increase in discharge at latencies of 135 and 155 ms.
4. With a further fourteen muscle spindle endings, the dynamic responses to stretch were measured 100–400 ms after the trains of cutaneous stimuli. For four spindle afferents there was a statistically significant change in the dynamic response to stretch occurring at conditioned-stretch intervals of 100–200 ms. For two afferents the dynamic response decreased by 17 and 26% and for two others it increased by about 24 and 37%.
5. While these results support the view that the level of background fusimotor drive is low in the relaxed state, they suggest that there is some dynamic fusimotor drive to completely relaxed muscles operating on the human hand, and that this drive can be altered reflexly by cutaneous afferent inputs from the hand.

Specialized cutaneous receptors in the human hand have an important role in the control of movement of the upper limb beyond their undeniable role in tactile acuity. Firstly, cutaneous afferents exert reflex effects on α -motoneurone pools of upper limb muscles (Caccia, McComas, Upton & Blogg, 1973; Garnett & Stephens, 1981). These reflexes may be mediated by segmental oligosynaptic spinal paths (shared with flexor reflex and Ib afferents) or intersegmental pathways involving propriospinal neurones (Malmgren & Pierrot-Deseilligny, 1988; Nielsen & Pierrot-Deseilligny, 1991; Burke, Gracies, Mazevet, Meunier & Pierrot-Deseilligny, 1992) or pathways of longer latency, possibly involving the motor cortex (Jenner & Stephens, 1982; cf. Maertens de Noordhout *et al.* 1992). Secondly, the cutaneous input from the finger modulates the grip force when objects are gripped (Johansson & Westling, 1984). Thirdly, activity in cutaneous and joint afferents from the digits can alter the perceived heaviness of weights lifted by muscles acting on the thumb and digits (Gandevia &

McCloskey, 1977; Marsden, Rothwell & Traub, 1979; Kilbreath & Gandevia, 1991). Finally, cutaneous inputs from the hand can contribute to the sensation of movement of specific joints (Ferrell, Gandevia & McCloskey, 1987).

Recent studies have examined the capacity of cutaneous afferents innervating the foot to alter the fusimotor output to flexors and extensors of the ankle when relaxed (Gandevia, Miller, Aniss & Burke, 1986), during voluntary contractions (Aniss, Gandevia & Burke, 1988), and during quiet unsupported standing (Aniss, Diener, Hore, Burke & Gandevia, 1990). There was no evidence for any fusimotor reflexes when at rest, and only sparse evidence during simple isometric contractions. Clearer evidence for fusimotor reflexes was observed during standing, and the ability of afferent inputs to activate the fusimotor system reflexly was only demonstrable for some spindle endings after they had been given a background discharge by passive stretch (Aniss *et al.* 1990).

Cutaneous input from the hand may exert a more dominant role in the motor control of the hand than the cutaneous input from the leg has in control of the leg. When subjects attempt to contract their acutely paralysed intrinsic hand muscles, some motoneurons cannot be activated without cutaneous feedback from the hand (Gandevia, Macefield, Burke & McKenzie, 1990), but this is not so for motoneurons innervating ankle flexor muscles (Gandevia, Macefield, Bigland-Ritchie, Gorman & Burke, 1993). Accordingly the cutaneous reflex control of the fusimotor system might be expected to differ for the leg and the hand. The present study was designed to examine the discharge characteristics of muscle spindle endings in wrist and finger extensor muscles when relaxed and to determine whether cutaneous afferents from the hand exert significant reflex effects via the fusimotor system on their discharge. An abstract based on preliminary data has been published (Wilson, Gandevia, Cordo & Burke, 1993).

METHODS

Studies were performed on thirteen subjects (six males and seven females) ranging in age from 21 to 48 years. All were healthy volunteers and the procedures were approved by the local institutional ethics committee.

Recordings

The subjects were seated comfortably in an armchair. To minimize the inadvertent contraction of muscles in the upper limb, the subjects wore a special shoulder brace designed to immobilize the entire upper limb (Smith & Nephew, Donjay, CA, USA). The shoulder was held in 70 deg abduction, the elbow flexed to 90 deg, the wrist pronated and in 30 deg extension, while the fingers and thumb were loosely flexed in the position of rest (Wood Jones, 1949). The volar aspect of the limb was supported on the lightweight frame and strapped in two or three places as necessary. The frame extended medially to the thorax and abdomen so that the weight of the

arm was supported via straps to the contralateral shoulder and hip (Fig. 1). The frame could also be attached directly to the experimental table. These manoeuvres provided sufficient external support to ensure that subjects were comfortable during the recordings and kept the relevant muscles relaxed.

Electromyographic activity (EMG) was recorded from the extensor muscles of the forearm using surface electrodes (1 cm diameter). One was positioned about 8 cm distal to the lateral epicondyle, and a second laterally over brachioradialis at the same level as the first. Both were referred to a third electrode located 5 cm distally. These positions allowed liminal contractions of the thumb and finger extensors, wrist extensors and brachioradialis to be readily detected on-line. Throughout each study, recordings were monitored on a large screen at high gain by the subject and experimenters (bandpass 1.6 Hz–1.6 kHz; gain 20 000).

The discharge of muscle afferents was recorded using insulated tungsten microelectrodes inserted into the radial nerve 7–12 cm above the elbow. Single afferents were sought during manual percussion of the relevant muscle or its tendon. Muscle spindle endings were distinguished from Golgi tendon organs using intrafascicular stimulation, as described elsewhere (McKeon & Burke, 1980; Burke, Aniss & Gandevia, 1987).

Nerve and mechanical stimulation

Electrical stimuli were delivered at two sites to produce cutaneous paraesthesiae: the superficial radial nerve where it crosses the abductor pollicis longus tendon; and the skin on the volar aspects of the proximal phalanges of the fingers (see Nielsen & Pierrot-Deseilligny, 1991; Burke *et al.* 1992). The electrodes for superficial radial stimuli were two strips of conductive tape (25 by 10 mm) about 2 cm apart with the cathode proximal. The stimuli produced paraesthesiae radiating laterally over the dorsum of the hand. Palmar stimulation was achieved through strips of conductive tape over the volar aspect of the proximal and middle phalanges, and stimulation produced paraesthesiae in all fingers. The stimulus trains consisted of five pulses at 300 Hz with the intensity usually set at twice perceptual threshold, and they were delivered unpredictably at 1–3 Hz, from a constant-current source. The threshold was checked regularly.

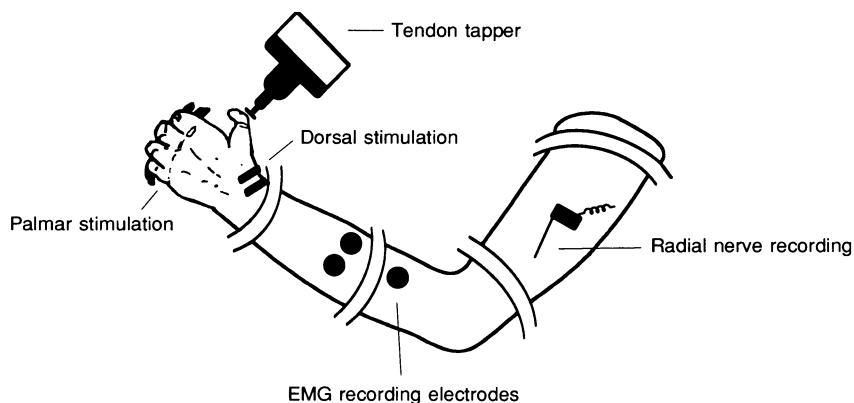


Figure 1. Experimental set-up

The subject was seated with the arm strapped in a semi-rigid frame. Trains of cutaneous stimuli were delivered to the superficial radial nerve (dorsal stimulation) or to the palmar aspect of the fingers (palmar stimulation). The vibrator was positioned over the tendon of the receptor-bearing muscle to allow assessment of the spindle response to abrupt stretch.

To increase the likelihood that reflex effects on the discharge of muscle spindle afferents would be detected, two additional procedures were used. Firstly, for eight of fifteen spindle afferents with no background discharge, cutaneous stimuli were delivered with the afferent silent (10–30 trains) and then when the ending had been given a background discharge by sustained pressure applied by the experimenter to its tendon or to its receptive field over the muscle. Secondly, muscle stretch was delivered via a servo-controlled vibrator which allowed separate control of the background force of the pulse and the tap amplitude (Cordo, Gandevia, Hales, Burke & Laird, 1993). Taps were delivered with a background force of 30 N, amplitude 1 mm and duration of 200 or 250 ms to the distal tendon or its bony insertion using a probe (22 by 4 mm). The indentation velocity was 400 mm s^{-1} . In different sequences the interval between the train of cutaneous stimuli and the tap varied from 100 to 400 ms. Within any sequence, the cutaneous stimulus trains preceded half of the taps in pseudorandom order so that small movements by the subject or changes in the electrical stimuli or tap conditions would not mitigate against a positive result.

Data recording and analysis

All data were monitored on a large screen during the experiment (Gould ES 2000) and recorded on tape for reanalysis (8-channel Vetter PCM). Spikes from single units were selected using a dual time-amplitude window discriminator (DDIS-1, BAK Electronics, Rockville, MD, USA) and displayed on a storage oscilloscope. Some analyses were performed on-line, but the main investigations were

conducted with data replayed from tape. Peristimulus time histograms (PSTHs) of the discharge of muscle spindle endings were constructed with the Cambridge Electronics Design 1401 interface. The usual bin width was 1 or 2 ms. Attention was paid to eliminating EMG during the study, and in the off-line analysis any sections contaminated by low-level EMG were excluded.

The statistical significance of peaks in the histograms following the stimulus trains was assessed using the cumulative sum technique. Estimates of variance were based on the background discharge rate of the spindle afferent and the regularity of discharge. The coefficient of variation was computed for 100 or more intervals in the immediate pre-stimulus period. Statistical significance was set at the 5% level (Davey, Ellaway & Stein, 1986; Aniss *et al.* 1990). For the responses to tendon taps 'difference' histograms were constructed by subtracting the control from the conditioned responses. The statistical significance of peaks in these histograms was assessed using Student's two-tailed *t* test.

RESULTS

Background discharge rates

Recordings were made from fifty-four muscle spindle afferents innervating muscles supplied by the radial nerve, while the upper limb was held comfortably in a frame designed to minimize EMG throughout the 3–4 h

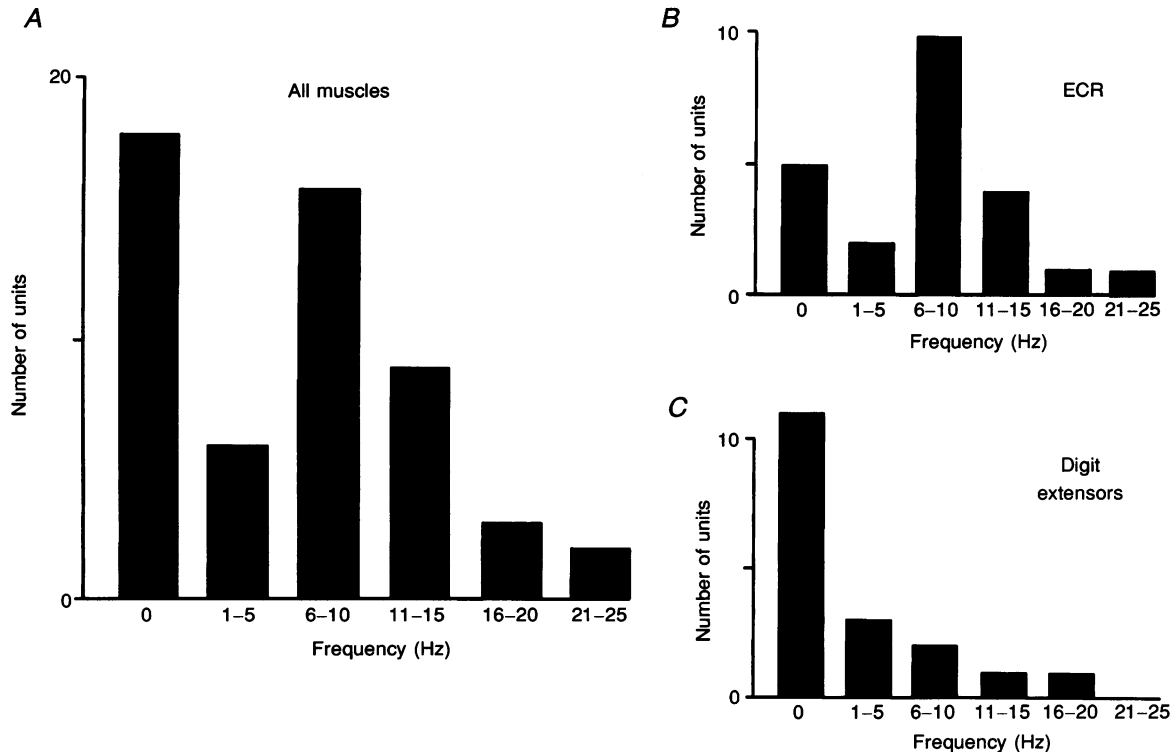


Figure 2. Background discharge frequency for muscle spindle afferents

Data for the full sample of spindle afferents ($n = 54$, *A*), extensor carpi radialis (ECR, $n = 23$, *B*) and extensors of the digits (extensor pollicis longus and extensor digitorum communis, $n = 18$, panel *C*).

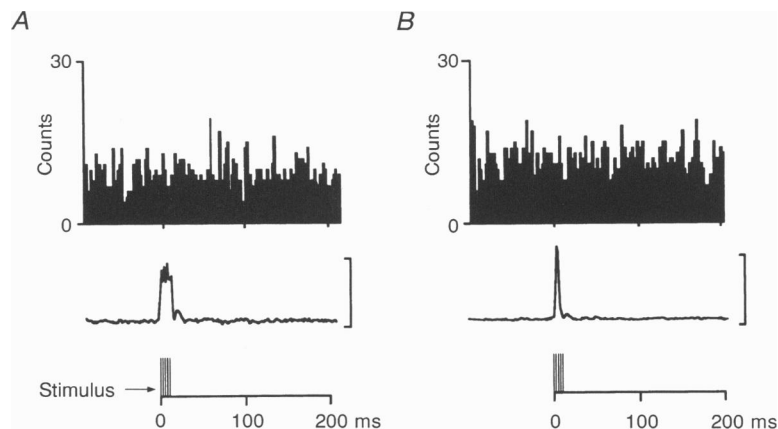


Figure 3. Two of the forty muscle spindle afferents recorded during cutaneous stimulation One muscle spindle afferent innervated extensor carpi radialis (*A*, palmar stimulation, $n = 300$) and another innervated extensor carpi ulnaris (*B*, dorsal stimulation, $n = 430$). In each panel, the upper trace is a PSTH of the discharge of the spindle afferent. The middle trace is the averaged rectified EMG (dominated by stimulus artifact because the muscles were relaxed). The lower trace shows the time of delivery of the cutaneous stimuli. Vertical calibrations are $15 \mu\text{V}$ in *A*, $10 \mu\text{V}$ in *B*.

experiment (see Methods). Eighteen of the spindle afferents (33%) had no background discharge. The mean discharge frequency for all endings (with or without a background discharge) was 7.1 ± 6.4 Hz (mean \pm s.d., range 0–24 Hz). The mean discharge frequency of the actively discharging endings was 10.6 ± 4.8 Hz. The distribution of background rates is shown for all endings in Fig. 2*A*, while Figs 2*B* and 2*C* show data for extensor

carpi radialis ($n = 23$) and the digit extensors ($n = 18$), respectively. The remaining spindle afferents innervated extensor indicis ($n = 4$), brachioradialis ($n = 3$), extensor carpi ulnaris ($n = 2$), extensor pollicis brevis ($n = 2$), abductor pollicis longus ($n = 1$) and supinator ($n = 1$). Spindles in extensor carpi radialis had a background discharge significantly more often than those in digit extensors (79 versus 42%; χ^2 test: $P < 0.05$). The wrist was

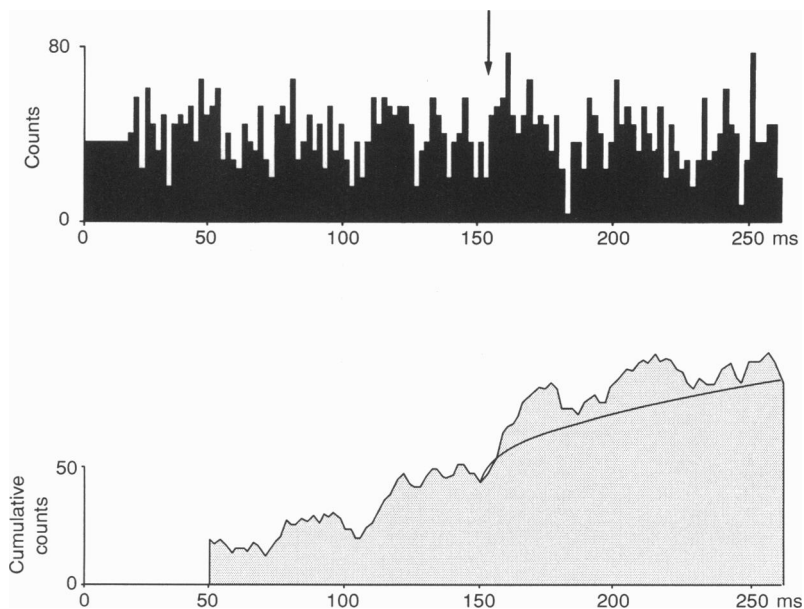


Figure 4. Muscle spindle afferent innervating brachioradialis

Upper trace, PSTH for stimulus trains to the superficial radial nerve. Because of stimulus artifact the first 20 bins of the PSTH have been set to the mean prestimulus count. Lower trace, cumulative counts for the histogram. The curved line indicates the statistical boundaries (set at the 5% level; see Methods) and this reveals a significant increase in spindle discharge at 155 ms (arrow in upper panel).

in a neutral position of radial deviation, so that the high discharge rate for spindle endings in wrist extensors could not have been anticipated on the basis of resting muscle length. The coefficients of variation for the background discharge rates ranged from 0.03 to 0.57, a range similar to that reported previously for spindle afferents in finger extensors (Nordh, Hulliger & Vallbo, 1983). There was no tendency for this to vary between muscles.

Responses to cutaneous stimulation: changes in background spindle discharge

To determine whether cutaneous stimuli could induce fusimotor reflexes of sufficient strength to affect the background discharge of spindle endings, trains of stimuli were applied to cutaneous nerves when recording the discharge of fifty-four muscle spindle afferents. Cutaneous stimulation was delivered to the superficial radial nerve at the wrist for thirty muscle spindle afferents, and to the palmar aspect of the fingers for thirty-seven afferents (both stimuli were delivered with thirteen afferents). For fourteen spindle afferents, the ability to alter spindle sensitivity to stretch was also examined (see next section). The stimulus intensity was non-noxious, 2–3 times perceptual threshold. The sequence of stimulus trains occurred unpredictably.

No reproducible discharge was evoked by the cutaneous stimuli in the eighteen spindle afferents with no background activity. To determine whether the stimuli had evoked 'subthreshold' intrafusal effects, eight of the eighteen afferents without a background discharge were also studied after activity had been induced by direct pressure on the relevant tendon or the receptive field in the muscle. The discharge of afferents with stretch-induced background firing was unaffected by the electrical stimulation of cutaneous afferents as assessed by PSTHs containing a mean of 304 stimulus trains (median 215, range 47–971).

The discharge of spindle afferents with a background discharge at the resting muscle length was nearly always unaffected by the electrical stimuli (Fig. 3). This was assessed by PSTHs based on a mean of 320 stimulus trains (median 250, range 50–950). These stimuli also produced no detectable reflex effects in the averaged rectified EMG of the relaxed forearm extensors during these sequences.

However, for two of the fifty-four spindle afferents there was a significant change in background discharge within 160 ms of the cutaneous stimuli. For a spindle afferent innervating brachioradialis (background discharge 24 Hz), the discharge became phase-locked to the superficial radial nerve stimuli (at about 70 ms), with a statistically

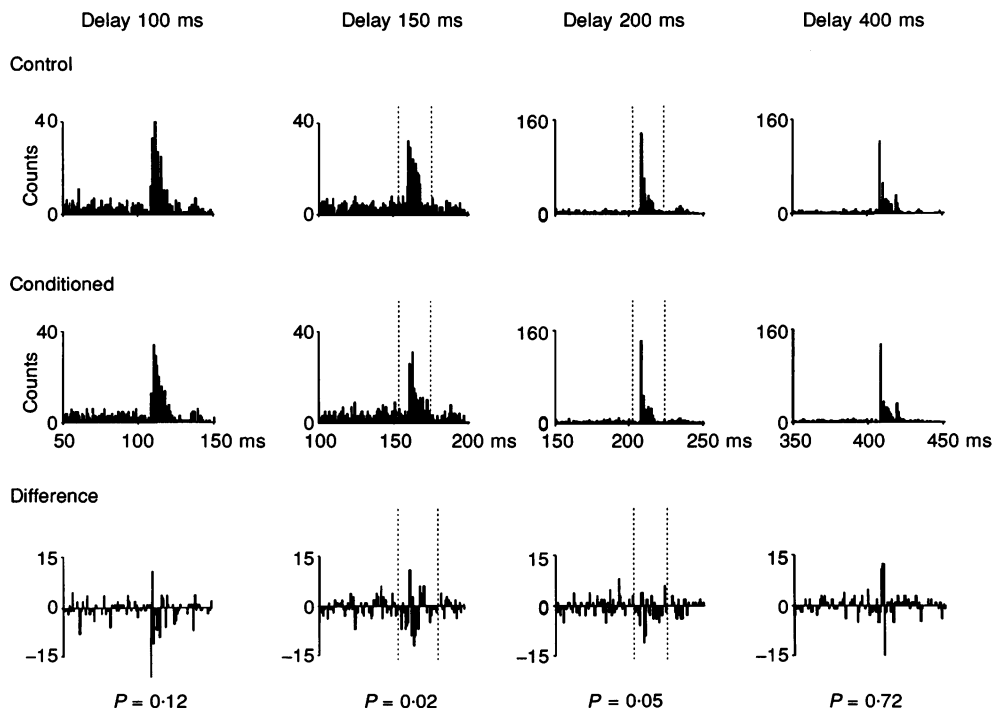


Figure 5. PSTHs for a muscle spindle afferent innervating extensor carpi radialis

The upper histograms show the responses to the control tap, and the lower histograms show the responses when palmar cutaneous stimuli preceded the taps at intervals of 100, 150, 200 or 400 ms. Data for each interval were collected in a single sequence with the control and conditioned responses randomly intermingled (see Methods). The cutaneous stimuli were delivered at time zero and there are between 200 and 250 stimuli in each histogram. The lowest traces depict histograms in which the control responses have been subtracted from the conditioned responses. The discharges in response to the tap were significantly reduced when conditioning stimuli were delivered 150 and 200 ms prior to the tap (highlighted by the two dashed vertical lines).

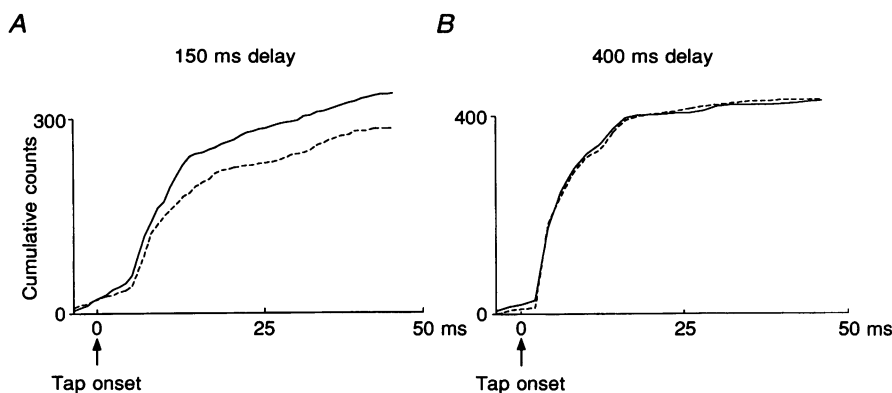


Figure 6. Cumulative counts for the spindle afferent for which data are shown in the histograms in Fig. 5

The number of discharges in response to taps when conditioning stimuli (dashed line) were delivered 150 ms prior to the tap (*A*) were significantly reduced. However, when conditioning stimuli were delivered 400 ms prior to the tap (*B*) there was no effect on the dynamic sensitivity of the spindle afferent. The continuous line is the control.

significant increase in discharge at 155 ms (Fig. 4). This effect was observed in two of three sequences with this unit in response to superficial radial but not palmar stimulation. In another subject, a spindle afferent in extensor pollicis longus (background discharge 13 Hz) showed a significant increase in firing at 135 ms following stimulation of the superficial radial nerve.

Changes in stretch responsiveness of spindle afferents

To assess whether the cutaneous input affected dynamic fusimotor neurones, the responsiveness of fourteen muscle spindle afferents was tested using stretch applied to the distal tendon of the relevant muscle. Trials in which

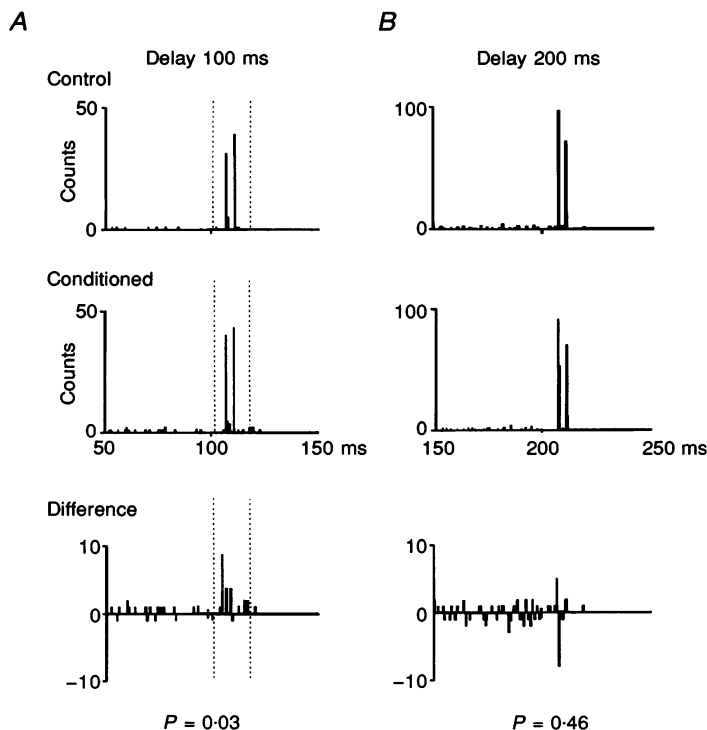


Figure 7. PSTHs for a muscle spindle afferent innervating extensor pollicis longus for two stimulus-tap delays (*A*, 100 ms; *B*, 200 ms)

Data depicted as in Fig. 5, with the control responses above and the conditioned responses below. The lowest traces are the difference histograms. Palmar cutaneous stimuli were delivered at time zero. The changes shown in the difference histograms were significant at 100 ms but not at 200 ms.

cutaneous stimulation preceded the stretch were intermingled with the control stretch trials. For four spindle afferents the cutaneous stimuli, delivered 100–200 ms prior to the stretch, produced significant changes in the response to stretch. An example is shown in Fig. 5. This spindle afferent innervated extensor carpi radialis (background discharge 13 Hz) and was assessed with conditioned-stretch intervals of 100, 150, 200 and 400 ms. As seen in the 'difference' histograms, palmar cutaneous stimuli reduced responsiveness at intervals of 100 ms (17% less counts than in the control histogram, $P=0.12$), 150 ms (26% reduction, $P=0.02$), 200 ms (12% reduction, $P=0.05$) but not 400 ms (2% increase, $P=0.72$). For this afferent, a decrease in counts occurred for palmar but not superficial radial stimuli. The reduction in the spindle afferent response to stretch applied 150 ms after conditioning cutaneous stimuli is highlighted in the cumulative counts shown in Fig. 6. The reproducibility of the reduced spindle afferent response was assessed by generating histograms for five sequential sections each of 100 s. The decreased count was recorded in each of the five conditioned stretch histograms. The response to stretch of a second afferent innervating extensor carpi radialis (no background discharge) also decreased at intervals of 100 ms

(16% reduction, $P=0.16$) and 200 ms (10% reduction, $P=0.03$) but not 400 ms (3% reduction, $P=0.84$) with palmar cutaneous stimuli.

With two afferents there was an increased response to muscle stretch at the 100 ms interval. One afferent innervated extensor pollicis longus (Fig. 7), had a background discharge of 5 Hz, and responded to palmar cutaneous stimulation with a 24% increase in the dynamic response to stretch ($P=0.03$). The other afferent innervated extensor digitorum communis and responded to superficial radial stimulation with a 37% increase ($P=0.03$).

For the remaining spindle afferents (ten of the fourteen) there was no change in stretch responsiveness produced by conditioning cutaneous stimuli delivered at intervals of 100–400 ms prior to the stretch (Fig. 8). A total of nineteen negative sequences were analysed with a mean of eighty control and conditioned stretches (median 70, range 40–150).

With five of the fourteen spindle afferent recordings, the tap produced a small tendon jerk, visible in the high gain recording of EMG at a mean latency of 20–21 ms. It showed no consistent change following the cutaneous stimulus trains, even when there was a significant change in the response to stretch of the spindle ending. An

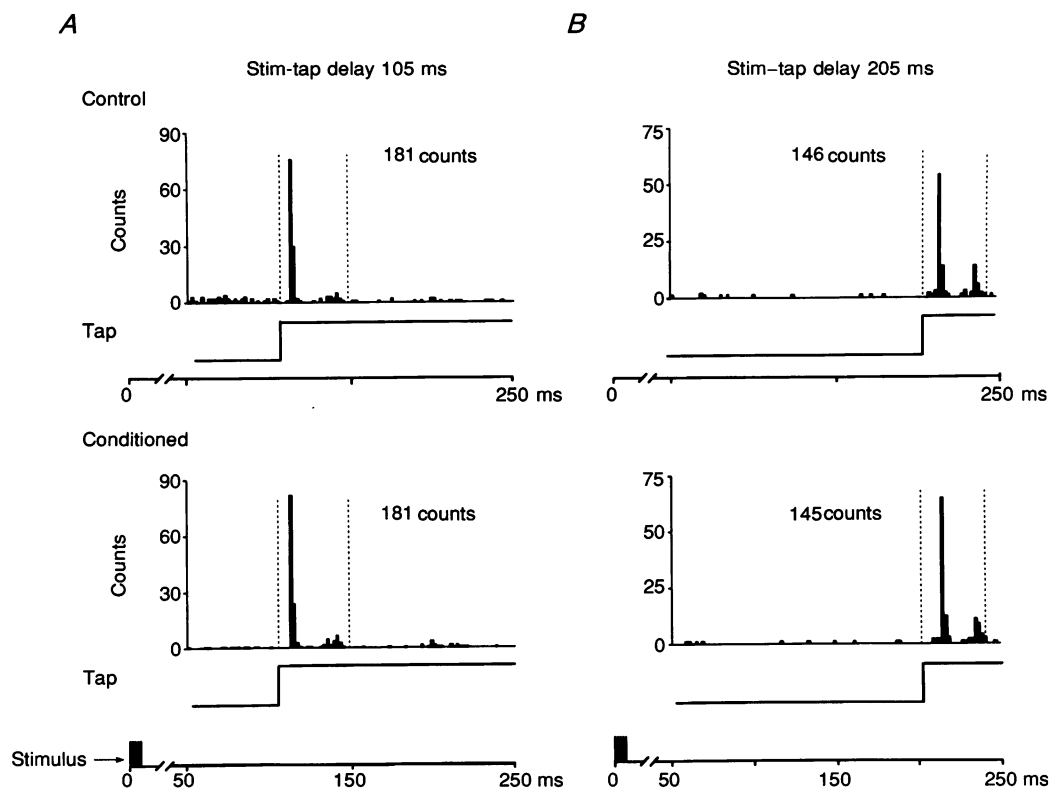


Figure 8. PSTHs for a muscle spindle afferent which had no change in dynamic sensitivity following cutaneous stimuli

The spindle afferent innervates extensor pollicis longus. Data is depicted as in Figs 5 and 7, with the control responses above and the conditioned responses below. The delays between the cutaneous stimuli and tap were approximately 105 ms in *A* and 205 ms in *B*. Below all panels is a diagrammatic indication of the muscle stretch.

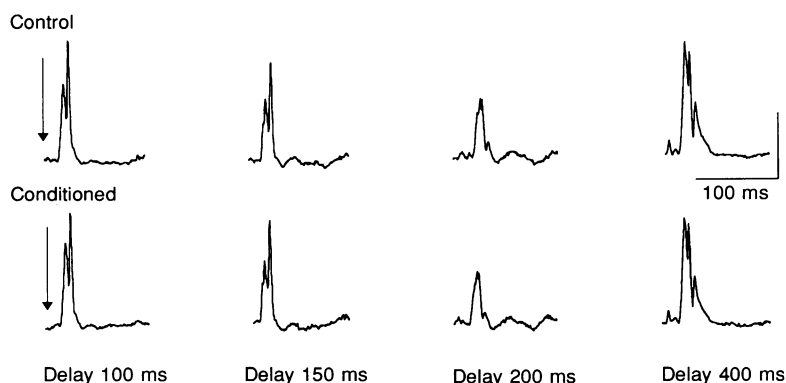


Figure 9. EMG responses produced by the controlled taps for the spindle afferent
The data for these EMG responses are shown in Fig. 5. Vertical calibrations are 12.5, 12.5, 6 and 8 mV, from left to right.

example is shown in Fig. 9. In this run there was a decrease in the stretch responsiveness of the spindle afferent after conditioning cutaneous stimuli (as shown in Figs 5 and 6), but the EMG response produced by the tap-induced discharge from the population of spindle afferents was unchanged.

DISCUSSION

This study assessed whether cutaneous afferents from the hand can reflexly affect fusimotor neurones innervating relaxed forearm extensor muscles. Of fifty-four muscle spindle endings, six showed significant changes in their behaviour in response to non-noxious stimulation of cutaneous afferents. This result could not have been anticipated given that the literature on human muscle spindle afferents suggests that there is little, if any, background fusimotor drive to relaxed muscles (Vallbo, Hagbarth, Torebjörk & Wallin, 1979; Burke, 1981; Edin & Vallbo, 1990) and that fusimotor reflexes have not been demonstrable previously at the spindle level, unless the subject was engaged in purposeful activity such as standing (Aniss *et al.* 1990) or the reflex input was especially noxious (Gandevia *et al.* 1986).

There are no data for upper limb muscles directly comparable to those obtained here. In the one study which examined the behaviour of muscle spindle afferents from relaxed tibialis anterior and triceps surae, there was no change in the discharge of eighteen muscle spindle afferents following electrical stimuli to the sural or posterior tibial nerves at non-noxious levels; nor did the averaged single- and multi-unit afferent responses to stretch change following conditioning by non-noxious stimuli (Gandevia *et al.* 1986). By contrast, electrical stimulation of cutaneous afferents innervating the hand produced either a change in background discharge of spindle afferents ($n = 2$) or a change in response to muscle stretch ($n = 4$) from a population of fifty-four muscle spindle afferents innervating upper limb muscles. Given

that the muscles were relaxed, and that the electrical stimuli evoked no EMG, the changes presumably reflect a reflex effect onto γ -motoneurons supplying the spindles. Latencies for the two increases in background discharge rates were about 135 and 155 ms. These would allow time for a fusimotor reflex given a cutaneous afferent conduction time to the spinal cord of 10–15 ms (Desmedt & Cheron, 1980), intraspinal conduction delays (perhaps 2–3 ms), efferent conduction time of 20–30 ms (via γ -motor axons conducting at half the velocity of rapidly conducting motor axons; Cheney & Preston, 1976), and subsequent intrafusal activation and conduction to the recording electrode. Given the emphasis on muscle relaxation, it seems unlikely that the increased discharge rates were produced by activity in skeletofusimotor (β) neurones. Indeed, with β -motoneurons even shorter reflex latencies might have occurred.

Because the stretch sensitivity diminished for two of the spindle afferents, there was presumably some background dynamic fusimotor activity which was inhibited by the cutaneous input. A previous microneurographic study of putative fusimotor axons suggested the presence of background activity that was insufficient to alter the discharge of spindle afferents (Ribot, Roll & Vedel, 1986). Given this result, and the fact that in a previous study some fusimotor reflex effects remained undetected in standing subjects unless the spindle afferents were given a background discharge (by tendon pressure; Aniss *et al.* 1990), it is possible that the present study has underestimated the strength of fusimotor reflexes acting on individual spindles. Either way the present results support the view (i) that there may be a background dynamic drive directed to spindle endings even in relaxed muscles, and (ii) that fusimotor activity need not necessarily alter background discharge rates of spindle endings.

The changes in response to an indirectly applied, but controlled, muscle stretch in four of fourteen afferents suggested that dynamic fusimotor drive had been altered.

The time course of this effect was such that it was apparent within 100 ms of the conditioning cutaneous stimulation and had subsided within a further 300 ms. Given the time course of the effect, it was probably mediated via slowly contracting nuclear bag fibres (Bessou, Laporte & Pagès, 1968; Matthews, 1972). However, this change in spindle output did not produce a detectable change in size of the 'tendon jerk' evoked by the test stretches. There are two likely explanations: (i) there were mixed reflex effects on the spindle response to stretch, with both increases and decreases in discharge; and (ii) such changes were only seen for a minority of afferents.

The background discharge rates for the spindle afferents in both the upper and lower limb are similar to those of deafferented spindles in the cat, i.e. quite low when compared with those reported for reduced or anaesthetized animal preparations (Vallbo *et al.* 1979). Such findings have formed part of the evidence that the level of background static fusimotor drive is usually low (Vallbo *et al.* 1979; Burke, 1981; Edin & Vallbo, 1990). Our data for background discharge rates and discharge variability are comparable to those previously reported for other spindle afferents in the radial nerve (Nordh *et al.* 1983; Edin & Vallbo, 1990), and this is indirect evidence that the positive reflex responses in the present study were not because our subjects were 'less relaxed'. However, the difference in prevalence of spindle afferents with a background discharge in the wrist and digit extensors (79%, mean discharge rate 8.2 Hz; and 42%, mean discharge rate 3.8 Hz, respectively) was unexpected. It is unlikely that the degree of muscle stretch placed on the wrist extensors differed from that on the digit extensors sufficiently to account for the differences in spindle discharge. From the data of Vallbo (1974) for forearm flexors and Edin & Vallbo (1990) for forearm extensors, a difference in muscle length of more than 3 mm would probably be required to produce the differences observed in the present study.

There are several additional implications of this study. Firstly, the presence of 'inhibitory' and 'facilitatory' cutaneous reflex effects on muscle spindle discharge (and stretch responsiveness) has been reported previously in reduced cat preparations (Hunt, 1951; Eldred & Hagbarth, 1954; Hunt & Paintal, 1958; Grillner, 1969; Davey & Ellaway, 1989). Cutaneous inputs are known to produce a variety of effects on identified fusimotor neurones in the cat (Appelberg, Johansson & Kalistratov, 1977; Hulliger, 1984). The findings in the present study are consistent with these mixed effects and serve to bring the results of human studies on the fusimotor system closer into line with those in animals. Secondly, the mixed effects could result from a somatotopic organization which is concealed by pooling data. For example, superficial radial stimulation increased background discharge or response to stretch with all three affected endings, and palmar stimulation decreased responses for two of three endings. This functional somatotopicity is different from that reported for the

human propriospinal system (Nielsen & Pierrot-Deseilligny, 1991; Burke *et al.* 1992). Thirdly, given the low incidence of the effects, their small magnitude, and particularly their variable sign, it is likely that significant influences would be undetectable in multi-unit recordings. A corollary to this may be that the net result of a fusimotor reflex ultimately reaching the motoneurone pool may be small, but this would depend on many other factors, including which cutaneous afferents and fusimotor neurones were excited.

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