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MAINTENANCE OF CONSTANT ARM POSITION OR FORCE: REFLEX AND VOLITIONAL COMPONENTS IN MAN

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SUMMARY

1. Normal subjects, with closed eyes, attempted to keep constant either the force exerted at the wrist or the position of the wrist against an elastic load. The load was attached to the wrist 275 mm from the axis of rotation of the elbow joint. During recording, the far end of the elastic load was displaced slowly enough that it was not immediately perceived but far enough for perception to occur before its completion.

2. The over-all relation between wrist force and position for the two conditions was approximately linear and could be described in terms of effective stiffness. The effective stiffness for the constant-position task averaged 2·8 N/mm (210 N m/rad), while for the constant-force task the mean effective stiffness was −0·028 N/mm (−2·1 N m/rad), indicative of slight over-compensation.

3. Averaging the performance at the onset of the imposed disturbance indicated that the subjects' behaviour consisted of two parts: an initial, small-range response followed by a second phase over the remainder of the displacement. The transition corresponded to the subjects' threshold for detection of the disturbance.

4. The stiffness measured for the response prior to perception was taken as a measure which included the tonic stretch reflex. The stiffness was altered appropriately for the two tasks, being lower when the subjects tried to maintain the force exerted constant (average 1·1 N/mm, 83 N m/rad) than when they attempted to keep the position constant (average 2·3 N/mm, 170 N m/rad). A small degree of co-contraction occurred but could be dissociated from the stiffness changes.

5. Scaling the results allowed comparison of the initial stiffness with values for the decerebrate cat. When analysed in this way, the values recorded in man during the constant-position task were similar to those reported for short-range stiffness in the decerebrate cat.

6. The thresholds for detection of the disturbance were much lower than those reported for subjects with relaxed muscles.

7. The stretch reflex in man has a direct role in compensating for small disturbances during motor tasks. It may also function to improve detection of applied disturbances by magnifying the corresponding force change. Once the stimulus is perceived and voluntary intervention is possible, a greater contrast is seen between the subjects' performance of the two tasks.

INTRODUCTION

The discharges of skin, joint and muscle afferents together allow subjective appreciation of kinaesthetic sensations of limb position and movement and also sensations related to achieved muscular tension (McCloskey, 1978). The role of these afferents in normal motor control is still not completely defined. Early experiments with monkeys deprived of sensory input indicated a severe deficit with virtual paralysis of the anaesthetic limb (Mott & Sherrington, 1895). More recent experiments in which the animals were encouraged to use the affected limbs have demonstrated that quite complicated movements are still possible, despite complete deafferentation (Bossom, 1974; Taub, 1976). The motor performance of humans deprived of normal sensory input by disease has been studied (Rothwell, Traub, Day, Obeso, Thomas & Marsden, 1982; Jeannerod, Michel & Prablanc, 1984; Sanes, Mauritz, Dalakas & Evarts, 1985). While quite complex movements can still be performed with the anaesthetic limbs, in practice the functional deficit is severe. One component of this deficit is the inability to maintain constant limb position or constant force.

The present study was designed to investigate the ability of normal subjects to maintain either constant position of the limb or to exert a constant force, without visual feed-back. In order to avoid the use of large perturbations which may be poorly suited to the study of physiological responses (Evarts, 1981), we used small perturbations and applied them slowly enough to require significant time before detection. The delay to conscious awareness of the perturbation has additionally allowed separate analysis of the involuntary and voluntary components of the subjects' behaviour.

Some of these results have been reported in brief form (Colebatch & McCloskey, 1984).

METHODS

Fifteen healthy males (including both the authors) were subjects in these experiments. Several were studied on more than one occasion. One subject was excluded on the basis of erratic performance. All gave informed consent to the experimental procedures.

Each subject sat with the right elbow flexed to approximately 90 deg and the wrist enclosed within a wristlet. A light handle projected from a mounting on the wristlet and was gently held by the subject. This prevented any twisting or slipping of the wristlet on the forearm. A wire, attached to a force transducer mounted on the front of the wristlet, was connected to a spring (stiffness approximately 0·5 N/mm) and thence to a position-controlled servomotor. The wire attachment on the wristlet was on average 275 mm from the elbow joint. (Throughout this paper stiffness has been expressed as N/mm. It has also been converted to N m/rad, angular stiffness, to facilitate comparison with data from other laboratories.) The compliant coupling ensured that it was possible for subjects to keep constant either the position or the force exerted at the wrist, despite movements applied to the remote end of the spring by the servomotor. An additional weak spring (0·01 N/mm) was attached between the front surface of the wristlet and a fixed force transducer and the signal used to measure the position of the wrist. Electromyographic activity (e.m.g.) was recorded over the surface of the biceps muscle and rectified and smoothed with a time constant of either 50 or 100 ms. E.m.g., the force at the wristlet, the position of the arm and the position of the servomotor were recorded on a four-channel polygraph (Fig. 1).

Before a series of trials, the subject was instructed to keep constant either the position of the forearm or the force at the wrist. The subject flexed the elbow and used an oscilloscope beam displaying the position signal to reach the required starting position. Given the elastic nature of the load, this ensured an identical initial force, 9·8 N (1 kg), because the servomotor shaft was always in the mid-position of its travel at the onset. The subject then shut his eyes and the oscilloscope beam was extinguished. The subject indicated when ready for a trial to begin and kept the eyes shut for the remainder of the trial. If there was clear drift of the arm from the visually set starting conditions during this preparatory period then no recording was made. This was uncommon. After a variable delay, the servomotor shaft was moved slowly away from or towards the subject. Typically this was 7 mm of travel in either direction as a ramp over 5 s.

The position and force at the wrist were also recorded in an $X-Y$ format on a storage oscilloscope and photographed. To study the behaviour at the onset of ramp movement, in some experiments a series of trials was collected and the position and force signals were averaged (Neurolog NL 750 with a four-channel multiplexer). For each average, eight trials were collected, four for each direction of servomotor movement, mixed with some trials in which no servomotor movement occurred.

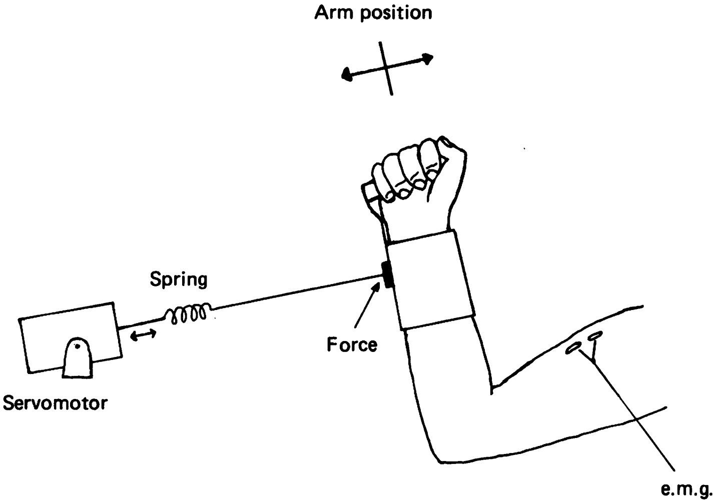

Fig. 1. Diagrammatic representation of the experimental method. A wristlet was fitted snugly to the right arm of the subjects. A force transducer mounted on the wristlet was connected by an elastic coupling to the shaft of the servomotor. Visual feed-back of forearm position was only available to the subjects prior to starting a trial to ensure constant initial conditions. During recording the subjects had to rely entirely upon proprioceptive feed-back from the arm. Subjects were required to keep constant either the force exerted at the wrist or the position of the wrist, despite movement of the servomotor shaft. Surface e.m.g. over the biceps muscle was also recorded.

Stiffness was estimated by fitting a straight line by eye to the force *versus* position data. The presence of consistent drift of the arm during the recording trials would have the effect of apparently increasing the stiffness recorded for one direction of applied perturbation while reducing it for the other. All values for stiffness were therefore calculated as the mean (S_{av}) of the stiffness recorded for the two directions of elbow displacement (S_1, S_2 respectively), weighted equally. The formula used was:

$$S_{av} = \tan[\{\tan^{-1}(S_1) + \tan^{-1}(S_2)\}/2].$$

This formula calculated the gradient from the mean of the two angles corresponding to the stiffness gradient in each direction.

RESULTS

Voluntary reponses

The full range of servomotor-induced displacement was used in studies of voluntary responses. Recordings were made from eleven subjects who attempted to keep either the position or force at the wrist constant; six did both tasks. After one or two practice trials, the subjects readily understood what was required of them. The applied perturbation was sufficiently large to be always above the threshold for detection by completion of the trial.

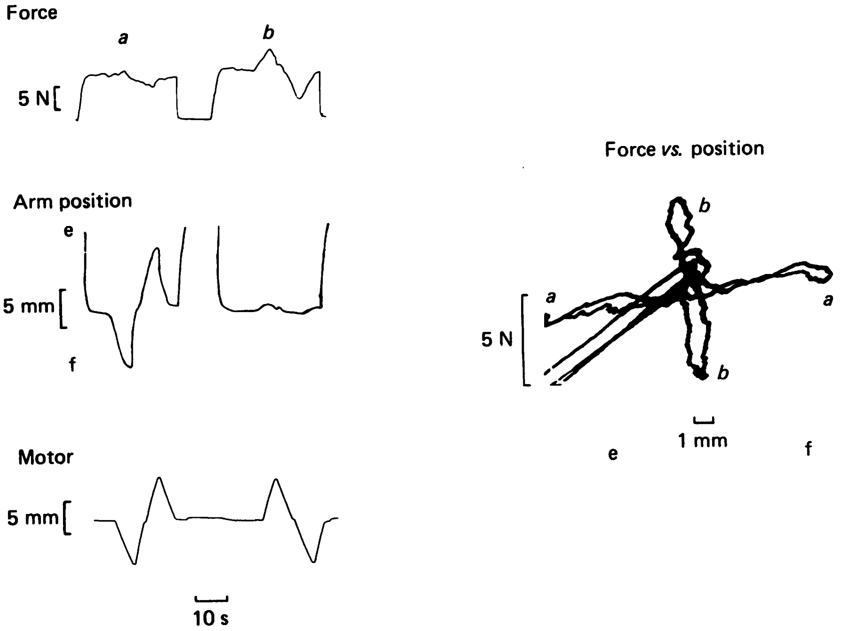

Fig. 2. Results from two consecutive trials performed by one of the authors (D. I. McC.). On the left are chart recordings of wrist force and position of both the wrist and the servomotor. On the right the force at the wrist is plotted against the position of the forearm. Trials began from the centre of this plot and the diagonal lines were made when, at the beginning, the subject flexed his arm to the starting position and when he voluntarily extended it at the end. In the first trial the subject was instructed to keep the force exerted at the wrist constant. During the trial, the subject flexed and then extended the forearm, closely matching the servomotor displacement so that there was little change in the force at the wrist. This is shown on the right as curve '*a–a*' with gradient −0·23 N/mm. The negative gradient indicates that this subject overcompensated slightly. In the second trial, the subject was instructed to keep the position of the forearm constant. In this trial, there was little alteration in the initial position despite considerable changes in force, plotted on the right as curve '*b–b*'. The gradient of this curve was 6·8 N/mm. Normally the four limbs of this relation were collected in separate trials. The letters 'e' and 'f' refer to elbow extension and flexion respectively.

The behaviour during the two tasks was quite different (Fig. 2). During attempts to keep the position of the wrist constant, the movement of the servomotor shaft caused little movement of the wrist but instead caused a large change in the force at the wrist (high effective stiffness). This was the result of the subjects voluntarily contracting or relaxing appropriately. During attempts to keep the force at the wrist constant, most of the servomotor movement was matched by the subjects' movement of their wrists so force at the wrist was altered little (low effective stiffness). The effective stiffness averaged 2·8 ± 1·5 N/mm (210 ± 110 N m/rad) (mean ± S.D.) for the eight subjects who attempted to keep wrist position constant and −0·028 ± 0·13 N/mm (−2·1 ± 9·8 N m/rad) for nine subjects who attempted to keep the force at the wrist constant. All subjects who performed both tasks showed greater effective stiffness for the position task than for the force task. The negative gradient of the effective stiffness during attempts to keep the wrist force constant indicated that subjects over-compensated for potential alterations in wrist force: thus, in response to an expected reduction in force, these subjects flexed their elbows so as to increase the force to a level greater than that present initially, and the reverse for a potential increase in force.

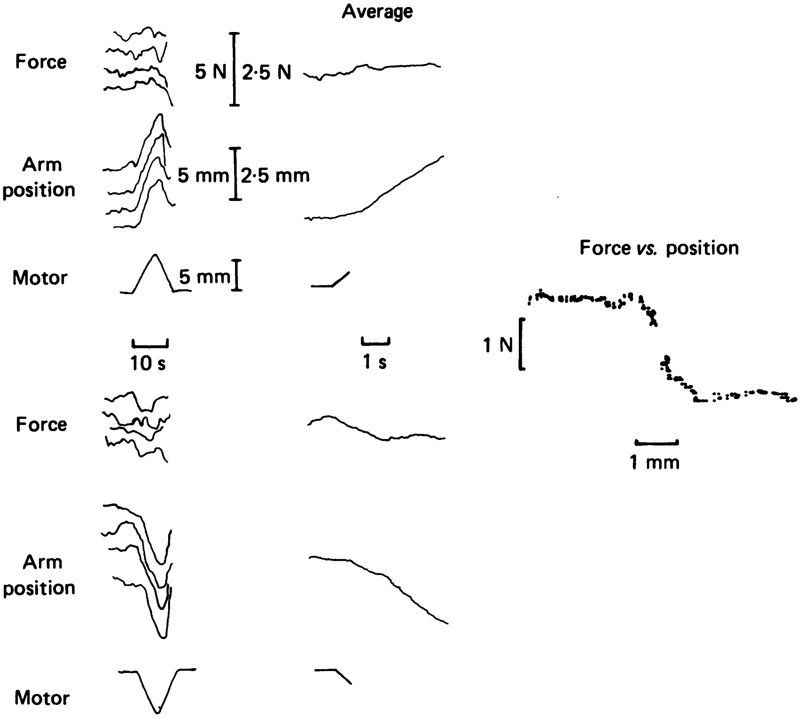

Fig. 3. A series of recordings from subject M.D. who was instructed to keep the force at his wrist constant. The Figure shows both the four pairs of individual trials and the averaged responses. On the left are the records of forearm position and force for each of the individual trials, each slightly offset for clarity. The force exerted at the wristlet changed little compared with the alterations in position. In the centre are the averaged records from these trials, from 1 s prior to the onset of servomotor movement (indicated diagrammatically below the traces) to 4 s afterwards. On the right the averages have been plotted as force at the wrist against wrist position with the two limbs of the plot separated for clarity. This subject shows the typical finding of an initial phase (stiffness 1·1 N/mm) followed by a second phase of much lower effective stiffness. The change in behaviour appeared to occur at the time of perception of the stimulus (see text).

Responses prior to detection

The perturbation was chosen to occur so slowly that it could not be detected immediately. This part of the study concentrated on events at the beginning of servomotor movement. Again, the subjects were instructed to keep constant either position or force and the applied perturbations were the same. The performances of eleven subjects were recorded; all performed both tasks. Eight trials, four for each direction of servomotor movement, were collected and averaged for each of the two conditions. Plots were made at higher gain than used in the first part of the study.

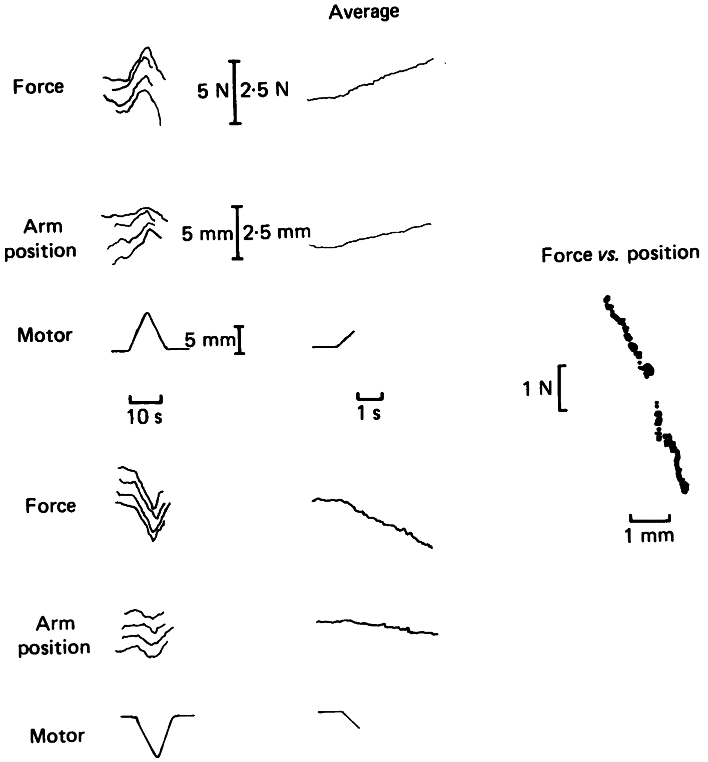

Fig. 4. A series of recordings from a subject (R.W.) instructed to keep the position of the wrist constant. Same general format as Fig. 3. The single trials show relatively little displacement of the arm, despite changes in the force at the wristlet. On the far right the averaged values of force at the wrist are plotted against wrist position. The initial stiffness is positive (here 1·8 N/mm). The contrast between the initial behaviour and the subsequent performance is less marked than for subjects performing the constant-force task.

When the subjects attempted to keep the force constant, the plot of wrist force against forearm position was divided by a distinct inflexion into two parts (Fig. 3). At the onset of the applied disturbance, the stiffness of the arm was positive. This then changed abruptly to the lower stiffness characteristic of the subject's previous over-all behaviour. The average stiffness for the initial segment was 1·1 ± 0·5 N/mm (83 ± 38 N m/rad). In contrast, the constant-position task resulted in plots in which, from the start, stiffness was higher than for the constant-force task and remained so (Fig. 4). There was often no clear inflexion between the initial stiffness and that for the remainder of the perturbation. The average stiffness of the initial segment of the relationship was $2{\cdot}3 \pm 1{\cdot}3$ N/mm (170 ± 98 N m/rad), significantly greater than during the constant-force task ($P < 0{\cdot}02$, paired t test).

The change in behaviour after the beginning of servomotor movement appeared to correspond to the onset of conscious intervention, so indicating the threshold for detection. To test this hypothesis, the threshold for detection of the perturbation was estimated for six subjects. All were instructed that they were required only to detect the beginning of the perturbation and not to specify its direction. In practice, this distinction proved to be unnecessary. In all subjects there was an initial period before detection of the perturbation of similar duration to that preceding the inflexion for the two other tasks (Fig. 5). On average, it took the subjects 2·4 s after the onset of servomotor movement to detect any change. The average stiffness during this period was $1{\cdot}7 \pm 0{\cdot}8$ N/mm (130 ± 61 N m/rad), intermediate between those for the constant-force and constant-position tasks. As the subjects did not perceive anything in the period over which these stiffnesses were measured the behaviour observed could not have been a voluntary response to the perturbation.

Despite the delay in perception, the slow rate of arm movement meant that the displacement of the wrist at the time of perception was still small. The average changes in initial force and position of the wrist at the time of perception were 0·92 N (94 g) and 0·69 mm respectively.

Two subjects performed the tasks before and after ischaemic anaesthesia of the forearm and hand (for 30 and 34 min). Ischaemia of the forearm was initiated with a sphygmomanometer cuff around the upper arm but maintained for the duration of recording with a second cuff inflated around the upper forearm. The cuff around the upper arm more effectively achieved complete ischaemia but, as all the elbow flexor muscles were also rendered ischaemic by it, the second cuff was substituted several minutes before recording. Even so, three of the five elbow flexors have their bellies within the forearm so some alteration in the usual behaviour was not unexpected. During ischaemia of the forearm and hand, the over-all pattern of behaviour in the two tasks was unaltered. In both subjects the initial stiffness remained greater for the constant-position task than for the constant-force task despite anaesthesia, although the difference between the two was reduced. These observations indicate that performance in neither task was dependent on afferent information originating within the forearm or hand such as, for example, from cutaneous receptors excited by the pressure of the wristlet. Other observations also indicated that cutaneous afferents were unlikely to be responsible for detection of the applied perturbation. Two subjects were asked to repeat the constant-force and constant-position tasks during voluntary co-contraction of elbow flexors and extensors but with the same net force at the wrist. Mean biceps e.m.g. was increased to an average of 4·1 times the level in the absence of deliberate co-contraction. Both subjects' ability to detect the perturbation during co-contraction was markedly reduced. The first, who had detected all the perturbations initially, detected only nine out of sixteen during co-contraction. The second, who had detected six of eight perturbations initially, detected none during co-contraction. Since the forces at the wristlet were unaltered by this manoeuvre the deterioration indicated that detection of the stimulus was unlikely to have depended upon afferents excited by the pressure of the wristlet.

Intrinsic muscle stiffness and stretch reflex gain increase approximately in proportion to muscular activation (Rack & Westbury, 1974; Nichols & Houk, 1976; Joyce, Rack & Ross, 1974; Marsden, Merton & Morton, 1976). The e.m.g activity of biceps just prior to the onset of the perturbation was compared for the two tasks in ten of the eleven subjects who performed the averaging trials. Over-all, there was a modest increase in mean e.m.g. when the subjects performed the constant-position task (mean 20 %, six increased, four reduced), indicative of a degree of co-contraction. This increase was, however, considerably smaller than the relative increase in stiffness for the group (110 %) and in individual subjects there was a dissociation between the change in mean e.m.g. and stiffness. Two subjects had less e.m.g. activity during the position task, despite an increase in measured stiffness. In three other subjects this dissociation was deliberately achieved by requiring them to perform the constant-

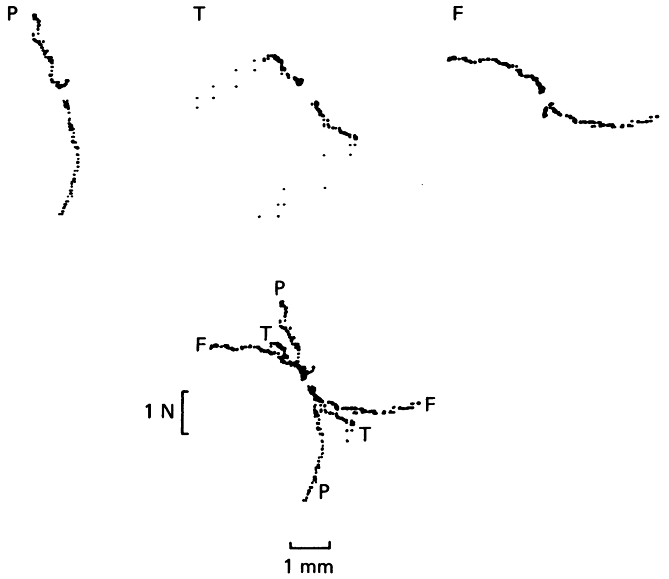

Fig. 5. A series of averaged results, plotted as force at the wrist against wrist position, for subject S.M. In the plot labelled 'P', the subject was instructed to keep the position of the forearm constant. The initial stiffness was high (3·4 N/mm). In the series shown on the upper right, labelled 'F', the subject was instructed to keep the force exerted at the wrist constant. The initial stiffness (0·59 N/mm) was higher than later in the curve, but less than that for the constant-position task. In the centre, labelled 'T', the subject was instructed to extend the forearm as soon as he became aware of any imposed perturbation. An initial period of change of force and position of the forearm occurred prior to the subject becoming aware of any disturbance. The three sets of observations are shown superimposed in the lower half of the Figure. The stiffness during the detection task (0·92 N/mm) was intermediate between that for the constant-position and constant-force tasks. The servomotor movement displaced the arm slowly enough that voluntary reaction time would not have been a significant limitation upon the thresholds recorded (points were recorded each 78 ms).

force task with a higher starting tension. A further subject who performed the constant-force task during voluntary co-contraction was still able to achieve a lower initial stiffness than during the position task without co-contraction, despite a threefold increase in biceps e.m.g. activity.

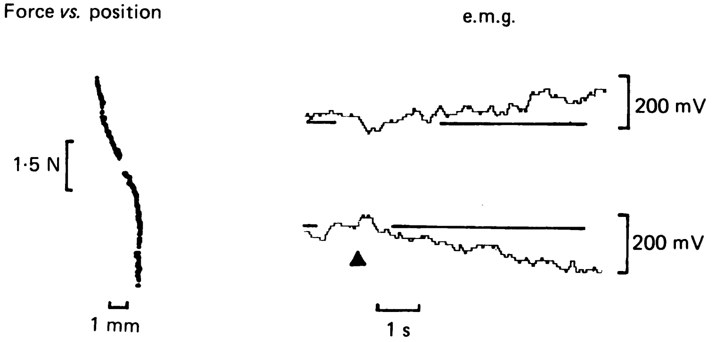

Fig. 6. Averaged e.m.g. for twenty-four pairs of trials performed for the constant-position task. The left part of the Figure shows the two limbs of the averaged force *vs.* displacement plot for this subject, separated for clarity. The initial stiffness was 1·4 N/mm. The right side of the Figure shows the averaged results of integrated (time constant 200 ms) biceps e.m.g. Servomotor movement began after a 1 s delay, at the time arrowed. The e.m.g. changes induced by each direction of applied disturbance are shown separately. At the onset of servomotor movement, there was a brief, paradoxical change in the e.m.g. followed by an approximately linear increase in parallel with the changes in force recorded. This result indicates that changes in neural activity occurred during the period in which stiffness was measured.

E.m.g. averaging was used in one subject to demonstrate directly that the initial stiffness measured during the constant-position task could not be entirely due to intrinsic muscle properties. A large number of trials (twenty-four in each direction of servomotor movement) was required to reduce the variability of the e.m.g. signal. The mean level of e.m.g. was altered as soon as the perturbation began, confirming that neural changes in excitability contributed to the stiffness measured (Fig. 6).

DISCUSSION

We have used small, slowly applied perturbations to human limbs to study physiological responses. These responses can be divided into two categories. When the perturbation is small or slow enough to be undetected, subjects are able to produce different responses depending on whether they are attempting to keep the position of the limb constant or the force exerted constant. When the perturbations are larger, and detected, subjects can voluntarily modify the contractions to achieve a greater range of control of limb position or tension.

The afferents upon which the subjects' judgements were based did not arise from cutaneous receptors within the forearm but most probably arose from receptors within the elbow flexor muscles (see also Rothwell *et al.* 1982). There is both electrophysiological (Oscarrson & Rosén, 1963; Landgren & Silfvenius, 1969; McIntyre, Proske & Rawson, 1984) and psychophysical (Goodwin, McCloskey &

Matthews, 1972; McCloskey, Ebeling & Goodwin, 1974; Roland & Ladegaard-Pederson, 1977) evidence to support a role for the primary spindle ending and the Golgi tendon organ in kinaesthetic sensations. Our results suggest that this proprioceptive information can be utilized in the volitional control of the limbs. Under our experimental conditions, the more exactly a subject is able to keep constant the position of the limb, the smaller are signals of altered position upon which he might rely and the larger are the signals of altered force. Similarly, when tension is kept constant, signals of altered tension are minimized and signals of altered position are maximized. Watson, Colebatch & McCloskey (1984) demonstrated that subjects were unable to ignore completely signals of tension when asked to align the position of their arms. A similar limitation could contribute to the residual errors seen in our subjects' performance.

Most previous studies of the function of the stretch reflex in man have used large, rapid perturbations and have depended upon e.m.g. latency to distinguish between reflex and voluntary components. This approach has the disadvantage of being unphysiological (Evarts, 1981), depends crucially upon estimates of voluntary reaction times, and is confined to studying the short period before voluntary intervention although only part of the reflex response may occur in this time (Houk, 1978).

In the present studies, the rate of stretch was slow enough to permit one to ignore the forces due to the mass of the arm (proportional to acceleration) and the viscous component of intrinsic muscle stiffness (proportional to velocity, Joyce *et al.* 1974). The initial stiffness recorded before detection of the stimulus could not have been a conscious response to it as deliberate anticipation was avoided by randomly intermingling the direction of the perturbation. Thus the values for initial stiffness represent a new method of measuring the combined effects of changes in reflex excitability plus the elastic component of intrinsic muscle stiffness. The lowest values recorded for stiffness in any subject must have represented conditions in which the stretch reflex was least involved, and so must give an indication of the maximum stiffness attributable to intrinsic, non-reflex mechanisms. If the range of stiffness measured in these experiments is due to changes in reflex gain (see below) then it is possible to estimate the contribution of reflex and intrinsic factors. These can be scaled, and they then give similar values to those for the soleus muscle of the decerebrate cat (Appendix).

Our subjects were able to change their involuntary responses to the perturbation and alter stiffness when required. The mild degree of co-contraction during the constant-position task appeared to be a natural reaction of the subjects to the task itself rather than the basis of the changes in stiffness measured (see also Akazawa, Milner & Stein, 1983). There was no direct correlation between the change in e.m.g. and the change in stiffness and the two could be dissociated if required. The change in stiffness must therefore represent presetting of the reflex response to stretch, consistent with evidence for presetting of responses to rapid stretch (Hammond, 1956, 1960; Tatton & Lee, 1975; Evarts & Granit, 1976; Iles, 1977; Colebatch, Gandevia, McCloskey & Potter, 1979; Kanosue, Akazawa & Fujii, 1983; Loo & McCloskey, 1985), although others have failed to demonstrate this (Marsden *et al.* 1976; Crago, Houk & Hasan, 1976).

The threshold for detection of the applied disturbance was extremely small. The average displacement at the time of perception is equivalent (using a lever ratio of 6 : 1, see Appendix) to 0·14 deg of elbow rotation at an average velocity of 0·06 deg/s. Comparison of these thresholds with the data of Hall & McCloskey (1983) shows that they are at least an order of magnitude less than for the performance of subjects for similar rates of movement at relaxed joints. The corresponding length change of the elbow flexors, approximately 110 μm, is within the range of maximum sensitivity of the primary spindle receptors (Matthews & Stein, 1969; Hasan & Houk, 1975). (This ignores the effects of the muscle tendon which acts as a compliance in series with the muscle fibres. The relative compliance of the tendon compared to the muscle fibres determines the proportion of any over-all length change 'seen' by the muscle fibres and spindles (Rack & Westbury, 1984). It is likely that the tendons of the elbow flexors have a relatively low compliance so that most of the stretch is transmitted to the muscle fibres. This is supported by changes in reflex excitability occurring at the onset of the perturbation in the subject in whom e.m.g. was averaged and also by the vigorous reflex response of these muscles to sinusoidal stretch of amplitudes similar to those used here (Joyce *et al.* 1974).)

Subjects must fail to detect the spindle discharge occurring with these small displacements in relaxed muscle (for example, Fig. 1*d* of Hagbarth, Wallin & Löfstedt, 1975). The improvement in detection with activity might be due to an increase in the total spindle discharge due to recruitment of previously silent endings or to increased spindle sensitivity due to increased fusimotor drive (Burke, Hagbarth & Löfstedt, 1978). Such a mechanism fails to explain the deterioration in detection which was seen with deliberate co-contraction. Although the threshold for activation of Golgi tendon organs by passive stretch is quite high, the threshold for excitation by active muscle contraction is low (Jansen & Rudjord, 1964). In view of their parallel increase in sensitivity, Goodwin (1976) speculated that Golgi tendon organs might be responsible for the improvement in detection that occurs with muscle contraction (for example, Gandevia & McCloskey, 1976). A role for tendon organ discharge is teleologically plausible in that, while the lever ratio in most muscles acts to reduce the muscle length change, changes in force are magnified. Threshold for our subjects, roughly 10 % of the initial force, corresponds to a change in actual muscle force of 5·62 N (573 g), an alteration large by comparison with the length change. A stretch reflex may perhaps, by magnifying the force change for a given displacement, also act to improve detection of disturbances.

APPENDIX

Comparison of reflex stiffness in man and decerebrate cat

Any comparison of reflex stiffness measured in man and decerebrate cat must allow for the obvious differences in muscle bulk and the range of operating length between the two. One suggested method of scaling is to compare:

$$K_{\mathrm{n}} = \frac{\text{force change}}{\text{force range}} \bigg/ \frac{\text{length change}}{\text{length range}} = K_{\mathrm{m}} \left(\frac{\text{length range}}{\text{force range}} \right),$$

where K_n is normalized stiffness and K_m is stiffness at the muscle tendon (Houk & Rymer, 1981).

A typical value for K_n for the soleus muscle of the decerebrate cat is 1 (stiffness 1 N/mm, force range 25 N, length range 25 mm: Houk & Rymer, 1981). Short-range extensions of soleus give higher values for stiffness and the example quoted by Matthews (1969) gives a K_n of 6·0.

TABLE 1. Stiffness in man and cat

	Man		
	Measured (N/mm)	Scaled	Cat soleus (scaled)
Intrinsic muscle stiffness	0·59	1·3	0·6–1·0
Stretch reflex plus intrinsic muscle stiffness	3·4	7·7	6·0

The corresponding calculation in man must allow for the presence of five muscles contributing to elbow flexion and also for the fact that measurements have not been made directly at the muscle tendons. The principles involved in calculating K_n from the values obtained in man are illustrated by assuming initially that there is only a single flexor muscle with the anatomy of biceps brachii. The results obtained in the experiment shown in Fig. 5 have been used.

For a given stiffness measured at the wrist, the actual stiffness at the muscle tendon (K_m) is increased by the square of the lever ratio. An average value for the equivalent lever arm for biceps at 90 deg of elbow flexion is 44·7 mm (Braune & Fischer, 1890; Wilkie, 1950) and the wristlet was attached 275 mm from the joint axis, giving a lever ratio of 6·15. During the subject's attempt to keep the position constant, $K(\text{wrist}) = 3{\cdot}4$ N/mm, so $K_m = 130$ N/mm.

Using the same value for effective lever arm, and assuming a maximum torque of 63·8 N m (Colebatch, Gandevia & Spira, 1986), the force range for biceps is 1430 N. The length range for biceps for a given angle, x, can be calculated from published values for the insertion and origin of the muscle as:

$$\text{length} = \sqrt{(\text{OA}^2+\text{OB}^2+2\text{OA OB}\cos(x))} \quad \text{(Wilkie, 1950)},$$

where OA and OB are the distances of the origin and insertion of the muscle from the elbow joint. A range of angular movement of 15 to 155 deg gives a length range of 84 mm.

Thus, for a measured stiffness at the wristlet of 3·4 N/mm, $K_n = 7{\cdot}6$, similar to that calculated for short-range stiffness for the decerebrate cat.

Recalculating the value of K_n for a combination of five elbow flexors requires weighting each muscle's effects by its lever ratio, fraction of the total torque and its length range. Using the data of Braune & Fischer (1890) (see also Bankov & Jørgensen, 1969), this calculation leads to a marginally higher value for K_n of 7·7.

The lowest stiffness that could be achieved by any subject is limited by intrinsic muscle stiffness. The value of stiffness measured in this subject during his attempts to keep force constant can also be scaled and compared with those reported for intrinsic muscle stiffness for the soleus muscle of the cat. For man, K_n is 1·3. Short-range intrinsic muscle stiffness for soleus muscle plus tendon has been estimated as 0·6–1·0 N/mm per Newton mean force (Rack & Westbury, 1974). The present measurements in man were made at approximately 1/25th of the expected maximum, corresponding to a force of about 1 N in the cat. Scaling this stiffness by the above formula gives a value of K_n for the cat of simply 0·6–1·0.

Both values for man are in good agreement with what have been argued to be analogous conditions in the cat, summarized in Table 1.

An alternative method of scaling has also been considered. In it, resting fascicle length is used instead of length range in the scaling formula to give K_f. The values for the cat are unchanged (typical fascicle length for soleus is 26 mm, Walmsley & Proske, 1981). In man, using the lengths reported by Hall & McCloskey (1983), significantly higher values are obtained. For the measured stiffness of 0·59 N/mm, $K_f = 2{\cdot}4$, and for a stiffness of 3·4 N/mm, $K_f = 14$.

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