CONDUCTION VELOCITIES OF MUSCLE AND CUTANEOUS AFFERENTS IN THE UPPER AND LOWER LIMBS OF HUMAN SUBJECTS

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SUMMARY

In the cat and monkey the fastest axons in the peripheral nerve are group I afferents from muscle, but there are no definitive data on conduction velocity for these afferents in human subjects. Knowledge of the relative conduction velocities of muscle and cutaneous afferents is important for the interpretation of reflex studies, evoked potentials and other aspects of motor control. To rectify this deficiency, the conduction velocities of the fastest muscle and cutaneous afferents were determined for the median, ulnar and tibial nerves of normal subjects. Low-threshold muscle afferents innervating abductor pollicis brevis, abductor digiti minimi and abductor hallucis were stimulated selectively through a microelectrode inserted percutaneously at the motor point. Low-threshold cutaneous afferents were stimulated with ring electrodes around the proximal phalanx of digits II or V for the upper limb and digit II for the lower limb. Compound action potentials were recorded with bipolar near-nerve electrodes at two sites in the proximal limb segment and conduction velocities of the fastest afferents in the neural volley calculated. The mean conduction velocities of the muscle and cutaneous afferents were, respectively, 74.7 ± 6.5 m·s⁻¹ and 80.3 ± 6.7 m·s⁻¹ for the median nerve, 67.5 ± 10.2 m·s⁻¹ and 67.5 ± 10.5 m·s⁻¹ for the ulnar nerve, and 54.7 ± 3.4 m·s⁻¹ and 52.8 ± 3.2 m·s⁻¹ for the tibial nerve. For upper and lower limb nerves the conduction velocities of low-threshold muscle and cutaneous afferents were not significantly different when measured over the same proximal segment.

INTRODUCTION

Little is known about the conduction velocities of human group I muscle afferents and most texts accept data from the cat as being appropriate for man. In the hindlimb of the cat the modal conduction velocity of individual Ia afferents from soleus is 100–110 m·s⁻¹ (range 60–125 m·s⁻¹; Hunt and Kuffler, 1951), whereas that for a population of low-threshold cutaneous afferents in the saphenous nerve is 54–60 m·s⁻¹ (range 33–95 m·s⁻¹; Brown and Iggo, 1967). Conduction velocities in the primate are slower but, as in the cat, muscle afferents conduct faster than cutaneous afferents in the baboon—the majority of Ia afferents from soleus conduct at 80–85 m·s⁻¹ (Cheney and Preston, 1976), and in the monkey the mean conduction velocity of low-threshold mechanoreceptors from the skin of the foot is 38 ± 6 m·s⁻¹ (Lindblom, 1965).

The conduction velocities of low-threshold muscle afferents in human subjects have been estimated indirectly from differences in H reflex latency either of the thenar muscles

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when stimulating the median nerve at two sites in the forearm (Eisen et al., 1984; Deuschl et al., 1985) or of the tibial nerve when stimulating at two sites in the thigh (Abbruzzese et al., 1985). Estimates have also been made by Abbruzzese et al. (1985) using afferent volleys evoked by tendon percussion. However, tendon percussion does not activate intramuscular afferents selectively; the resultant volleys are contaminated by cutaneous afferent activity (Burke et al., 1983). Electrical stimulation of the tibial and sural nerves at the ankle allows conduction velocities of muscle and cutaneous afferents from the foot to be compared, albeit indirectly (Burke et al., 1981; Gandevia et al., 1982; Bartel et al., 1985; Vogel et al., 1986). The tibial nerve at the ankle is a mixed nerve, containing afferents of muscle, cutaneous and articular origin; the sural nerve is primarily cutaneous from the lateral aspect of the foot but also conveys joint afferents from the ankle (Gardner et al., 1975). The most rapidly conducting afferents of the tibial nerve appear to be 5—10 m·s⁻¹ faster than those of the sural nerve across the distal limb segment, and this has been attributed to the presence in the tibial nerve of group I muscle afferents (Burke et al., 1981; Gandevia et al., 1982). This comparison, however, is based on the assumptions that nerve length and temperature were the same.

To activate human muscle afferents directly, without the coactivation of cutaneous and joint afferents when stimulating a mixed nerve, low-threshold sensory and motor axons were activated by constant-current pulses delivered through an insulated microelectrode inserted percutaneously at the motor point (Gandevia and Burke, 1986, 1988). The technique has been employed to demonstrate the cortical projections of low-threshold muscle afferents from several proximal and distal muscles of the upper limb (Gandevia and Burke, 1988) and from abductor hallucis (Macefield et al., 1988a).

The present study was designed to measure the conduction velocities of the fastest afferents of muscle origin and those of cutaneous-articular origin in the proximal segment of the upper and lower limbs of human subjects. In each limb conduction velocities were compared over the same conduction distance using identical recording conditions. The results indicate that, in contrast to data from the cat and monkey, low-threshold muscle afferents do not conduct more rapidly than low-threshold cutaneous afferents in normal human subjects. A preliminary report of some of the results has been published (Macefield et al., 1988b).

**METHODS**

Nerve conduction data from the upper limb were obtained in 8 healthy subjects, each of whom provided informed consent. The experiments were conducted with the approval of the institutional ethics committees. Six of the subjects were 21—33 yrs of age, 1 was 43 and another 59. Nerve conduction data from the lower limb were obtained in 6 of the 8 subjects (age 21—43 yrs). Experimental sessions were generally of 2—3 h duration.

*Stimulation procedures*

The median or ulnar nerve at the wrist was stimulated by constant-current pulses (0.3 ms, 3 Hz) delivered through bipolar surface electrodes (cathode proximal) at a level sufficient to produce pronounced activation of the appropriate intrinsic muscles and radiating cutaneous sensations, neither of which the subjects
considered noxious. The digital nerves of digit II or V were stimulated at 2–3 times perceptual threshold via ring electrodes around the proximal phalanx (cathode proximal) or, in 3 subjects, around the distal phalanx. In addition, 3 subjects the proximal phalanx of digits II and/or III were stimulated at 1.5–2.0 times perceptual threshold. Low-threshold muscle afferents of abductor pollicis brevis (median innervation) or abductor digitii minimi (ulnar innervation) were stimulated with constant-current pulses (0.3 ms, 3 Hz, 1–3 mA) delivered through a tungsten microelectrode, insulated except for approximately 200 µm at its tip, inserted percutaneously at the motor point (Gandevia and Burke, 1986, 1988; Macefield et al., 1988a,b). The motor point was initially localized using stimuli delivered through a surface probe. The anode was a surface electrode on the dorsum of the hand. The intramuscular stimuli caused a clear twitch confined to the appropriate muscle but no cutaneous sensations (local or radiating) and no deep sensations referred to distal joints (see Gandevia and Burke, 1988). They were not considered noxious.

The tibial nerve at the medial malleolus was stimulated through surface electrodes (cathode proximal) with constant-current pulses (0.3 ms, 3 Hz) at a level sufficient to produce a clear twitch contraction of the intrinsic muscles of the foot and radiating cutaneous sensations that were not noxious. The sural nerve at the lateral malleolus and the digital nerves of digit II (proximal phalanx) were stimulated at 2–3 times sensory threshold. Low-threshold muscle afferents of abductor hallucis were stimulated through an insulated tungsten microelectrode inserted percutaneously at the motor point with the anode on the dorsum of the foot.

**Recording procedures**

For the studies of conduction in the upper limb the subject lay supine with the shoulder abducted 30–40° and the arm extended. Constant-current stimuli delivered through a surface probe (2 mm diameter) were used to locate the median nerve in the cubital fossa and axilla and the ulnar nerve behind the medial malleolus and in the axilla. Platinum-alloy needle electrodes (shaft length 10 mm) were inserted subdermally in a longitudinal bipolar configuration, with an interelectrode separation of 40 mm. This configuration is considered to be optimal in minimizing the contribution of the reference electrode to the recorded compound action potential (Eduardo and Burke, 1988). Referential recordings were also made using a common reference electrode inserted lateral to the course of the nerve and intermediate to the proximal and distal electrode sites. For the studies of conduction on the lower limb the subject lay prone and the optimal recording sites of the tibial nerve at the popliteal fossa and upper thigh were located using a surface probe. Tungsten microelectrodes (shaft length 55 mm), insulated to within 10 mm of the tip, were inserted percutaneously in a bipolar configuration (interelectrode separation 40 mm) and their final location adjusted while delivering constant current stimuli through the electrode. A ground electrode was applied distal to the recording sites. Skin temperature over the conduction path was maintained at ±0.5° C within the range 32–35° C. The conduction distance along the proximal limb segment was determined with a tape measure applied to the skin between the active recording electrodes and its value verified at the conclusion of the experiment. The ranges of conduction distances were 110–180 mm and 180–225 mm for the upper and lower limbs, respectively.

Compound nerve action potentials were amplified (5×10⁴), filtered (bandpass 10 Hz–1.5 kHz) and digitized at 10 kHz (Medelec Sensor ER-94A). For studies of the upper limb, potentials were analysed over 20 ms following delivery of the stimulus; for the lower limb studies the potentials were analysed over 30 ms. Repeated averages of 256 sweeps were directed alternately to two stores, generating duplicate averages each totalling 256–4096 sweeps. Multiple sets of averages were obtained in some subjects. Data were stored on disc and analysed off-line.

**Analysis**

For each subject grand averages of the bipolar and referential data were derived from the duplicate or multiple records. Latencies of the potentials were measured by cursor from the onset of the stimulus to the onset of the major negative phase (initial positive peak). Correct placement of the cursor at the peak was facilitated by monitoring the difference in amplitude between the marking cursor and a reference cursor.
No attempt was made to improve the temporal resolution of the system by interpolating between two steps of the cursor; the error in measurement of latency should be equally distributed in the directions of over-estimation and under-estimation. For recordings in the upper limb amplitudes were determined from the referential records as the peak of the initial positive phase to the peak of the major negative phase. However, in the lower limbs, the afferent volleys were more dispursed and the amplitude of the potential reflected the intensity of the volley less accurately.

It has been repeatedly demonstrated that, in normal human subjects, the fastest axons contributing to the compound nerve action potential produced by stimulating a mixed nerve are afferent, not efferent, having conduction velocities some $5-10 \text{ m} \cdot \text{s}^{-1}$ faster than the fastest motor axons in that nerve (Dawson, 1956; Gilliatt et al., 1961; Buchthal and Rosenfalck, 1966; Melvin et al., 1966; Behse and Buchthal, 1971; Dorfman, 1984; Abbruzzese et al., 1985). This has been confirmed for 4 of the 8 subjects in the present study (see Burke et al., 1981, 1983; Gandevia et al., 1982). It is therefore assumed that the fastest fibres in the mixed nerve action potential are afferent not efferent and that with motor point stimulation the fastest axons are afferent (presumably group I) not efferent (see Discussion).

Analysis of variance was employed to evaluate the statistical significance of the data. Differences were considered significant at the $P<0.05$ level.

RESULTS

Conduction velocities of afferents in the upper limb

Compound action potentials generated by electrical stimulation of the median or ulnar nerves at the wrist, the proximal phalanx of digits II or V, and the motor point of abductor pollicis brevis or abductor digiti minimi were recorded at the elbow and axilla using both bipolar and referential electrode configurations. Representative examples of afferent conduction in the whole nerve and its constituent muscle and cutaneous-articular fascicles are illustrated for the median and ulnar nerves in figs 1 and 2, respectively. As indicated in Table 1, the conduction velocities of the fastest muscle afferents of abductor pollicis brevis and abductor digiti minimi were not significantly different from those of the fastest afferents (cutaneous and articular) innervating digits II and V, respectively. Also, the conduction velocities were not significantly different from the most rapidly conducting components of the volley produced by stimulation of the parent nerve at the wrist (Table 1). In 3 subjects the digital nerves were stimulated at the distal phalanx to avoid the activation of interphalangeal joint afferents that occurs when stimuli are delivered at the proximal phalanx (see Discussion). There was no difference in conduction velocity of the digital potentials evoked from the two sites, suggesting that the conduction velocities of the fastest articular afferents were not greater than those of the fastest cutaneous afferents.

Amplitudes of the neural volleys at the proximal and distal sites, measured from the referential recordings, are presented in Table 2 and expressed both in absolute and relative terms. Data for the median and ulnar nerves were pooled because there were no significant differences in the sizes of their compound action potentials. The diminution in amplitude at the proximal recording site relative to the distal site (Kimura et al., 1986; Olney et al., 1987) was independent of size of the afferent volley. However, temporal dispersion of the afferent volley, measured as the increase in rise-time of the potential across the $110-180 \text{ mm}$ separating the distal and proximal recording sites (mean conduction
distance 138 mm), was dependent on the amplitude of the afferent volley. The smaller volleys generated by stimulation of only cutaneous or only muscle afferents exhibited significantly less temporal dispersion than the potentials produced by stimulation of the parent nerve (Table 2).
FIG. 2. Compound action potentials generated by stimulation of the ulnar nerve at the wrist and its cutaneous-articular (proximal phalanx of digit V) and muscle (abductor digiti minimi) afferent components in 1 subject (male, age 26 yrs). Upper and lower records in each panel are the potentials recorded with bipolar electrodes behind the medial malleolus and at the axilla, respectively. The calculated conduction velocities of the fastest muscle and cutaneous-articular afferents are identical.

Both amplitude and temporal dispersion of the potential influence the shape of the initial positive peak and therefore the definition of onset latency. The greater definition afforded by a potential with a larger amplitude may be confounded by the problems of temporal dispersion. The effect of amplitude on the measured difference in latency between the distal and proximal recording sites was examined in 3 subjects by delivering
CONDUCTION VELOCITIES IN HUMAN NERVES

TABLE I. MEAN ± SD CONDUCTION VELOCITY DATA (m·s⁻¹) FOR THE PROXIMAL SEGMENT OF THE UPPER LIMB, DETERMINED FROM BIPOLAR AND REFERENTIAL RECORDS*

<table>
<thead>
<tr>
<th></th>
<th>Bipolar</th>
<th>Referential</th>
<th>Bipolar</th>
<th>Referential</th>
</tr>
</thead>
<tbody>
<tr>
<td>Median</td>
<td>81.1 ± 6.7</td>
<td>81.4 ± 10.8</td>
<td>72.7 ± 11.1</td>
<td>74.2 ± 13.6</td>
</tr>
<tr>
<td>(69.0–89.3)</td>
<td>(63.9–94.1)</td>
<td>(56.5–83.3)</td>
<td>(54.3–83.3)</td>
<td></td>
</tr>
<tr>
<td>Digit II</td>
<td>80.3 ± 7.1</td>
<td>75.8 ± 10.8</td>
<td>67.5 ± 10.5</td>
<td>68.5 ± 12.3</td>
</tr>
<tr>
<td>(65.2–85.9)</td>
<td>(65.2–88.9)</td>
<td>(52.3–78.1)</td>
<td>(48.7–81.7)</td>
<td></td>
</tr>
<tr>
<td>APB</td>
<td>74.7 ± 6.5</td>
<td>74.8 ± 8.0</td>
<td>67.5 ± 10.2</td>
<td>63.9 ± 10.7</td>
</tr>
<tr>
<td>(63.9–89.3)</td>
<td>(63.9–84.2)</td>
<td>(59.0–78.9)</td>
<td>(50.4–78.7)</td>
<td></td>
</tr>
<tr>
<td>n = 7</td>
<td>n = 6</td>
<td>n = 5</td>
<td>n = 5</td>
<td>n = 6</td>
</tr>
</tbody>
</table>

* Ranges in brackets; n = number of subjects, APB = abductor pollicis brevis, ADM = abductor digitii minimi.

TABLE 2. REDUCTION IN AMPLITUDE AND TEMPORAL DISPERSION OF THE NEURAL VOLLEY IN THE PROXIMAL SEGMENT OF THE UPPER LIMB, DETERMINED FROM REFERENTIAL RECORDS*

<table>
<thead>
<tr>
<th></th>
<th>Amplitude at elbow (µV)</th>
<th>Amplitude at axilla (µV)</th>
<th>Relative amplitude at axilla</th>
<th>Temporal dispersion (%/100 mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Median and ulnar</td>
<td>53.8 ± 19.6 (19.1–87.0)</td>
<td>23.7 ± 11.4 (12.5–51.8)</td>
<td>0.44</td>
<td>27.9 ± 16.9 (0–54.7)</td>
</tr>
<tr>
<td>n = 12</td>
<td>[1.00]</td>
<td>[1.00]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Digits II and V</td>
<td>7.5 ± 2.9 (2.5–14.8)</td>
<td>3.4 ± 1.8 (1.5–6.4)</td>
<td>0.45</td>
<td>19.9 ± 14.9 (0–56.8)</td>
</tr>
<tr>
<td>n = 13</td>
<td>[0.14]</td>
<td>[0.14]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>APB and ADM</td>
<td>1.4 ± 0.9 (0.2–3.2)</td>
<td>0.6 ± 0.4 (0.1–1.3)</td>
<td>0.43</td>
<td>18.1 ± 12.9 (0–37.7)</td>
</tr>
<tr>
<td>n = 12</td>
<td>[0.03]</td>
<td>[0.03]</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Ranges of amplitudes of the potentials recorded at the elbow and axilla are given in round brackets, relative amplitudes in square brackets; n = number of subjects. Temporal dispersion was calculated as the increase in rise-time of the potential recorded at the axilla, relative to the elbow, expressed as percentage increase per 100 mm.

Low-intensity stimuli (1.5–2.0 × sensory threshold) to the proximal phalanx of digits II or III, either independently or simultaneously. Neural volleys were recorded with bipolar electrodes over the median nerve at the wrist and cubital fossa (conduction distance 240–255 mm). In each subject, stimulus sites were adjusted so that the latencies of the potentials recorded at the wrist were the same for the two digits. When the size of the recorded potential was increased by delivering simultaneous stimuli to the two digits the onset latency of the potential decreased more at the proximal site than the distal (by up to 0.3 ms). These small differences translated into increases in conduction velocity of 2–4 m·s⁻¹. Comparable changes in conduction velocity with increasing stimulus intensity are seen in fig. 1 of Rosenfalck and Buchthal (1973). It is concluded that the amplitude of the recorded potential can influence the resolution of latency differences and hence the calculation of velocity (see also below).
**Conduction velocities of afferents in the lower limb**

Low-threshold muscle afferents of abductor hallucis did not conduct significantly faster than the low-threshold cutaneous afferents from digit II, as assessed from bipolar recordings (Table 3). The conduction velocities were slower than those of the parent nerve (tibial nerve at ankle) and those of the sural nerve, but the differences were not statistically significant. As noted above, the small differences in calculated conduction velocity may be a reflection of the larger size of the tibial and sural nerve volleys (see also Rosenfalck and Buchthal, 1973); when the stimulating current to the sural nerve was reduced in 2 subjects, such that the afferent volley approached the amplitude of the potential from digit II, the calculated conduction velocity was 4–8 m·s⁻¹ less (fig. 4).

As illustrated in fig. 3, all potentials were fractionated (Behse and Buchthal, 1971)

<table>
<thead>
<tr>
<th>TABLE 3. MEANS ± SD FOR CONDUCTION VELOCITY DATA (m·s⁻¹) FOR THE PROXIMAL SEGMENT OF THE LOWER LIMB, DETERMINED FROM BIPOLAR RECORDS*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tibial nerve</td>
</tr>
<tr>
<td>57.9 ± 1.9</td>
</tr>
<tr>
<td>(56.0–60.0)</td>
</tr>
<tr>
<td>n = 6</td>
</tr>
</tbody>
</table>

* Ranges in brackets; n = number of subjects.

**FIG. 3.** Compound action potentials generated by stimulation of the tibial and sural nerves at the medial and lateral malleoli, respectively, and the muscle (abductor hallucis) and cutaneous-articular (proximal phalanx of digit II) afferent components of the posterior tibial nerve, in one subject (female, age 31 yrs). Upper and lower records in each panel are the potentials recorded with bipolar electrodes at the popliteal fossa and at the upper thigh, respectively. Duplicate subaverages are provided to illustrate the reproducibility of the recordings; latencies were measured from the grand average, the number of sweeps comprising which is included at the lower right of each panel. Note that in this example the conduction velocity of the afferent volley from the digit is calculated for the fastest axons in the major component of the fractionated potential; the conduction velocity of the fastest afferents of the volley, i.e., the small potential preceding the initial major negativity, was calculated to be 71.4 m·s⁻¹.
Conduction velocities of muscle and cutaneous afferents

This study has determined the peripheral conduction velocities of low-threshold muscle afferents in the median, ulnar and tibial nerves of normal human subjects and demonstrated that the fastest muscle afferents do not conduct along the proximal limb segment more rapidly than the fastest cutaneous/articular afferents of the digital nerves. On the basis of electrical excitability of human nerves Dawson (1956) had concluded that the conduction velocities of low-threshold afferents from the thenar muscles are not greater than those of the digital nerves. By comparing the relationship of H and long-latency reflexes evoked by stimulation of the median nerve with the long-latency reflexes evoked...
by stimulation of the cutaneous superficial radial nerve, Deuschl et al. (1985) concluded that the conduction velocities of the cutaneous afferents mediating the long-latency reflex are in the range of the low-threshold muscle afferents. The present study provides direct support for these conclusions.

According to Stilwell (1957) the distal interphalangeal joint receives an articular branch of the digital nerve that enters the joint proximally. When the digital nerves are stimulated at the distal phalanx, the resultant afferent potential will therefore contain cutaneous activity from the finger tip without contamination by articular activity. The conduction velocities of the afferent volleys generated by stimulation of the distal phalanx and the proximal phalanx were similar, such that the digital nerve conduction data probably reflect the conduction of low-threshold cutaneous afferents. That the conduction velocities of low-threshold muscle and cutaneous afferents were not significantly different suggests that their populations share a similar range of axonal diameters. Certainly, the unitary action potentials recorded from identified sensory axons originating in muscle spindle, cutaneous and articular receptors of the hand are comparable in amplitude, as reported in a recent microneurographic study in normal subjects (Burke et al., 1988).

**Stimulation of low-threshold muscle afferents**

Intramuscular electrical stimulation allows selective activation of muscle afferents without some of the limitations inherent in microneurographic studies: intraneural stimulation of muscle afferents within motor fascicles is possible only with nerves that are readily accessible, such as the median, ulnar, radial and tibial nerves, and is not suitable for the study of proximal muscles (Gandevia and Burke, 1986, 1988). The afferents activated by microstimulation at the motor point were of low threshold, were activated at levels close to motor threshold, and conducted rapidly. It is well known that the fastest motor axons conduct slower than the fastest sensory axons in a mixed nerve (Dawson, 1956; Gilliatt et al., 1961; Buchthal and Rosenfalck, 1966; Melvin et al., 1966; Behse and Buchthal, 1971; Burke et al., 1981; Gandevia et al., 1982, 1984; Dorfman, 1984; Abbruzzese et al., 1985). Hence it can be assumed that the initial component of the neural volley initiated by stimulation at the motor point consisted of orthodromically activated sensory axons rather than antidromically activated motor axons and, in accordance with this view, well-defined sensory evoked potentials can be recorded over the scalp at appropriately short latencies (Gandevia and Burke, 1988; Macefield et al., 1988a). Along the distal limb segment the mean conduction velocities of the fastest motor axons to abductor pollicis brevis, abductor digitii minimi and abductor hallucis, as determined from compound muscle action potentials, are 57.2 ± 4.2 m s⁻¹, 56.2 ± 4.6 m s⁻¹ and 43.2 ± 4.9 m s⁻¹, respectively (Thomas et al., 1959); the corresponding conduction velocities of the compound sensory volleys along the proximal segment are 74.7 ± 6.5 m s⁻¹, 67.5 ± 10.2 m s⁻¹ and 54.7 ± 3.4 m s⁻¹ (present data).

The low-threshold afferents activated by intramuscular stimulation were not cutaneous in origin: the exposed tip of the insulated microelectrode was located at least 5 mm within the muscle belly such that it would be highly unlikely that the stimuli would cause local activation of cutaneous afferents. The subjects did not report local cutaneous
sensations associated with the stimuli, nor did they report radiating paraesthesiae. Cutaneous receptors would have been stimulated by the muscle twitch but not until appreciable skin distortion had occurred, too late to contribute to the neural volley. As discussed by Gandevia and Burke (1988), the afferents activated by intramuscular stimulation most likely belong to the group I population, originating in the primary ending of the muscle spindle (group Ia) and the Golgi tendon organ (group Ib). Devanandan et al. (1983) have demonstrated a rich supply of muscle spindles but a relative paucity of Golgi tendon organs in the intrinsic muscles of the monkey hand. In the course of microneurographic studies of afferents from the hand in normal human subjects we have encountered many afferents possessing the properties of muscle spindles but few possessing those of Golgi tendon organs (see Burke et al., 1988), suggesting that in the human hand the relative proportions of the two receptor types may be similar to those in the monkey. Intramuscular stimulation of intrinsic muscles of the hand may therefore be a relatively selective stimulus for muscle spindle afferents.

**Implications**

In previous studies from this laboratory, it has been asserted that, in the human lower limb, muscle afferents conduct some 5–10 m·s⁻¹ faster than cutaneous afferents (Burke et al., 1981, 1982, 1983; Gandevia et al., 1982). This view was based on comparisons of the conduction velocities of the tibial mixed nerve potential and the sensory potential of the sural nerve when stimulated at the ankle and recorded at the popliteal fossa. These studies used different stimulus intensities for the two nerves and assumed that the conduction paths were equally direct for the two neural volleys. In the present study, conduction time was measured across the identical segment of the sciatic nerve for each afferent volley and the effects of stimulus intensity were eliminated by determining the conduction time between two recording sites. Nevertheless, there was still a tendency for the larger, better defined volleys to have a slightly shorter conduction time than the smaller volleys.

Some of the conclusions from this laboratory should be reappraised in the light of the present findings. It has been a consistent theme of our studies that the cerebral potential evoked by stimulation of mixed nerves in the lower limb (such as the tibial nerve) is determined largely if not exclusively by muscle afferents. The shorter latency of P40 of the cerebral potential to tibial nerve stimulation when compared with that produced by sural nerve stimulation (some 5 ms) was attributed to a combination of faster peripheral conduction and faster central conduction of muscle afferent volleys (Burke et al., 1981, 1982; Burke and Gandevia, 1986). Vogel et al. (1986) provided evidence that most of the discrepancy in latency of P40 was due to faster central conduction, a view with which we fully concur. However, this is consistent with our argument that the cerebral potentials to stimulation of the tibial and sural nerves are determined by different afferent populations, presumably muscle afferent and cutaneous afferent, respectively (cf. Kakigi and Jones, 1986). This view is further supported by topographic differences in the cerebral projection of these nerves as recorded using magnetoencephalography (Huttunen et al., 1987) and conventional electroencephalography (Macefield et al., 1988a).
It has been argued that the compound EPSPs set up in soleus motoneurons by percussion on the Achilles tendon or by electrical stimulation of the tibial nerve in the popliteal fossa last so long (> 10 ms, < 5 ms, respectively) that contamination of the afferent volleys by cutaneous afferents could result in cutaneous inputs affecting the reflex discharge, particularly the ankle jerk (Burke et al., 1983, 1984). This was considered less likely with the H reflex because it was calculated that the cutaneous volley would reach the motoneuron pool too late. On the basis of the present findings cutaneous volleys would reach the spinal cord at a similar time as muscle afferent volleys and only the length and excitability of the interneuronal chain would prevent their participation in determining the size of the H reflex. The present findings thus reinforce the need to be cautious in interpreting the results of studies that have used the H reflex as a purely monosynaptic reflex to probe motoneuron excitability in human subjects.

Cutaneous mechanoreceptors are powerfully activated when the human hand performs a motor task (Hulliger et al., 1979; Westling and Johansson, 1987; Burke et al., 1988), perhaps as much so as intramuscular mechanoreceptors, and the afferent volleys so generated have similar conduction velocities (present study). Classical teachings have assigned a purely perceptual role to cutaneous afferents, denying them a role in motor control, and a purely motor role to muscle mechanoreceptors, denying them a role in conscious sensation. There is increasing evidence that the former view is as untenable as the latter. In the human hand, low-threshold cutaneous afferents from the digits influence the excitability of the muscles acting on the digits via a spinal pathway (e.g., Jenner and Stephens, 1982; Aniss et al., 1988), and tactile afferents from the finger tips have been shown to be crucial for adjusting the forces generated by the muscles involved in maintaining precision grip of an object (Johansson and Westling, 1987; Westling and Johansson, 1987).

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