

## Velocity sensitivity of human muscle spindle afferents and slowly adapting type II cutaneous mechanoreceptors

Stephen E. Grill and Mark Hallett

*Human Motor Control Section, Medical Neurology Branch, National Institute of Neurological Disorders and Stroke, National Institutes of Health, Bethesda, Maryland 20892-1430, USA*

1. Velocity information is used in the performance of movement. This study evaluated the ability of peripheral receptors to signal velocity in human subjects.
2. The velocity sensitivity of human muscle spindle afferents from the extensor digitorum muscles and slowly adapting type II cutaneous mechanoreceptors on the dorsum of the hand was evaluated with recordings from the radial nerve during imposed flexion movements about the metacarpophalangeal joint. Twenty-degree movements at velocities ranging from 5 to 80 deg s<sup>-1</sup> were used.
3. Three measures of dynamic response were calculated: the dynamic positional sensitivity (the relation between discharge rate and joint angle during the dynamic phase of movement), the dynamic index (the discharge rate just before ramp completion minus the rate 0.5 s later), and the incremental response (the discharge rate just before ramp completion minus the rate just before ramp onset).
4. Both muscle spindle afferents and slowly adapting type II cutaneous mechanoreceptors demonstrated significant velocity sensitivity. The magnitudes of the relations between dynamic response measures and velocity were similar in the two receptor types.
5. These findings are consistent with the view that both muscle spindle afferents and slowly adapting type II cutaneous mechanoreceptors provide reasonable velocity signals.

Humans are normally able to use kinesthetic velocity information when performing forearm movements (Sittig, Denier Van der Gon & Gielen, 1987; Gandevia & Burke, 1992) and in controlling multijoint movements (Cordo, 1990). Conscious perception of small changes in angular velocity is possible (Grill, Hallett, Marcus & McShane, 1994). These findings suggest that either a receptor is able to provide a true velocity signal or the nervous system is able to calculate one based on afferent signals not signalling velocity, for example, by differentiating a position signal. It is widely held that muscle spindle afferents are the main providers of kinesthetic signals, although signals from muscle afferents (Goodwin, McCloskey & Matthews, 1972; Gandevia, 1985), cutaneous mechanoreceptors (Moberg, 1983; Ferrell & Smith, 1988), and joint receptors (Ferrell, Gandevia & McCloskey, 1987; Ferrell & Craske, 1992) may all reach consciousness.

The relation between dynamic response and velocity has been studied extensively for muscle spindle afferents in the

cat (Jansen & Matthews, 1962; Matthews, 1963; Lennerstrand, 1968; Schafer, 1973; Cody, Harrison & Taylor, 1975; Houk, Rymer & Crago, 1981), but not in humans.

Cutaneous mechanoreceptors in humans have been studied with respect to their responses to finger and hand movements (Hulliger, Nordh, Thelin & Vallbo, 1979; Edin & Abbs, 1991). Slowly adapting type II cutaneous mechanoreceptors on the dorsum of the human hand provide directional responses to finger joint movements (Edin & Abbs, 1991; Edin, 1992). Ninety-two percent of these cutaneous mechanoreceptors respond to hand or finger movements. The velocity sensitivity of cutaneous mechanoreceptors has not been quantified.

We measured the responses of muscle spindle afferents from the extensor digitorum muscles and slowly adapting type II cutaneous mechanoreceptors on the dorsum of the hand during imposed constant velocity flexion movements about the metacarpophalangeal joint.

## METHODS

### Subjects

The subjects were fourteen normal volunteers, aged 24–59 years, from whom we recorded afferents from eleven muscle spindle afferents and eleven slowly adapting type II cutaneous mechanoreceptors. The protocol was approved by the Institutional Review Board, and all subjects gave their written informed consent for the study.

### Torque motor apparatus

The torque motor apparatus used in the study is fully described elsewhere (Grill *et al.* 1994). Briefly, movements about the metacarpophalangeal joint were under the explicit control of a computer-controlled rotary torque motor (Model 310B, modified, Cambridge Technology, Inc., Watertown, MA, USA) that was able to operate in both position and torque modes. The system provides analog force and position signals, allowing calculation of torque and angle about the metacarpophalangeal joint. Subjects were seated with the right arm flexed at the elbow approximately 120 deg and partially immobilized in a vacuum pillow. The finger under study was attached to a metal bar with a 7.5 cm long metal finger holder that surrounded the finger over the extensor surface. A flat wooden stick held in place with Velcro secured the finger to the metal portion of the finger holder. This arrangement permitted movements about the metacarpophalangeal joint only. The finger holder extended proximally to a point midway between the proximal interphalangeal joint and the metacarpophalangeal joint. The fingers not under study were secured with tape to prevent movement or contact with the moving finger. The metacarpophalangeal joint was initially set at an angle of approximately 30 deg, which was arbitrarily assigned a value of 0 deg. Movements in the flexor direction were considered positive.

### Microneurographic recordings

Single afferents were recorded from the radial nerve of the right arm, 5–10 cm above the elbow, using tungsten needle electrodes (Titronics Medical Instruments, Iowa Doppler Products, Iowa City, IA, USA) (Grill *et al.* 1994). The neurogram, which was amplified and bandpass filtered, was recorded on a digital tape recorder (TEAC RD-200T PCM, Tokyo, Japan) for later off-line analysis by our own computer program. For every recording, each waveform exceeding a 'trigger' threshold was viewed and compared quantitatively, using correlation analysis, to a template waveform in order to determine whether it indeed represented an action potential from the unit under consideration. The program provided the time of occurrence of each event with a resolution of 0.05 ms.

### Afferent characterization

Afferents sensitive to imposed flexion movements were sought in our search protocol, which imposed continuous sinusoidal movements of approximately 15 deg about the metacarpophalangeal joint. Each afferent was subjected to several experimental tests in order to classify it as either a muscle spindle afferent or a slowly adapting type II cutaneous mechanoreceptor.

Afferents whose discharge increased during the contraction phase of an electrically induced twitch were classified as Golgi tendon organs and were not studied further.

Muscle spindle afferents responded to imposed flexion movements and palpation of the muscle belly of either the extensor digitorum communis (EDC) or the extensor indicis proprius (EIP) muscle, and were silenced during the rising phase, or showed enhanced discharge during the falling phase, of an electrically induced muscle twitch. Muscle twitches were induced by stimulating over the motor point of the muscles. The raw data from an afferent characterized as a muscle spindle afferent are shown in response to an electrically induced muscle twitch contraction (Fig. 1A) and a ramp flexion movement (Fig. 1B). The discharge of most muscle spindle afferents increased during isometric contractions of the appropriate finger, although some were unloaded. We did not attempt to classify muscle spindle afferents as primary or secondary spindle afferents.

Receptors were classified as cutaneous mechanoreceptors if they did not respond to palpation of muscles in the forearm but did respond to light touch of the skin on the dorsum of the hand. Receptive field sizes were evaluated with Semmes-Weinstein monofilaments (North Coast Medical, Inc., San Jose, CA, USA), using a filament of 10 times the threshold. The receptive fields of the cutaneous mechanoreceptors were 1 to 2 cm in diameter and were distributed throughout the dorsal surface of the hand between the metacarpophalangeal joint and about half way to the wrist. The receptors were classified as slowly adapting type II cutaneous mechanoreceptors on the basis of their maintained discharge in response to tactile and finger movement stimuli and the regularity of their discharge (Knibestöl & Vallbo, 1970; Chambers, Andres, Dering & Iggo, 1972; Edin & Abbs, 1991). Coefficients of variation, using several 0.5 s segments of data of interspike intervals following flexion movements for each afferent, were calculated and ranged from 0.047 to 0.19 (median, 0.103). (In cats, coefficients of variation were < 0.25 for slowly adapting type II cutaneous mechanoreceptors and > 0.50 for slowly adapting type I cutaneous mechanoreceptors, in response to tactile stimuli (Chambers *et al.* 1972).) Only cutaneous afferents whose receptive fields were proximal to the metacarpophalangeal joint were studied because afferents with receptive fields distal to this joint may have been influenced by the mechanical effects of the finger holder on neighbouring skin. The finger producing the greatest afferent response when moved was used in testing.

### Experimental control

The control of the torque motor, acquisition of analog data, and delivery of instructions to the subjects were under computer control, with the use of our own software, using ASYST (Asyst Software Technologies, Inc., Rochester, NY, USA). Twenty-degree ramp flexion movements of different velocities, expressed in degrees per second ( $\text{deg s}^{-1}$ ), were imposed about the metacarpophalangeal joint. The velocity ranged from 5 to 80  $\text{deg s}^{-1}$ . The ordering of the velocities was pseudorandom. Acquisition of data proceeded automatically, with approximately 5 s between each trial, until data from at least four trials at each velocity were collected or the unit recording deteriorated. To ascertain that the subjects were relaxed and not reacting to the imposed movements, the electromyogram (EMG) was recorded from the flexor digitorum superficialis and EDC muscles. The EMG, recorded with surface electrodes, was amplified and bandpass filtered (300 Hz to 3 kHz) before sampling by the computer.

### Analysis of data

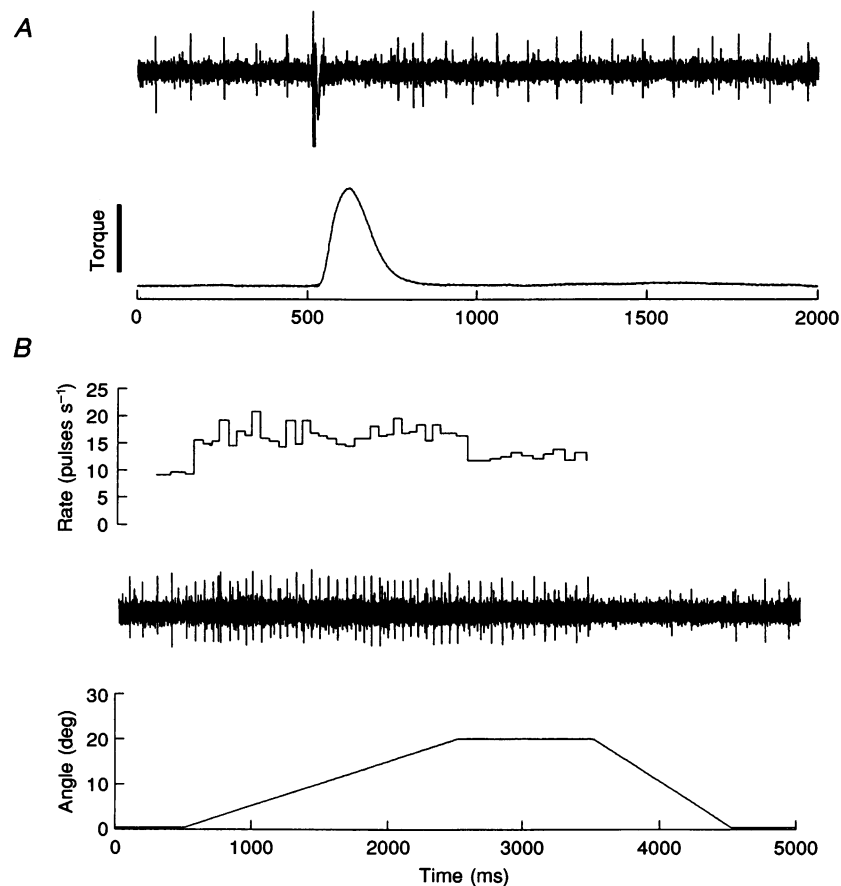
**Calculation of dynamic positional sensitivity.** The dynamic positional sensitivity is the slope of the relation between discharge rate, expressed in pulses per second ( $\text{pulses s}^{-1}$ ) and joint angle, expressed in degrees, during the ramp stretch. This is similar to the 'slow-velocity response' used in evaluating the velocity sensitivity of cat muscle spindles (Lennerstrand, 1968). We calculated the instantaneous frequency of each interspike interval and plotted the result against the joint angle at the time of each individual spike. Several trials were then overlaid. Only points during the dynamic flexion phase of the ramp movement were included in the analysis. In addition, where an initial burst was present, only intervals occurring after the burst were included. The slope of the relation between discharge rate and joint angle was then calculated using least-squares regression. This method avoided the difficulties associated with conversion of instantaneous frequency to an analog representation at discrete intervals.

**Calculation of incremental response.** The incremental response is the discharge rate just before ramp completion minus the discharge rate just before stretch initiation (Houk *et al.* 1981). This measure, therefore, includes the entire magnitude of the dynamic response.

**Calculation of dynamic index.** The dynamic index is defined as the discharge rate just before ramp completion minus the static discharge 0.5 s later (Jansen & Matthews, 1962).

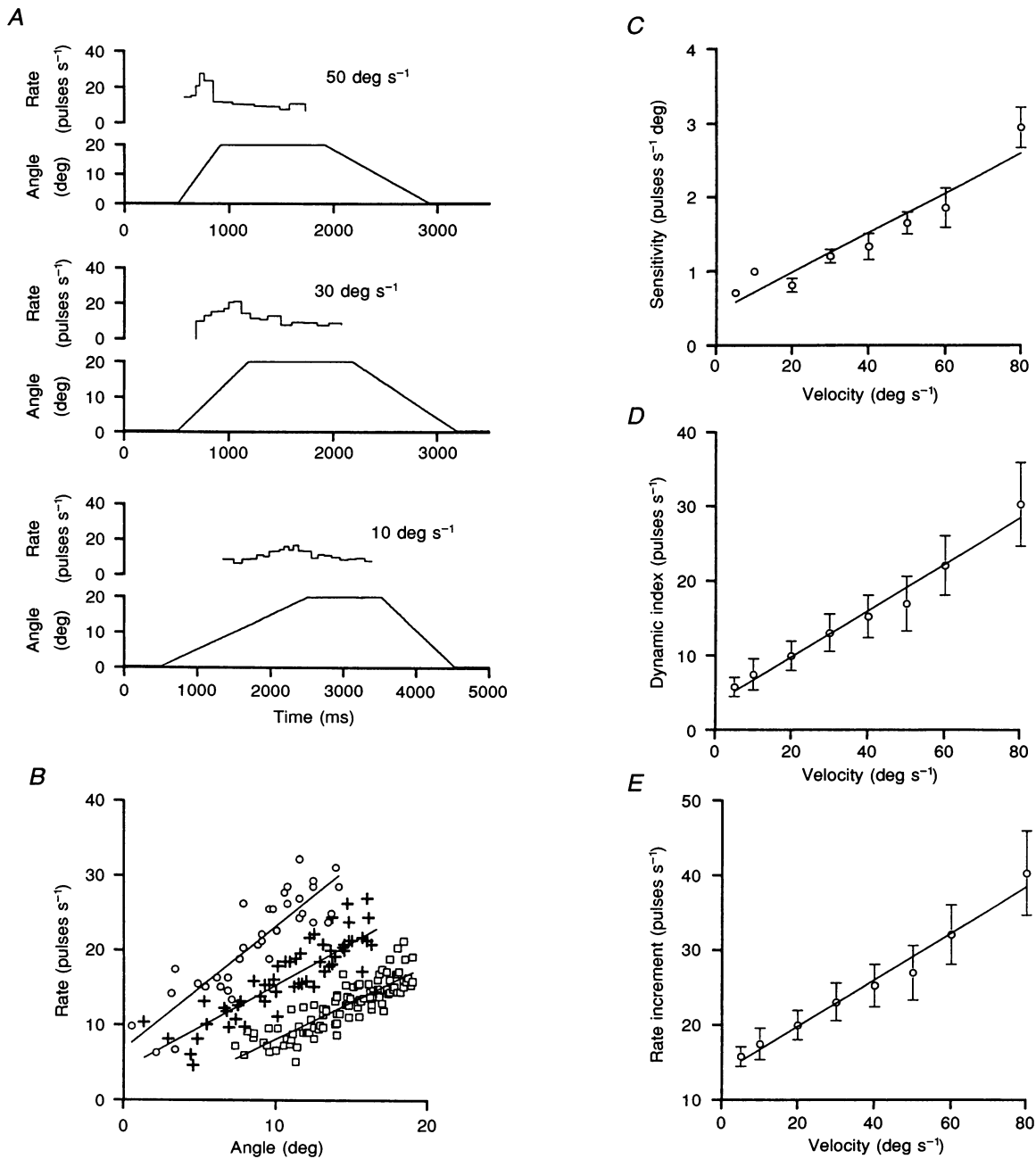
## RESULTS

Twenty-two afferents, consisting of eleven muscle spindle afferents (five from EDC I, two from EIP, three from EDC II, and one from EDC III) and eleven slowly adapting type II cutaneous mechanoreceptors were studied. The receptive fields, measured from the edge of the field, for six cutaneous mechanoreceptors were within 1 cm proximal to the metacarpophalangeal joint, and the remaining five were between 1 and 2.5 cm proximal to the joint. For the cutaneous mechanoreceptors, the finger producing the greatest afferent response when moved was the index finger in seven cases and the middle finger in four cases. Resting discharge was observed in seven of the muscle spindle afferents (discharge rate: mean,  $12.7 \text{ pulses s}^{-1}$ ; median,  $11.7 \text{ pulses s}^{-1}$ ), but in only five of the cutaneous mechanoreceptors (discharge rate: mean,  $8.2 \text{ pulses s}^{-1}$ ; median,  $7.9 \text{ pulses s}^{-1}$ ).



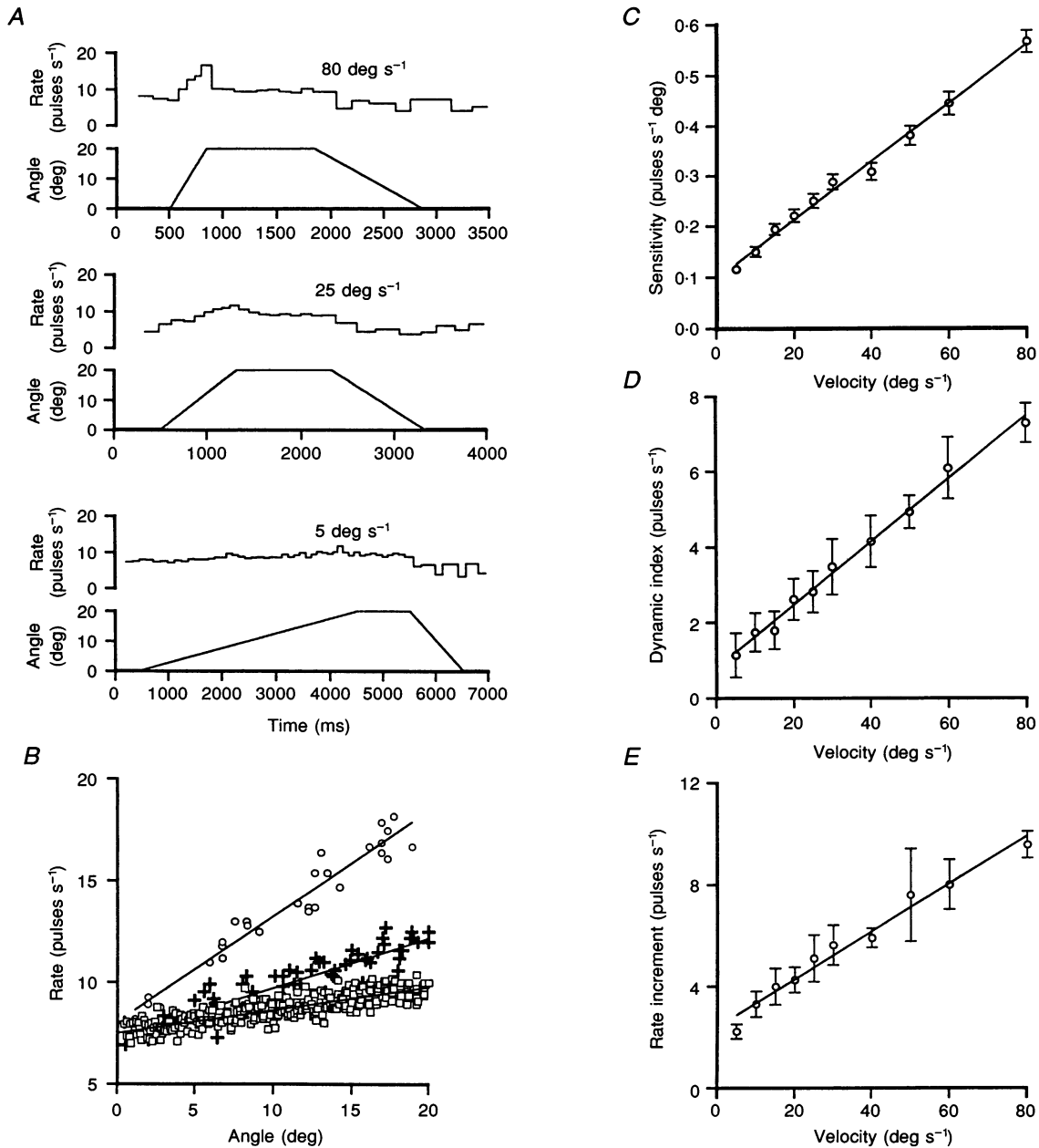
**Figure 1.** Responses of a muscle spindle afferent to electrically induced muscle twitch (*A*) and ramp stretch (*B*)

In *A*, the torque calibration bar indicates 10% maximal voluntary torque. In *B*, the middle trace is the neurogram, and the upper trace is the instantaneous frequency.



**Figure 2. Responses of a muscle spindle afferent to ramp movements of varying velocity**

*A*, instantaneous frequency of a muscle spindle afferent in response to three ramp movements of different velocities. *B*, dynamic positional sensitivity plot for the three movement velocities shown in *A*. Each point on the graph represents the instantaneous frequency of each interspike interval plotted against the joint angle for the flexion portion of the movement. Three trials at each velocity are superimposed. The lines represent the best-fit linear regression line for a given velocity of stretch. O, 50 deg s<sup>-1</sup>; +, 30 deg s<sup>-1</sup>; □, 10 deg s<sup>-1</sup>. *C*, slope of the dynamic positional sensitivity relation plotted as a function of velocity (slope =  $0.027 \pm 0.004$  pulses s<sup>-1</sup> deg (deg s<sup>-1</sup>)<sup>-1</sup>). Bars indicate the standard error of the slope (s.e.s.). *D*, dynamic index plotted as a function of velocity (slope =  $0.309 \pm 0.011$  pulses s<sup>-1</sup> (deg s<sup>-1</sup>)<sup>-1</sup>). Bars indicate the standard deviation (s.d.). *E*, incremental response plotted as a function of velocity (slope =  $0.311 \pm 0.019$  pulses s<sup>-1</sup> (deg s<sup>-1</sup>)<sup>-1</sup>). Bars indicate the s.d.



**Figure 3. Responses of a slowly adapting type II cutaneous mechanoreceptor to ramp movements of varying velocity**

*A*, instantaneous frequency of a cutaneous mechanoreceptor in response to three ramp movements of different velocities. *B*, dynamic positional sensitivity plot for the three movement velocities shown in *A*. Each point on the graph represents the instantaneous frequency of each interspike interval plotted against the joint angle for the flexion portion of the movement. Four to six trials at each velocity are superimposed. The lines represent the best-fit linear regression line for a given velocity of stretch. ○, 80 deg s<sup>-1</sup>; +, 25 deg s<sup>-1</sup>; □, 5 deg s<sup>-1</sup>. *C*, slope of the dynamic positional sensitivity relation plotted as a function of velocity (slope = 0.0067 ± 0.0004 pulses s<sup>-1</sup> deg (deg s<sup>-1</sup>)<sup>-1</sup>). Bars indicate the s.e.s. *D*, dynamic index plotted as a function of velocity (slope = 0.0834 ± 0.0025 pulses s<sup>-1</sup> (deg s<sup>-1</sup>)<sup>-1</sup>). Bars indicate the s.d. *E*, incremental response plotted as a function of velocity (slope = 0.213 ± 0.020 pulses s<sup>-1</sup> (deg s<sup>-1</sup>)<sup>-1</sup>). Bars indicate the s.d.

In single trials of the discharge of a muscle spindle afferent (Fig. 2A) and a slowly adapting type II cutaneous mechanoreceptor (Fig. 3A) in response to three different movement velocities, the responses were apparently enhanced as the velocity increased.

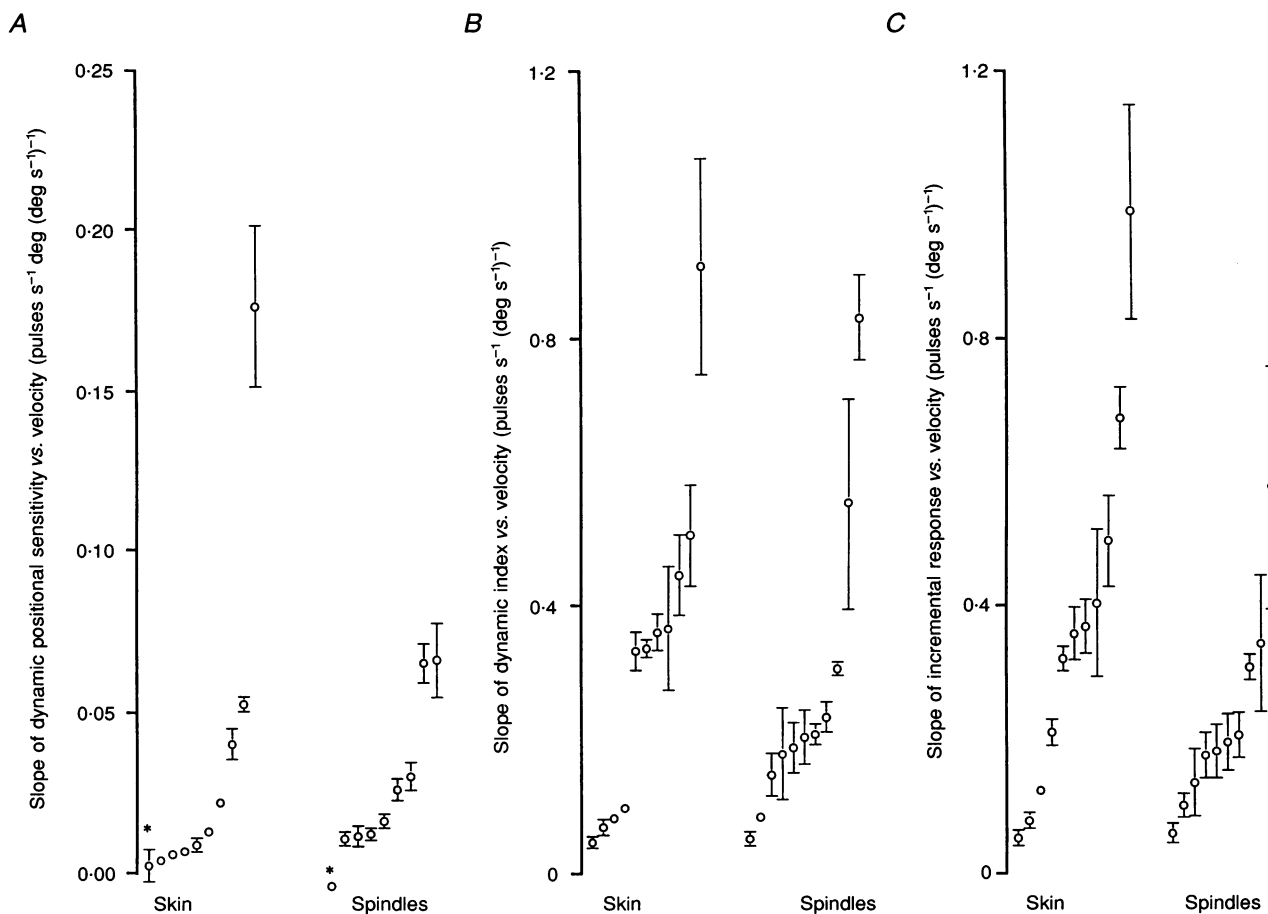
For nine of the eleven muscle spindle afferents and ten of the eleven cutaneous mechanoreceptors, the data for dynamic positional sensitivity were well fitted by linear regression. Only these afferents were subjected to the dynamic positional sensitivity analysis. For the discharge patterns of the two afferents shown, the dynamic positional sensitivity appeared to increase as the velocity increased (Figs. 2B and 3B). The increase is clearly evident in the plot of dynamic positional sensitivity *vs.* velocity for the muscle spindle afferent ( $P = 0.0003$ ) (Fig. 2C) and the cutaneous mechanoreceptor ( $P < 0.0001$ ) (Fig. 3C).

Similarly, the slope of the relation between dynamic index and velocity was significantly greater than zero for the muscle spindle afferent ( $P < 0.0001$ ) (Fig. 2D) and the

cutaneous mechanoreceptor ( $P < 0.0001$ ) (Fig. 3D). Likewise, the slope of the relation between incremental response and velocity was greater than zero for the muscle spindle afferent ( $P < 0.0001$ ) (Fig. 2E) and the cutaneous mechanoreceptor ( $P < 0.0001$ ) (Fig. 3E).

### Population responses

Measures of dynamic response increased significantly with velocity for all of the afferents studied. For eight of the nine muscle spindle afferents and nine of the ten cutaneous mechanoreceptors for which the dynamic positional sensitivity was well fitted by straight lines, the relation between dynamic positional sensitivity and velocity was significant (Fig. 4A). For all eleven muscle spindle afferents and all eleven cutaneous mechanoreceptors, both the dynamic index (Fig. 4B) and the incremental response (Fig. 4C) increased significantly with velocity. For all three of the dynamic measures, there was extensive overlap between muscle spindle afferents and cutaneous mechanoreceptors (Fig. 4A–C). With the exception of one cutaneous mechanoreceptor whose dynamic measures



**Figure 4. Magnitudes of the relation between the dynamic response measures and the velocity**

For dynamic positional sensitivity (A), dynamic index (B), and incremental response (C), the slopes of the relation between the dynamic measure and the velocity are plotted for each afferent arbitrarily in ascending order and separately for slowly adapting type II cutaneous mechanoreceptors (skin) and muscle spindle afferents (spindles). Asterisks indicate that the relation between the dynamic measure and the velocity was not significantly greater than zero. Bars indicate s.e.s.

**Table 1. Relation between dynamic response measures and velocity**

	Cutaneous mechanoreceptor		Muscle spindle afferent	
	Mean $\pm$ s.d.	Median	Mean $\pm$ s.d.	Median
Dynamic positional sensitivity (pulses s <sup>-1</sup> deg (deg s <sup>-1</sup> ) <sup>-1</sup> )	0.033 $\pm$ 0.053	0.011	0.027 $\pm$ 0.025	0.017
Dynamic index (pulses s <sup>-1</sup> (deg s <sup>-1</sup> ) <sup>-1</sup> )	0.33 $\pm$ 0.27	0.34	0.27 $\pm$ 0.23	0.21
Incremental response (pulses s <sup>-1</sup> (deg s <sup>-1</sup> ) <sup>-1</sup> )	0.36 $\pm$ 0.26	0.36	0.29 $\pm$ 0.23	0.20

exceeded those of all the other units, the distribution of the dynamic measures appeared quite similar for the two types of afferents. This cutaneous mechanoreceptor had its receptive field closest to the metacarpophalangeal joint, but another cutaneous mechanoreceptor with a similarly situated receptive field did not have large sensitivities. A third cutaneous mechanoreceptor whose receptive field was in a similar location had the third highest sensitivity. There was no significant difference between muscle spindle afferents and slowly adapting type II cutaneous mechanoreceptors with respect to the means of any of the dynamic measures ( $P > 0.05$ , Student's *t* test) (Table 1).

For the eleven muscle spindle afferents in the present study, the mean dynamic index evaluated at a velocity of 50 deg s<sup>-1</sup> was 22 pulses s<sup>-1</sup>. In a previous study (Edin & Vallbo, 1990), the dynamic index of human muscle spindle afferents was evaluated at a velocity of 50 deg s<sup>-1</sup>, and ranged from 0 to approximately 50 pulses s<sup>-1</sup>, with a mean of 22 pulses s<sup>-1</sup> for the primary muscle spindle afferents and a mean of 14 pulses s<sup>-1</sup> for the secondary muscle spindle afferents.

**Static positional sensitivity**

Although we were concerned mainly with the dynamic response of the afferents, we also calculated a quasi-static measure of afferent response. Using the slowest movements (5 deg s<sup>-1</sup>), we calculated the rate 0.5 s after ramp completion minus the rate just before the stretch and divided the result by the angular change (20 deg). The quasi-static positional sensitivity for muscle spindle afferents ranged from 0.20 to 0.76 pulses s<sup>-1</sup> deg (median, 0.38 pulses s<sup>-1</sup> deg; mean, 0.40 pulses s<sup>-1</sup> deg) and for cutaneous mechanoreceptors ranged from 0.66 to 1.81 pulses s<sup>-1</sup> deg (median, 0.41 pulses s<sup>-1</sup> deg; mean, 0.20 pulses s<sup>-1</sup> deg). The values for static sensitivity of muscle spindle afferents are comparable with previous estimates calculated similarly, in which the mean quasi-static positional sensitivity was 0.23 pulses s<sup>-1</sup> deg for primary muscle spindle afferents and 0.37 pulses s<sup>-1</sup> deg for secondary muscle spindle afferents (Edin & Vallbo, 1990). Similarly, an indirectly estimated median static positional sensitivity for slowly adapting type II cutaneous mechanoreceptors was between 0.36 and 0.54 pulses s<sup>-1</sup> deg (Edin, 1992). The quasi-static positional sensitivity is likely to overestimate the true static positional sensitivity. For one of the cutaneous mechanoreceptors, there was an absence of sustained discharge 0.5 s after ramp completions,

so static positional sensitivity was zero and, therefore, was omitted from static positional sensitivity analysis.

**DISCUSSION**

Human muscle spindle afferents and slowly adapting type II cutaneous mechanoreceptors demonstrate velocity sensitivity. For the eleven muscle spindle afferents and the eleven slowly adapting type II cutaneous mechanoreceptors, the dynamic index and incremental response increased significantly with velocity. For eight of the nine muscle spindle afferents and nine of the ten cutaneous mechanoreceptors that were subjected to calculation of dynamic positional sensitivity, that measure increased significantly with velocity. Therefore, both muscle spindle afferents and slowly adapting type II cutaneous mechanoreceptors provide signals with velocity information. The finding that the slope of the dynamic positional sensitivity relation is not constant, but instead increases with velocity, implies that, similar to cat muscle spindle afferents (Houk *et al.* 1981), the dynamic response is dependent on a multiplicative relationship between muscle length and velocity.

**Muscle spindle afferent responses**

Our finding of a mean dynamic index of 22 pulses s<sup>-1</sup> at a velocity of 50 deg s<sup>-1</sup> is in good agreement with that of a previous study (Edin & Vallbo, 1990). In characterizing the dynamic responses of muscle spindle afferents for a range of velocities, we have shown that the three dynamic measures we used vary with velocity.

Most studies of cat muscle spindle afferents indicate that the dynamic response does not provide a true linear response in an engineering sense, where a doubling of the input results in a doubling of the output (Cooper, 1961; Jansen & Matthews, 1962; Matthews, 1963; Lennerstrand, 1968; Cody *et al.* 1975; Houk *et al.* 1981), although an exception has been reported (Schafer, 1973). As noted by Matthews (1963), part of the non-linearity may be a result of the finding that with extrapolation to zero velocity, the dynamic response is not zero. The main non-linearity for the receptors we studied appears to be a result of a non-zero intercept in that the relations between the dynamic measures and velocity are well fitted by straight lines for the range studied.

It is likely that the relations between the dynamic measures and the velocity fall steeply as zero velocity is approached.

However, it is unlikely that velocities below  $5 \text{ deg s}^{-1}$  have much physiological importance, because most normal finger movements are made at higher speeds. We consider that there may be a distinct change in the state of muscle spindle responsiveness in going from static to dynamic conditions and that, at least above a certain minimal velocity, the dynamic response increases with velocity in a straight-line relationship. If the nervous system is able to perform the simple calculation of subtracting an extrapolated intercept, the muscle spindle dynamic response could provide a signal linearly related to velocity in the engineering sense.

Most studies of velocity sensitivity of muscle spindle afferents in cats used muscle pullers connected to tendons detached from their joints and involved velocities of up to  $100 \text{ mm s}^{-1}$ , which assuming a mean muscle fibre length of  $42 \text{ mm}$  (Rack and Westbury, 1984) corresponds to over  $200\%$  muscle fibre lengths  $\text{s}^{-1}$ . The highest velocities in the present study are probably on the order of  $10\%$  muscle fibre lengths  $\text{s}^{-1}$  based on calculations converting angular changes about the metacarpophalangeal joint to longitudinal tendon extension of finger extensor muscles (Edin & Vallbo, 1990). Cat muscle spindle afferents may fire at rates greater than  $200 \text{ pulses s}^{-1}$ , whereas human muscle spindle afferents rarely fire at rates of more than  $40 \text{ pulses s}^{-1}$ . Our use of higher velocities would have been inappropriate because human muscle spindle afferents could not accurately signal faster velocities. For instance, a  $20 \text{ deg}$  movement at  $200 \text{ deg s}^{-1}$  would last only  $100 \text{ ms}$ , whereas a  $20 \text{ deg}$  movement at  $150 \text{ deg s}^{-1}$  would last  $133 \text{ ms}$ . At best, a human muscle spindle afferent would fire one or two additional action potentials for the faster of these movements. Given the variability of muscle spindle afferent discharge, it is unlikely that these velocities could be distinguished on the basis of only one or two additional interspike intervals (cf. Matthews & Stein, 1969). Therefore, the limited firing rate of human muscle spindle afferents would not allow them to signal higher velocities accurately. Because feedback is not thought to contribute to control of fast or ballistic movements (Wadman, Denier Van der Gon, Geuze & Mol, 1979; Sanes & Jennings, 1984), the inability of muscle spindle afferents to discriminate fast velocity movements is not surprising, even when a role for them in feedback control is considered.

The movements used in the present study were all under passive conditions. If muscle spindle afferent signals are to be used during active movements, the nervous system must be able to deal with the confounding effects of fusimotor actions. This could involve the use of efference copy (Matthews, 1981). Another possibility is the use of the antagonist muscle spindle afferents, which are passively stretched during agonist shortening (Hasan & Stuart, 1984; Gandevia, McCloskey & Burke, 1992). During active movements, vibration of the antagonistic tendon produces undershoots of intended movements (Capaday & Cooke,

1981). This suggests that afferent information from antagonist muscles is important in movement sensation. Presumably, fusimotor actions are limited during times when muscles are passively lengthened.

### Cutaneous mechanoreceptor responses

The slowly adapting type II cutaneous mechanoreceptors provide a velocity signal very similar to that of muscle spindle afferents. The fact that they provide a reliable velocity signal does not necessarily imply that they are used by the nervous system in that way. Cutaneous mechanoreceptors are thought to serve mainly an exteroceptive role. Slowly adapting type II cutaneous mechanoreceptors can be exquisitely sensitive to tactile stimuli, often firing at rates in excess of  $200 \text{ pulses s}^{-1}$  (Edin, 1992), whereas their responses to joint movements are similar to those of muscle spindle afferents, usually firing at rates of less than  $50 \text{ pulses s}^{-1}$ . This may imply that the movement responses of slowly adapting type II cutaneous mechanoreceptors are relatively unimportant or, alternatively, that they may function in two modes of operation. Interestingly, cutaneous sensitivity is reduced during voluntary movements (Angel & Malenka, 1982; Milne, Annis, Kay & Gandevia, 1988), which conceivably may represent a central switch from signalling tactile to proprioceptive information (Prochazka, 1989).

Psychological studies support a role for cutaneous mechanoreceptors in perception. Digital nerve block, which blocks input from both cutaneous and joint receptors, results in impairment, although not complete loss, of kinesthetic sensation (Goodwin *et al.* 1972; Ferrell & Smith, 1988). Furthermore, this technique would not affect the cutaneous mechanoreceptors located on the dorsum of the hand, which is where a large portion of the cutaneous mechanoreceptors sensitive to finger movements are located (Edin & Abbs, 1991). Cutaneous mechanoreceptors are more likely to be a source of kinesthetic information because joint afferents respond mostly at the extremes of movement (Clark & Burgess, 1975; Ferrell, 1980; Burke, Gandevia & Macefield, 1988, but see Edin, 1991).

Only slowly adapting type II cutaneous mechanoreceptors were found in the present study, which used finger movement as a search procedure. Manual palpation of the skin was used predominantly in a study (Edin & Abbs, 1991) which found an equal proportion of type I and type II receptors, whereas in a subsequent study (Edin, 1992) which found a predominance of type II cutaneous mechanoreceptors, reliance on finger movement was used to a greater extent (Edin, 1995, personal communication). The use of finger movement as a search procedure may cause a bias in finding the more regularly firing receptors. There is no significant difference in the proportion of slowly adapting type II cutaneous mechanoreceptors found in the present study and in the study by Edin (1992) ( $P = 0.1134$ , Fisher's exact test).



### Origin of signal properties

It is interesting to find that the responses of muscle spindle afferents and slowly adapting cutaneous mechanoreceptors are so similar, given their different anatomical locations and structures. The static and dynamic characteristics of the muscle spindle afferent response to stretch have been attributed to intrafusal muscle fibre mechanics (Jansen & Matthews, 1962; Lennerstrand, 1968).

Slowly adapting type II cutaneous mechanoreceptors correspond to the Ruffini ending (Chambers *et al.* 1972). These receptors are spindle shaped, oriented parallel to the long axis of the limb, and lie free in the dermis. The capsule and inner-capsule space structure corresponds to some extent to that of muscle spindles, and the suspension of the inner core by collagenous fibres is suggestive of a stretch receptor (Chambers *et al.* 1972). They are sensitive to both the position and the velocity of vertical displacements. Thus, both receptors lie parallel to the long axis of the limb and so are able to respond to joint movements. Both are spindle shaped and respond to both static and dynamic characteristics of stimuli.

### Role of velocity signal

There is much evidence that kinesthetic information is used for co-ordinating movement. Control of multijoint sequences uses information on joint velocity (Cordo, Carlton, Bevan, Carlton & Kerr, 1993). It is likely that proprioceptive signals are used in a feedforward predictive, rather than feedback fashion, since the mechanical state would probably have changed once feedback corrections could act (Sainburg, Poizner & Ghez, 1993). For the control of multijoint sequences using feedforward processes, accurate velocity information is essential. Because, in the nervous system, the time needed for processing proprioceptive information for co-ordination of movement is on the order of only 60 ms (Cordo *et al.* 1993), it would be advantageous to have a peripheral signal of velocity that requires relatively little processing. The signals from muscle spindle afferents and slowly adapting type II cutaneous mechanoreceptors appear to provide reasonable signals for use in this way.

- ANGEL, R. W. & MALENKA, R. C. (1982). Velocity-dependent suppression of cutaneous sensitivity during movement. *Experimental Neurology* **77**, 266–274.
- BURGESS, P. R. & CLARK, F. J. (1969). Characteristics of knee-joint receptors in the cat. *Journal of Physiology* **203**, 317–335.
- BURKE, D., GANDEVIA, S. C. & MACEFIELD G. (1988). Response to passive movement of receptors in joint, skin and muscle of the human hand. *Journal of Physiology* **402**, 347–361.
- CAPADAY, D. & COOKE, J. D. (1981). The effects of muscle vibration on the attainment of intended final position during voluntary human arm movements. *Experimental Brain Research* **42**, 228–230.

- CHAMBERS, M. R., ANDRES, K. H., DUERING, M. V. & IGGO, A. (1972). The structure and function of the slowly adapting type II mechanoreceptor in hairy skin. *Experimental Physiology* **57**, 417–445.
- CLARK, F. J. & BURGESS, P. R. (1975). Slowly adapting receptors in the cat knee joint: can they signal joint angle? *Journal of Neurophysiology* **39**, 925–935.
- CODY, F. W. J., HARRISON, L. M. & TAYLOR, A. (1975). Analysis of activity of muscle spindles of the jaw-closing muscles during normal movements in the cat. *Journal of Physiology* **253**, 565–582.
- COOPER, S. (1961). The responses of the primary and secondary endings of muscle spindles with intact motor innervation during applied stretch. *Quarterly Journal of Experimental Physiology* **46**, 389–398.
- CORDO, P. (1990). Kinesthetic control of a multijoint movement sequence. *Journal of Neurophysiology* **63**, 161–172.
- CORDO, P., CARLTON, L., BEVAN, L., CARLTON, M. & KERR, G. K. (1993). Proprioception of movement sequences: Role of velocity and position information. *Journal of Neurophysiology* **71**, 1848–1861.
- EDIN, B. B. (1991). Finger joint movement sensitivity of non-cutaneous mechanoreceptors in the dorsal skin of the human hand. *Journal of Neurophysiology* **65**, 657–670.
- EDIN, B. B. (1992). Quantitative analysis of static strain sensitivity in human mechanoreceptors from hairy skin. *Journal of Neurophysiology* **67**, 1105–1113.
- EDIN, B. B. & ABBES, J. H. (1991). Finger movement responses of cutaneous mechanoreceptors in the dorsal skin of the human hand. *Journal of Neurophysiology* **65**, 657–670.
- EDIN, B. B. & VALLBO, Å. (1990). Dynamic response of human muscle spindle afferents to stretch. *Journal of Neurophysiology* **63**, 1297–1306.
- FERRELL, W. R. & CRASKE, B. (1992). Contribution of joint and muscle afferents to position sense at the human proximal interphalangeal joint. *Experimental Physiology* **77**, 331–342.
- FERRELL, W. R., GANDEVIA, S. C. & McCLOSKEY, D. I. (1987). The role of joint receptors in human kinaesthesia when intramuscular receptors cannot contribute. *Journal of Physiology* **386**, 63–71.
- FERRELL, W. R. & SMITH, A. (1988). Position sense at the proximal interphalangeal joint of the human index finger. *Journal of Physiology* **399**, 49–61.
- GANDEVIA, S. C. (1985). Illusory movements produced by electrical stimulation of low-threshold muscle afferents from the hand. *Brain* **108**, 965–981.
- GANDEVIA, S. C. & BURKE, D. (1992). Does the nervous system depend on kinesthetic information to control natural limb movements? *Behavioral and Brain Sciences* **15**, 614–632.
- GANDEVIA, S. C., McCLOSKEY, D. I. & BURKE, D. (1992). Kinaesthetic signals and muscle contraction. *Trends in Neurosciences* **15**, 61–65.
- GOODWIN, G. M., McCLOSKEY, D. I. & MATTHEWS, P. B. C. (1972). The contribution of muscle afferents to kinaesthesia shown by vibration induced illusions of movement and by the effects of paralyzing joint afferents. *Brain* **95**, 705–748.
- GRILL, S. E., HALLETT, M., MARCUS, C. & McSHANE, L. (1994). Disturbances of kinaesthesia in patients with cerebellar disorders. *Brain* **117**, 1433–1447.
- HASAN, Z. & STUART, D. G. (1984). Mammalian muscle receptors. In *Handbook of the Spinal Cord*, vol. 3, ed. DAVIDOFF, R. A., pp. 559–607. Marcel Dekker, New York.
- HOUK, J. C., RYMER, W. Z. & CRAGO, P. E. (1981). Dependence of dynamic response of spindle receptors on muscle length and velocity. *Journal of Neurophysiology* **46**, 143–166.

- HULLIGER, M., NORDH, E., THELIN, A.-E. & VALLBO, Å. B. (1979). The response of afferent fibres from the glabrous skin of the hand during voluntary finger movements in man. *Journal of Physiology* **291**, 233–249.
- JANSEN, J. K. S. & MATTHEWS, P. B. C. (1962). The central control of the dynamic response of muscle spindle receptors. *Journal of Physiology* **161**, 357–378.
- KNIBESTÖL, M. & VALLBO, Å. (1970). Single-unit analysis of mechanoreceptor activity from the human glabrous hand. *Acta Physiologica Scandinavica* **80**, 178–195.
- LENNERSTRAND, G. (1968). Position and velocity sensitivity of muscle spindles in the cat. I. Primary and secondary endings deprived of fusimotor activation. *Acta Physiologica Scandinavica* **73**, 281–299.
- MATTHEWS, P. B. C. (1963). The response of de-efferented muscle spindle receptors to stretching at different velocities. *Journal of Physiology* **168**, 660–678.
- MATTHEWS, P. B. C. (1981). Evolving views of the internal operation and functional role of the muscle spindle. *Journal of Physiology* **321**, 1–30.
- MATTHEWS, P. B. C. & STEIN, R. B. (1969). The regularity of primary and secondary muscle spindle afferent discharges. *Journal of Physiology* **202**, 59–82.
- MILNE, R. J., ANISS, A. M., KAY, N. E. & GANDEVIA, S. C. (1988). Reduction in perceived intensity of cutaneous stimuli during movement: a quantitative study. *Experimental Brain Research* **70**, 569–576.
- MOBERG, E. (1983). The role of cutaneous afferents in position sense, kinesthesia, and motor function of the hand. *Brain* **106**, 1–19.
- PROCHAZKA, A. (1989). Sensorimotor gain control: A basic strategy of motor systems? *Progress in Neurobiology* **33**, 281–307.
- RACK, P. M. H. & WESTBURY, D. R. (1984). Elastic properties of the cat soleus tendon and their functional importance. *Journal of Physiology* **347**, 479–495.
- SAINBURG, R. L., POIZNER, H. & GHEZ, C. (1993). Loss of proprioception produces deficits in interjoint coordination. *Journal of Neurophysiology* **70**, 2136–2147.
- SANES, J. N. & JENNINGS, V. A. (1984). Centrally programmed patterns of muscle activity in voluntary motor behavior of humans. *Experimental Brain Research* **54**, 23–32.
- SCHAFFER, S. S. (1973). The characteristic curves of the dynamic response of primary muscle spindle endings in the absence and presence of stimulation of fusimotor fibres. *Brain Research* **59**, 395–399.
- SITTIG, A. C., DENIER VAN DER GON, J. J. & GIELEN, C. C. A. M. (1987). The contribution of afferent information on position and velocity to the control of slow and fast human forearm movements. *Experimental Brain Research* **67**, 33–40.
- WADMAN, W. J., DENIER VAN DER GON, J. J., GEUZE, R. H. & MOL, C. R. (1979). Control of fast goal-directed arm movements. *Journal of Human Movement Studies* **5**, 3–17.

### Acknowledgements

The authors are grateful to Drs W. Zev Rymer and Steve Massaquoi for constructive comments on the manuscript and to B. J. Hesse for skillful editing.

Received 18 October 1994; accepted 31 May 1995.