Journal of Physiology (1992), **457**, *pp.* 503–513
With 6 *figures*
Printed in Great Britain

DETECTION OF SLOW MOVEMENTS IMPOSED AT THE ELBOW DURING ACTIVE FLEXION IN MAN

BY JANET L. TAYLOR AND D. I. McCLOSKEY

From the Prince of Wales Medical Research Institute, School of Physiology and Pharmacology, University of New South Wales, PO Box 1, Kensington, Sydney 2033, Australia

(*Received 29 May 1991*)

SUMMARY

1. Subjects' ability to detect movements imposed at the elbow during active flexion was measured. Movements of three different angular velocities (0·04, 0·4 and 4·4 deg/s) were applied to the arm while subjects maintained one of two force levels of active flexion. The threshold magnitudes for detection of the direction of imposed movement were found.

2. All thresholds were very small. At the lowest velocity of movement the average threshold was 0·13 deg and no subject had a threshold of greater than 0·3 deg. This contrasts with thresholds of over 2 deg measured in a previous study when the muscles about the joint were relaxed. Thresholds decreased further with increasing velocity of movement.

3. No difference was found between the two levels of contraction of the elbow flexors. However, extension (stretch of the contracting muscle) and flexion thresholds were calculated separately, and smaller extensions than flexions could be detected.

4. These findings indicate that conscious detection of imposed movements is greatly enhanced during active muscle contraction. Movements which cause unloading of the contracting agonist, as well as movements which result in stretch, are more easily detected than when the muscle is contracting. The discussion focuses on possible mechanisms for this enhancement.

INTRODUCTION

Detection of passive movements about a joint can be used as a measure of proprioceptive acuity in human subjects (Goldscheider, 1889; Laidlaw & Hamilton, 1937; Cleghorn & Darcus, 1952; Gandevia & McCloskey, 1976; Hall & McCloskey, 1983). The magnitude of the movement that can be detected varies with the velocity of the imposed movement and with the joint being tested (Hall & McCloskey, 1983). The ability to detect movements depends on a combination of input from muscle, joint and cutaneous receptors (Gandevia, Hall, McCloskey & Potter, 1983) although the contributions of these may vary from joint to joint.

In general, passive movements have been imposed on a relaxed limb. However, Gandevia & McCloskey (1976) observed that tensing the flexors of the distal interphalangeal joint of the middle finger led to an improvement in subjects' ability to detect passive movements of the joint. The test was performed while the finger was anaesthetized so that only muscle input was available, and in some subjects tensing the muscles completely compensated for the loss of acuity resulting from the exclusion of joint and skin input. In addition, Colebatch & McCloskey (1987) reported that slow movements of the elbow, imposed during a maintained flexor contraction could be detected at a magnitude one-tenth of that previously reported for the relaxed arm (Hall & McCloskey, 1983).

When an arm has been actively positioned its location can be more accurately indicated, using another part of the body, than when it has been passively positioned (Paillard & Brouchon, 1968), and a recent study suggests that a difference of 0·075 mm in distance between the pads of the finger and thumb can be detected with active control of the fingers (John, Goodwin & Darian-Smith, 1989), whereas the threshold passive displacement that can be detected at the distal interphalangeal joint is 0·3 mm at an angular velocity of 40 mm/s (Hall & McCloskey, 1983).

These studies suggest that proprioceptive acuity at a joint is very much improved by active contraction of the muscles operating the joint. The present study examined proprioceptive acuity at the elbow, as measured by subjects' ability to detect imposed movements, at two levels of contraction of the elbow flexors and over a range of velocities.

METHODS

Five normal volunteer subjects, students and staff of the University of New South Wales, including one of the authors (D.I.McC.), took part in experiments to determine thresholds for the detection of the direction of passive movements of the elbow during active contraction of the elbow flexors. All experiments described were conducted with the informed consent of the subjects and with the approval of the University's Ethical Committee.

Set-up

Subjects sat at a bench with the right arm held in the horizontal plane in front of them, with the elbow bent to 90 deg and the radial border of the forearm uppermost. A support fixed the upper arm in place. The forearm was supported against gravity but was free to move horizontally. The elbow was left free from 5 cm above, to more than 10 cm below the joint. A firmly fitting metal cuff was worn around the distal forearm. A pin joint linked the cuff to an electromagnetic vibrator (Fig. 1). A ramp movement of the vibrator shaft moved the arm toward or away from the body, flexing or extending the elbow. A force transducer mounted on the vibrator signalled the force between the arm and the vibrator, and a position transducer signalled movement of the forearm. Both signals were amplified and displayed on the screen of a storage oscilloscope. Force was also displayed on an oscilloscope and could be seen by the subject when the experimenters elected to display it. A screen prevented subjects seeing the arm.

Experimental protocol

Each subject performed six sets of sixty to sixty-five trials over three experimental sessions of 2 to 2½ hours each. For each trial, subjects first contracted the flexors of the elbow isometrically until the force signal matched a designated target level. This target force, either 4·9 or 19·6 N, was constant in any set of trials. The display of the force signal was then turned off while the subject continued to hold the same force. After several seconds, a flexion or extension of the elbow was imposed by the electromagnetic vibrator. Three velocities of movement of the vibrator were used, 0·2, 2 or 20 mm/s, so that each subject performed a set of trials of each velocity, at both initial loads. Because subjects had slightly different arm lengths from the elbow to the point of attachment of the vibrator shaft (between 25 and 26·5 cm), angular velocity varied slightly between subjects. Average velocities were 0·04, 0·44 and 4·4 deg/s. The magnitudes of the imposed flexions and extensions were varied within each set of trials.

Subjects were instructed to indicate the direction of the imposed movement as soon as they were sure they could do so correctly. The indication they gave was a prompt increase in flexor force if the movement was a flexion of the elbow, or a decrease in force if the movement was an extension. Subjects were allowed 4 s in which to respond after the completion of a movement, before the vibrator reset and returned the arm to the initial position. However, for some large, slow movements subjects responded before the movement was completed. The magnitudes of the imposed movements were chosen so that correct detection of the direction of the movement could be made for about half the trials in a set. When the direction of a movement was not correctly detected subjects generally made no response, as the instruction 'not to guess' was emphasized. Subjects made the wrong response for fewer than one in twenty trials. These were scored with those for which no response was made as incorrectly detected trials.

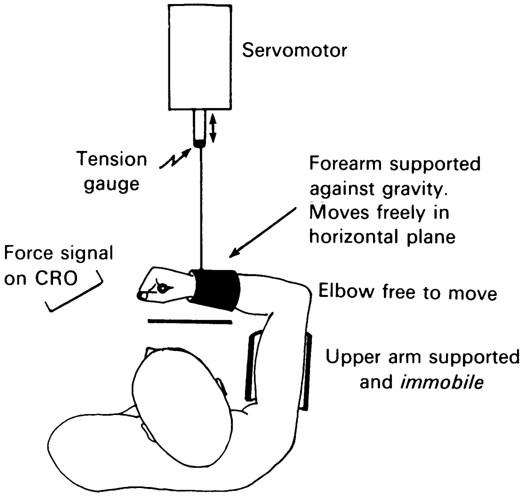

Fig. 1. This is a diagrammatic representation of the experimental set-up. Subjects flex the elbow until the force signal reaches a target on the oscilloscope screen (CRO). After a variable delay, movement of the servomotor then flexes or extends the elbow.

After each trial, the change in position and force measured at the wrist, from the beginning of the imposed movement, either to the end of the movement or, for detections made before the displacements were complete, to the time of detection of the movement, were recorded from the oscilloscope screen. Within each set of trials for each subject the smallest movements were not detected, whereas the largest movements were detected. Between the extremes, there was a cross-over region in which the direction of movements was sometimes correctly detected and sometimes not. Figure 2 shows individual trials in a plot of position against velocity for one subject. The trials here were performed with a 4·9 N initial flexor load. Open circles are correctly detected movements and filled triangles are movements not detected or not detected correctly. Flexion and extension movements are shown on separate graphs. At each velocity there is an overlap between the correctly and the undetected/incorrectly detected trials. A 'threshold' magnitude for the detection of the direction of an imposed movement can be derived from the trials which fall within this cross-over region. For each set of trials, for each subject, the mean of the correctly detected trials from the cross-over was found, as was the mean of undetected/incorrectly detected trials. The average of these means was taken as the threshold magnitude (Taylor & McCloskey, 1988). The thresholds calculated for the subject in Fig. 2 are marked by filled squares.

An ischaemic block of the distal forearm and hand was performed on one subject and the determination of threshold magnitudes for the detection of flexion and extension of the elbow at one velocity (2 mm/s) and one initial load (4·9 N) were repeated. The anaesthesia of the distal forearm ensured that any changes in pressure at the wrist, where the perturbations were applied, could not be used as a clue to the movements imposed in this experiment. Because of the time constraints imposed by the duration for which the ischaemic block could reasonably be maintained, sixteen trials (rather than thirty) were used to define each of the thresholds, and a single velocity and initial load were tested.

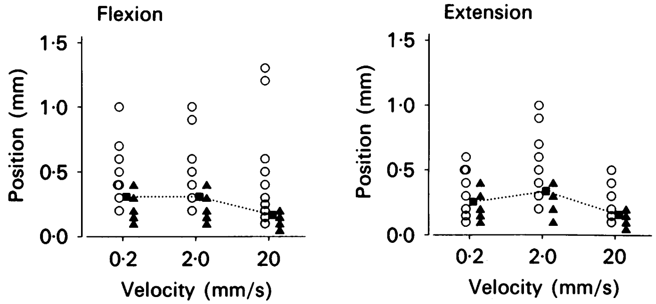

Fig. 2. Flexion and extension movements were imposed at the wrist to move the arm about the elbow. The two graphs are a summary of one subject's responses with an exerted force of 4·9 N. Change in position at the wrist is plotted against velocity for each trial. ○, correctly detected perturbations; ▲, perturbations that were not correctly detected. Trials are displaced slightly in velocity, for illustration only. A 'threshold' for detection was calculated for each velocity and direction of imposed movement. ■, thresholds.

RESULTS

The thresholds for the detection of the direction of passive movements about the elbow, during active contraction of the elbow flexors, were determined for three velocities of movement and two initial loads. For each condition, a threshold for the detection of flexion and a threshold for the detection of extension were measured as millimetres of movement at the wrist. These threshold magnitudes were then converted to angular movements of the elbow for further statistical analysis. In all the conditions, subjects could detect the direction of very small movements during active contraction.

All the thresholds calculated for individual subjects are shown in Fig. 3. Even at the slowest velocity ($< 0{\cdot}05$ deg/s), no subject had a threshold for detection of flexion or extension of more than 0·3 deg, and only one subject had thresholds of more than 0·2 deg. At higher velocities of movement, thresholds were even lower. An analysis of variance on the data showed a significant difference between thresholds at different velocities ($P < 0{\cdot}001$) and a Student–Newman–Keuls test revealed that thresholds for detection of 4·4 deg/s (20 mm/s) movements were less than for 0·44 deg/s (2 mm/s) movements ($P < 0{\cdot}05$) which were less than for 0·04 deg/s (0·2 mm/s) movements ($P < 0{\cdot}01$).

The thresholds found for one subject during anaesthesia of the distal forearm and hand are shown as asterisks in Fig. 3. Thresholds for the same subject without ischaemic block are represented by triangles (△, ▲). When cutaneous pressure clues were possible, the threshold for detection of extension of the elbow for movements of 0·44 deg/s was 0·08 deg. This was unchanged by the exclusion of any possible detectable changes in pressure. For detection of flexion, the corresponding thresholds were 0·09 deg without anaesthesia and 0·07 deg with anaesthesia. The close correspondence between these thresholds makes it unlikely that the subject was using skin pressure changes at the wrist to detect imposed movements.

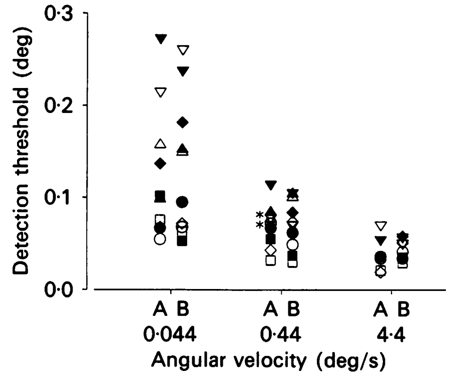

Fig. 3. Five subjects' thresholds for detection of the direction of imposed movement are shown as degrees of elbow movement at each of three angular velocities. Each subject is represented by a different symbol. Filled symbols are subjects' thresholds for detection of flexion (shortening of the contracting muscle) and open symbols for detection of extension. At each velocity, thresholds were found for an initial exerted force at the wrist of 4·9 N (A) and of 19·6 N (B). For one subject (△, ▲) thresholds for extension and flexion of 0·44 deg/s and 4·9 N initial load were also determined during an ischaemic block of the distal forearm. These thresholds during ischaemia are shown in the figure as asterisks.

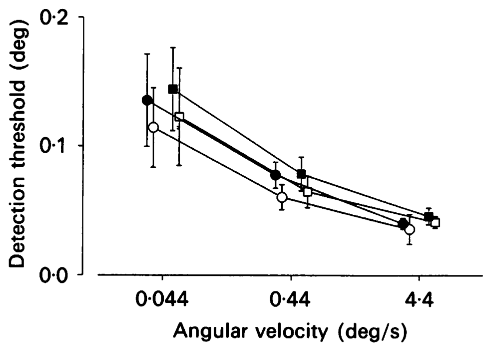

Fig. 4. The means (±s.e.m.) of five subjects' thresholds for detection of extension and flexion are shown for two levels of exerted force. Four detection thresholds (in degrees of elbow movement) are shown at each angular velocity. For illustration, points are offset from the marked angular velocities and are joined by lines between velocities. Circles represent detection thresholds measured with an initial force of 4·9 N at the wrist. Squares show thresholds for 19·6 N. Filled symbols represent flexion and open symbols, extension.

The means (±s.e.m.) of the thresholds of the five subjects are shown in Fig. 4. At each velocity, thresholds for flexion and extension at each of the initial loads is shown. There was no significant difference between thresholds at 4·9 and at 19·6 N load (paired *t* test). However, comparison of extension and flexion thresholds (paired *t* test) reveals that thresholds for extension, stretching the contracting muscle, are lower than for flexion ($P < 0{\cdot}02$). The error bars in this figure provide an indication of the considerable variability between subjects at low angular velocities.

Although all results have been given here in terms of the change of position imposed on the arm, it is not possible to impose a movement on the arm when it is actively maintaining a load, without also causing a change in force. It is possible that, rather than detecting the direction of the imposed movements by detecting a change in position, subjects might detect this change in force. Thus, for each trial, both the position change and the force change that occurred with each movement were recorded. Figure 5 is a plot of force against position for individual trials for one subject. All were made at an initial load of 4·9 N. The same trials are shown in the position *vs.* velocity plot of Fig. 2. It is apparent that at some velocities of movement, a force detection threshold could have been calculated as easily as a position detection threshold. The change in force and change in position were closely related. However, at slower velocities, movements were sometimes correctly detected when the force change was zero or even negative. The direction of these trials could not have been identified through force changes, and therefore at least some of the trials must have been correctly identified through detection of position changes alone. The presence of such trials made it impossible to calculate a force to match the position threshold.

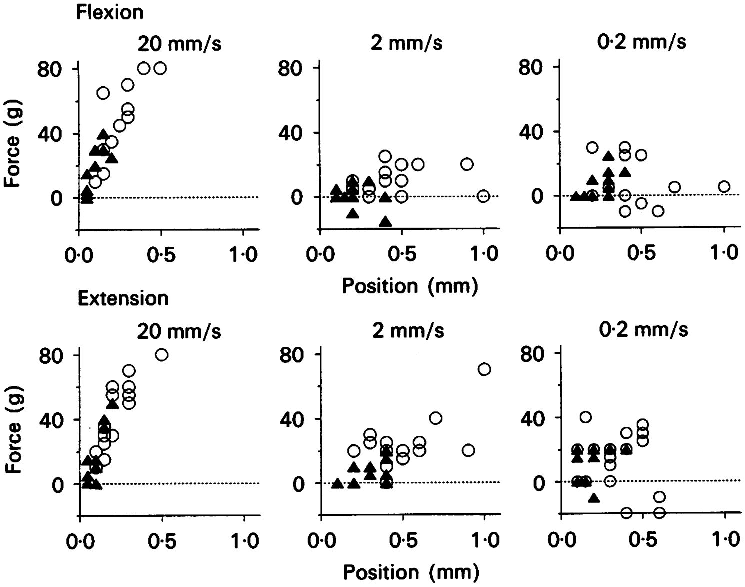

Fig. 5. A set of one subject's trials at 4·9 N initial force are shown. Flexion and extension movements of three different velocities were imposed at the elbow. Each velocity, for each direction, is illustrated separately. As well as a change of position, perturbations also resulted in a change of force. Change of force in each trial is plotted here against change of position. Trials that were correctly detected are represented by open circles, and those that were not correctly detected, by filled triangles. Some symbols represent more than one trial in which identical perturbations were applied.

DISCUSSION

The magnitude of passive movements of the elbow detected during active contraction of the flexors is very small compared to movements that can be detected when imposed on the relaxed arm. Using figures on changes in muscle fascicle length with joint rotation from Hall & McCloskey (1983), the thresholds reported here can be expressed in terms of millimetres of stretch of muscle fascicles. They are 0·07 mm at 0·02 mm/s, 0·035 mm at 0·24 mm/s and 0·02 mm at 2·4 mm/s. Threshold magnitudes found in the present study can be compared with the results that Hall & McCloskey (1983) found for movements of the relaxed arm (Fig. 6). Although the 70% detection levels for the relaxed arm are compared with the 'thresholds' obtained here (see Methods) for the arm with contracting elbow flexors, it is clear that active muscle contraction improves detection of imposed movements. In a different, but related study (Colebatch & McCloskey, 1987), a threshold for detection at an angular velocity of 0·6 deg/s was noted during active muscle contraction. This is also shown in Fig. 6 and agrees well with the present results.

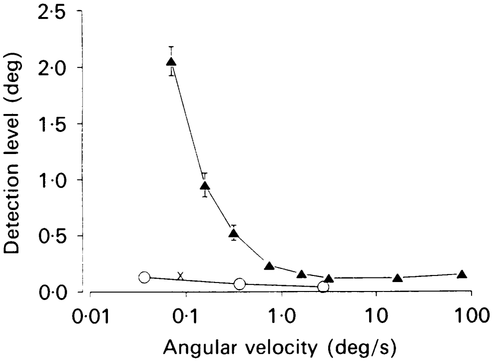

Fig. 6. This is a graph of detection thresholds for movements of the elbow over a range of angular velocities. ○, mean thresholds found in the present study. Error bars fall within the symbols. ▲, thresholds found for the relaxed arm (70% detection levels from Hall & McCloskey, 1983). ×, a threshold for detection with active flexion of the elbow (Colebatch & McCloskey, 1987).

Signals arising from cutaneous, joint and muscle receptors can all contribute to kinaesthesia (McCloskey, 1978; Matthews, 1987). However, the functional importance of each input may vary from joint to joint. In this study at the elbow, it is likely that muscle receptors are the most important sources of proprioceptive information. Cutaneous receptors around the joint are unaffected by muscle contraction so that the improved proprioceptive acuity described here cannot be attributed to an increase in their sensitivity. In addition, it has been demonstrated at the knee that anaesthesia of skin receptors does not impair detection of passive movements (Clark, Horch, Bach & Larson, 1979). Changes in pressure of the cuff through which perturbations were applied at the wrist may have provided clues to movement. However, the tight fit of the cuff means that the changes were small compared to the constant pressure and were spread over a wide band. In our experience, the clues provided through cutaneous receptors by perturbations of the magnitude used here are sometimes sufficient to signal that a perturbation has occurred, but do not indicate its direction, as was required in the tests performed here, and as would be expected of a system able to provide true proprioceptive signals. Furthermore, when the distal forearm was anaesthetized to prevent such pressure clues, detection of perturbations was not impaired. This suggests that cutaneous clues from the experimental apparatus were not necessary for the detection of imposed movement.

A contribution from joint receptors cannot be ruled out. Although it is generally agreed that joint receptor firing is greatest at the extremes of range of movement, some receptors have mid-range changes in discharge that relate to joint angle and more fire phasically with movement (Proske, Schaible & Schmidt, 1988). However, Baxendale & Ferrell (1983) have reported no effect of increased muscle tone on mid-range discharge in afferents from the cat elbow. Furthermore, Gandevia & McCloskey (1976) showed that tensing the muscles operating the distal interphalangeal joint improved proprioceptive acuity during a digital nerve block. Thus, even when no joint or cutaneous signals are available, muscle contraction improves proprioceptive sensibility.

It is possible that subjects used the force changes associated with the imposed movements to detect direction in some of the trials. Although Golgi tendon organs have high thresholds to passive stretch, their thresholds to active muscle contraction are low (as low as 5–10 mg) and their sensitivity to force changes during contraction is high (Houk & Henneman, 1967; Binder, Kroin, Moore & Stuart, 1977). However, in some trials, particularly with low velocity movements, the direction of movements was correctly detected despite being accompanied by positive, negative or zero force changes. Therefore, on these trials at least, position, or change of position, rather than force was the variable monitored.

It seems likely that subjects used signals from muscle spindles to detect the movements imposed on the arm in this study, but the means by which active contraction of the flexors improved detection of both flexion and extension are not clear. There are several possible mechanisms that could lower the detection threshold for movement: contraction may alter the biomechanics of the muscle and tendon and cause more of the perturbation to be related to the spindle; sensitivity of individual spindles may be increased; firing of the population of spindles may be enhanced; transmission of kinaesthetic afferent signals to the cortex may be improved.

The length changes in muscle with a given stretch will depend on the relative stiffness of muscle and tendon, and supporting a load can increase the stiffness of both. Thus, although a low level of contraction may improve the transmission of a perturbation to the muscle by eliminating tendon slack (Rack & Ross, 1984), increasing contraction strength may well decrease the muscle fibre movement seen by the muscle spindles (Prochazka & Trend, 1986; Fellows & Rack, 1987; Hoffer, Caputi, Pose & Griffiths, 1989). At the elbow, the number of synergists used in active flexion and their short tendon length (especially of brachialis) means that the connection between bone and muscle is quite stiff before tension is applied, and so most of an imposed perturbation can probably be assumed to be already relayed to the muscle, particularly at the relatively slow velocities employed here. Furthermore, the initial position used in this study and in that of Hall & McCloskey (1983) was mid-range where there is no tendon laxity even with relaxed muscle. Therefore, biomechanical factors are unlikely to play a large part in the improvement of detection of movement seen here. Thresholds for detection of the imposed movement did not change when the initial load was increased from 4·9 to 19·6 N. This indicates that the changes in stiffness of the tendon and muscle resulting from this fourfold increase in tension were not functionally significant.

Muscle contraction increases the resting discharge rate of spindle afferents and recruits afferents that were not previously firing (Burke, Hagbarth & Skuse, 1978; Vallbo, Hulliger & Nordh, 1981). It thus increases the possible range for modulation of discharge of individual spindles and of the population. The increase in discharge is almost certainly due to fusimotor discharge accompanying the contraction. At short to medium muscle lengths, dynamic fusimotor activity can increase the sensitivity of the Ia ending to small stretches (Goodwin, Hulliger & Matthews, 1975; Hulliger, Matthews & Noth, 1977*a*; Hulliger, 1987), but concurrent static fusimotor discharge acts to reduce this (Hulliger , Matthews & Noth, 1977*b*). The increase in resting discharge with contraction suggests the action of static fusimotor discharge along with any dynamic activity. Thus, it is unlikely that an increase in the responsiveness of individual spindles accounts for the decrease in the threshold magnitude for detection of movements seen here. Some recordings from human spindle afferents have shown increased responses to load and position changes during contractions and high sensitivity to very small disturbances during isometric contractions and slow movements, but others have reported a diminished response (see Vallbo *et al.* 1981).

In relaxed human muscle, few spindles have a resting discharge (less than 10% in the forearm when the hand is in a position of rest). However, with an isometric contraction of as little as 5–10% of maximum, 60–70% of spindles are active (see Burke, 1981). Although the response to stretch of individual active spindles may be similar in relaxed and contracting muscle, the aggregate of the firing of the muscle's investment of spindles will be greater when the muscle is contracting, and this may account for the lower detection thresholds seen here. This is, in some ways, a contrast with the position response of the muscle during passive stretch. There, increased overall discharge, through increased firing rate and increased number of active afferents, corresponds to length change of the muscle and not to increased sensitivity to position changes (Burgess, Clark, Simon & Wei, 1982).

Comparison between thresholds for the detection of extension (stretch) and for the detection of flexion (shortening) show a small but significant difference (Fig. 5). Subjects can detect smaller extensions than flexions of the elbow, but even the detection of flexion is much improved over that for the relaxed arm. In relaxed muscle, the low resting discharge of muscle spindles means that, although spindle afferents can increase discharge in response to stretch, they cannot decrease firing with shortening. Detection of movement in both directions about a joint is therefore likely to involve both agonists and antagonists with the spindles in each muscle responding to stretch (Burgess *et al.* 1982). With a contracting muscle, there is a significant resting discharge in spindle afferents, therefore, shortening can cause a significant decrease in firing. Thus, in this study, both stretch (extension) and shortening (flexion) could have been signalled through receptors associated with the contracting muscle. The difference in thresholds between flexion and extension movements could be explained by the asymmetry of the spindle response to shortening and stretch. However, the decrease with increased velocity of movement of the detection threshold for flexion means that the unloading response of the flexors would need to be graded with velocity of unloading.

Contraction-associated improvement in transmission of afferent signals cannot be excluded. Facilitation of kinaesthetic afferents by pyramidal tract stimulation has been demonstrated in the thalamus in cats (Tsumoto, Nakamura & Iwama, 1975), whereas gating of somatosensory afferents during active movements is known to inhibit their effect at the cortex (Rushton, Rothwell & Craggs, 1981; Tapia, Cohen & Starr, 1987). An increase in signals reaching the cortex from both agonist and antagonist muscle would allow improved detection of both extension and flexion of the elbow.

This work was supported by the National Health and Medical Research Council of Australia. We thank Professors D. Burke and S. Gandevia for their comments on the manuscript.

REFERENCES

BAXENDALE, R. H. & FERRELL, W. R. (1983). Discharge characteristics of the elbow joint nerve of the cat. *Brain Research* **261**, 195–203.

BINDER, M. D., KROIN, J. S., MOORE, G. P. & STUART, D. G. (1977). The response of Golgi tendon organs to single motor unit contractions. *Journal of Physiology* **271**, 337–349.

BURGESS, P. R., CLARK, F. J., SIMON, J. & WEI, J. Y. (1982). Signaling of kinesthetic information by peripheral sensory receptors. *Annual Review of Neuroscience* **5**, 171–187.

BURKE, D. (1981). The activity of human muscle spindle endings in normal motor behavior. In *International Review of Physiology*, vol. 25, *Neurophysiology IV*, ed. PORTER, R., pp. 91–125. University Park Press, Baltimore, MD, USA.

BURKE, D., HAGBARTH, K.-E. & SKUSE, N. F. (1978). Recruitment order of human spindle endings in isometric voluntary contractions. *Journal of Physiology* **285**, 101–112.

CLARK, F. J., HORCH, K. W., BACH, S. M. & LARSON, G. F. (1979). Contributions of cutaneous and joint receptors to static knee-position sense in man. *Journal of Neurophysiology* **42**, 877–888.

CLEGHORN, T. E. & DARCUS, H. D. (1952). The sensibility to passive movement of the human elbow joint. *Quarterly Journal of Experimental Psychology* **4**, 66–77.

COLEBATCH, J. G. & McCLOSKEY, D. I. (1987). Maintenance of constant arm position or force: reflex and volitional components in man. *Journal of Physiology* **386**, 247–261.

EMONET-DENAND, F., LAPORTE, Y., MATTHEWS, P. B. C. & PETIT, J. (1977). On the subdivision of static and dynamic fusimotor actions on the primary ending of the cat muscle spindle. *Journal of Physiology* **208**, 827–861.

FELLOWS, S. J. & RACK, P. M. H. (1987). Changes in the length of the human biceps brachii muscle during elbow movements. *Journal of Physiology* **383**, 405–412.

GANDEVIA, S. C., HALL, L. A., McCLOSKEY, D. I. & POTTER, E. K. (1983). Proprioceptive sensation at the terminal joint of the middle finger. *Journal of Physiology* **335**, 507–517.

GANDEVIA, S. C. & McCLOSKEY, D. I. (1976). Joint sense, muscle sense, and their combination as position sense, measured at the distal interphalangeal joint of the middle finger. *Journal of Physiology* **260**, 387–407.

GOLDSCHEIDER, A. (1889). Untersuchungen uber den Muskelsinn. *Archiv für Anatomie und Physiologie* **3**, 369–502.

GOODWIN, G. M., HULLIGER, M. & MATTHEWS, P. B. C. (1975). The effects of fusimotor stimulation during small amplitude stretching on the frequency-response of the primary ending of the mammalian muscle spindle. *Journal of Physiology* **253**, 175–206.

HALL, L. A. & McCLOSKEY, D. I. (1983). Detections of movements imposed on finger, elbow and shoulder joints. *Journal of Physiology* **335**, 519–533.

HOFFER, J. A., CAPUTI, A. A., POSE, I. E. & GRIFFITHS, R. I. (1989). Roles of muscle activity and load on the relationship between muscle spindle length and whole muscle length in the freely walking cat. In *Progress in Brain Research*, vol. 80, ed. ALLUM, J. H. J. & HULLIGER, M., pp. 75–86. Elsevier Science Publishers, Amsterdam, New York, Oxford.

HOUK, J. C. & HENNEMAN, E. (1967). Responses of Golgi tendon organs to active contractions of the soleus muscle of the cat. *Journal of Neurophysiology* **30**, 466–481.

HULLIGER, M. (1987). The role of muscle spindle receptors and fusimotor neurones in the control of movement. In *The London Symposia* (*EEG Supplement 39*), ed. ELLINGSON, R. L., MURRAY, N. M. F. & HALLIDAY, A. M., pp. 58–66. Elsevier Science Publishers (Biomedical Division), Amsterdam, New York, Oxford.

HULLIGER, M., MATTHEWS, P. B. C. & NOTH, J. (1977*a*). Static and dynamic fusimotor stimulation on the response of Ia fibres to low frequency sinusoidal stretching of widely ranging amplitudes. *Journal of Physiology* **267**, 811–838.

HULLIGER, M., MATTHEWS, P. B. C. & NOTH, J. (1977*b*). Effects of combining static and dynamic fusimotor stimulation on the response of the muscle spindle primary ending to sinusoidal stretching. *Journal of Physiology* **267**, 839–856.

JOHN, K. T., GOODWIN, A. W. & DARIAN-SMITH, I. (1989). Tactile discrimination of thickness. *Experimental Brain Research* **78**, 62–68.

LAIDLAW, R. W. & HAMILTON, M. A. (1937). A study of thresholds in apperception of passive movement among normal control subjects. *Bulletin of the Neurological Institute of New York* **6**, 268–273.

MCCLOSKEY, D. I. (1978). Kinesthetic sensibility. *Physiological Reviews* **58**, 763–814.

MATTHEWS, P. B. C. (1987). Proprioceptors and their contribution to somatosensory mapping: complex messages require complex processing. *Canadian Journal of Physiology and Pharmacology* **66**, 430–438.

PAILLARD, J. & BROUCHON, M. (1968). Active and passive movements in the calibration of position sense. In *The Neuropsychology of Spatially Oriented Behavior*, ed. FREEDMAN, S. J., pp. 37–55. Dorsey Press, Homewood, IL, USA.

PROCHAZKA, A. & TREND, P. (1986). X-ray imaging of human muscle contraction. *Journal of Physiology* **377**, 15*P*.

PROSKE, U., SCHAIBLE, H.-G. & SCHMIDT, R. F. (1988). Joint receptors and kinaesthesia. *Experimental Brain Research* **72**, 219–224.

RACK, P. M. H. & ROSS, H. F. (1984). The tendon of flexor pollicis longus: its effects on the muscular control of force and position at the human thumb. *Journal of Physiology* **351**, 99–110.

RUSHTON, D. N., ROTHWELL, J. C. & CRAGGS, M. D. (1981). Gating of somatosensory evoked potentials during different kinds of movement in man. *Brain* **104**, 465–491.

TAPIA, M. C., COHEN, L. G. & STARR, A. (1987). Selectivity of attenuation (i.e., gating) of somatosensory potentials during voluntary movement in humans. *Electroencephalography and Clinical Neurophysiology* **68**, 226–230.

TAYLOR, J. L. & MCCLOSKEY, D. I. (1988). Proprioception in the neck. *Experimental Brain Research* **70**, 351–360.

TSUMOTO, T., NAKAMURA, S. & IWAMA, K. (1975). Pyramidal tract control over cutaneous and kinesthetic sensory transmission in the cat thalamus. *Experimental Brain Research* **22**, 281–294.

VALLBO, A. B., HULLIGER, M. & NORDH, E. (1981). Do spindle afferents monitor joint position in man? A study with active position holding. *Brain Research* **204**, 209–213.