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TASK-DEPENDENT CHANGES IN GAIN OF THE REFLEX RESPONSE TO IMPERCEPTIBLE PERTURBATIONS OF JOINT POSITION IN MAN

BY J. HORE*, D. I. McCLOSKEY AND JANET L. TAYLOR
From the School of Physiology and Pharmacology, University of New South Wales, PO Box 1, Kensington, Sydney, New South Wales 2033, Australia

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SUMMARY

1. It has been demonstrated recently that, when suitably instructed, subjects could alter the stiffness at the elbow in response to a slowly and imperceptibly changing elastic load. Although evidence was provided in favour of this occurring via changes in gain of the reflex response to stretch, changes in the degree of co-contraction could not be entirely ruled out. The major objective of the present experiments was to determine if subjects could alter stiffness at the wrist in a similar task, and then to determine whether they retained this ability when co-contraction was made impossible by anaesthetizing the nerve to the wrist extensors. A second objective was to determine if changes in stiffness could be controlled independently at the wrist and elbow.

2. Subjects, with eyes closed, initially held position constant against a constant force that loaded the flexors. For the wrist, they were instructed: (i) to keep the hand as still as possible (keep position constant) or (ii) to let the hand be moved by the perturbation (keep force constant). The perturbation was an initially imperceptible elastic load whose direction (loading or unloading) could not be predicted. Subjects were also asked to indicate when the perturbation was first perceived.

3. When asked to hold position constant or force constant at the wrist, subjects demonstrated task-dependent changes in stiffness prior to perception of the perturbation. These changes in stiffness were still achieved when the nerve to the wrist extensors was anaesthetized and thus co-contraction was prevented.

4. Five subjects demonstrated the ability to control stiffness independently at the wrist and the elbow although most subjects had difficulty with the task we employed to demonstrate this.

5. The results demonstrate: (i) that for the wrist, set-dependent changes in stiffness that occur prior to perception of a slowly developing perturbation can be mediated by changes in gain of reflex responses to those perturbations, and (ii) that stiffness can be controlled independently at the wrist and elbow, presumably in part by changes in gain of stretch reflexes.

* Present address: Department of Physiology, Health Sciences Centre, the University of Western Ontario, London, Ontario, Canada N6A 5C1.

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INTRODUCTION

Many studies have supported the view that human subjects can alter reflex responses according to their volitional 'set' (Hammond, 1956; Tatton & Lee, 1975; Evarts & Granit, 1976; Colebatch, Gandevia, McCloskey & Potter, 1979; Colebatch & McCloskey, 1987; Stein & Capaday, 1988). However, other studies have not confirmed this ability (Marsden, Merton & Morton, 1976; Crago, Houk & Hasan, 1976; Hoffer & Andreassen, 1981; Angel & Weinrich, 1986), and it has been suggested that demonstrated changes were brought about by variation in the initial level of muscle activation (Houk & Rymer, 1981), or that changes were not reflex in nature but were changes in early, triggered, voluntary reactions (Crago *et al.* 1976).

Recently, Colebatch & McCloskey (1987) presented evidence to support the existence of task-dependent changes in the reflex response to perturbation of the human arm. They applied small, slow, ramp perturbations that moved the forearm about the elbow. There were two special features of these perturbations. The first was that they were applied through a spring. By using such an elastic load it was demonstrated that, when suitably instructed, subjects could keep the forearm still (i.e. they could keep position approximately constant) or they could allow the forearm to be moved about the elbow by the perturbation (i.e. they could keep tension approximately constant). A second feature was that the perturbations were not perceived by the subject for the first few seconds. This prolonged the time before a voluntary response could be made and so extended the interval for study of the reflex response. During this extended reflex response interval, changes in the stiffness of the arm, appropriate to the task that subjects were asked to perform, were demonstrated.

The stiffness of a limb about a joint is the sum of the stiffness of all muscles acting about the joint (Feldman, 1980; Partridge, 1983). Thus, an increase in stiffness can be brought about with no change in net joint torque if agonist and antagonist muscles contract to oppose each other. Although electromyographic evidence presented in the study of Colebatch & McCloskey (1987) suggested that changes in co-contraction were not responsible for the observed alterations in stiffness, this mechanism could not be entirely excluded.

In the present study, we used the same experimental technique as Colebatch & McCloskey (1987). We determined that task-dependent changes in the reflex response to stretch described for the elbow also occurred at the wrist. By paralysing the antagonist muscle group we showed that these changes were not entirely dependent on co-contraction, but were the result, at least in part, of changes in the gain of the reflex response to stretch. In addition, we further investigated the ability of subjects to control reflex gain by studying the simultaneous responses of two related joints.

METHODS

Perturbations were applied to the arm of normal human subjects. An electromagnetic servomotor, attached by a spring to the arm at a point distal to the joint being studied, was driven by a ramp function. The shaft of the motor could move away from the arm increasing tension in the spring ('pull'), or it could ramp toward the arm decreasing tension ('let go'). A force transducer mounted on the motor recorded changes in tension, while a force/displacement transducer fixed to a stationary support and connected to the arm via a very weak spring (10 g/cm) signalled changes in position. The force and position signals were low-pass filtered and amplified before being digitized (Metrabyte APM-08 12-bit converter) and recorded by an Apple II+ personal computer. The signals were sampled every 6 ms for 3 s following the start of the perturbation. Subjects indicated their first awareness of the perturbation by pressing a button and if this occurred before 3 s had elapsed the trial was discarded. Thus, all responses recorded were made before a reaction to a perceived disturbance was possible. We understand 'perceived' in this context, to mean 'able to give a report about'.

At the completion of a set of ten trials, the five 'pull' signals were averaged, as were the five 'let goes'. Linear regression of force against position was performed for each set of averaged signals. The slopes of the regressions have the dimensions of stiffness and were combined for the two directions of perturbation according to the formula

$$\text{Stiffness} = \frac{\tan(\tan^{-1}(\text{slope } 1) + \tan^{-1}(\text{slope } 2))}{2},$$

where slope 1 is the slope of the response to 'pulls' and slope 2 is the slope of the response to 'let goes' (Colebatch & McCloskey, 1987), to give a measure of the effective stiffness of the arm about the joint.

Experiment 1

The ability to alter the reflex stiffness at the wrist was investigated in eleven subjects. Subjects were volunteer students and staff and gave informed consent to the procedure, which had institutional ethics approval.

Subjects sat with the left forearm resting on a bench in front of them with its radial border uppermost. The forearm was clamped and the hand was splinted in a wooden frame and supported against gravity, but allowed free horizontal rotation about the wrist. The required initial force of 5·9 N flexion at the wrist aligned the hand with the forearm. A slow ramp perturbation (5 mm or 1·5 N over 5 s) was applied through a spring attached at a metacarpophalangeal (MCP) joint and the change in force and position at this point recorded.

Subjects attended for two sessions. In the first session they were instructed on the tasks, allowed to practise and performed two sets of ten trials. For one set of trials they were instructed to keep the hand as still as possible ('keep position constant') and for the other set the instruction was to let the hand be moved by the perturbation ('keep the force or tension constant'). Each set of trials consisted of five 'pulls' and five 'let goes' randomly intermixed.

Seven subjects who showed a significant difference in stiffness between the two tasks (keeping position and keeping force constant) returned for a second experimental session. A radial nerve block at the elbow was performed by injection of 10 ml of 2% lignocaine (Eriksson, 1969). This paralysed the extensors of the wrist in six of seven subjects. These subjects (including two authors; D.I.McC., J.T.) were unable to extend the wrist against gravity. One subject was eliminated from the experiment as only a partial block was achieved.

Again after some practice, subjects performed two sets of ten trials, either keeping position constant or keeping force constant. Thus, in total, subjects performed four sets of trials, two control (holding position and holding force) and two with paralysed extensors where only the agonist flexors were operating at the wrist. For each set, the position and force records of the five trials in each direction were averaged and stiffness calculated as the slope of a linear regression of force on position.

Experiment 2

Having found that the reflex response at the wrist could be altered, we investigated the possibility that subjects could modify the reflex stiffness at two joints independently. Nine normal, right-handed subjects took part. Subjects were seated at a table with the right arm resting in front of them (see Fig. 1). The elbow was bent to 90 deg and the forearm rested on its ulnar border on a support that pivoted at one end. This allowed free horizontal movement (flexion or extension) at the elbow. In addition, the support was hinged at the wrist to allow flexion and extension at that joint. The arm was loaded as in expt 1 through a spring attached to a frame splinting the hand.

Perturbations were applied to the arm through the spring by movements of the shaft of the motor away from or towards the arm and changes in force were measured at this point. However, two separate measurements of position were recorded for each trial. Change of position of the whole arm (any movement at the elbow plus any movement at the wrist) was signalled by an externally

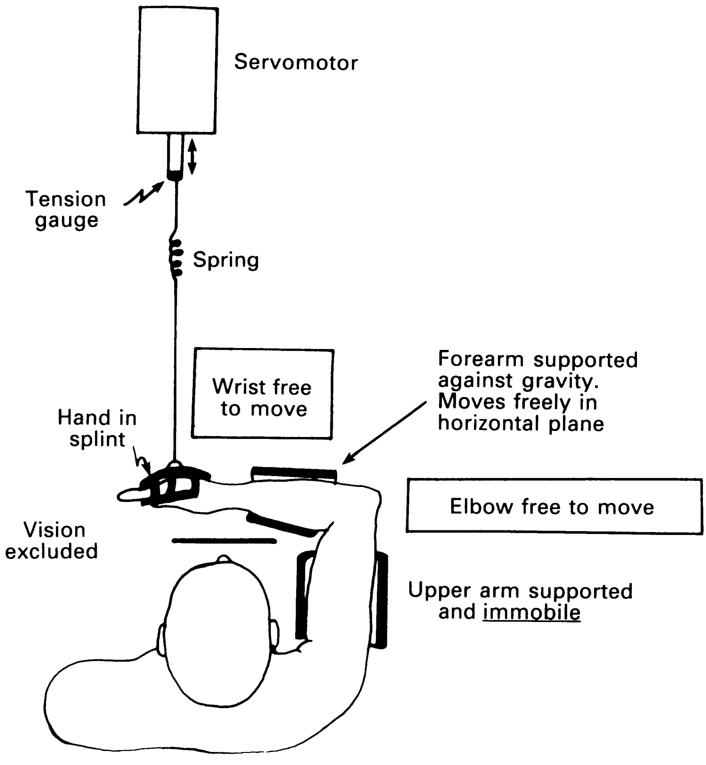

Fig. 1. Diagram of the experimental method for expt 2. Perturbations were applied to the subject's hand when both the wrist and the elbow were free to move in the horizontal plane. Subjects were instructed to keep the elbow still and let the wrist follow the force or, to keep the wrist still and let the elbow move. Position changes were measured by displacement transducers (not shown). One transducer was fixed to a stationary mount and measured movements of the whole arm at the hand. A second transducer was either, also fixed to the stationary mount and attached to the forearm to measure displacements about the elbow or, mounted on the forearm to measure movements of the hand relative to the forearm.

fixed, stationary force/displacement transducer connected by a very weak spring to the point of application of force on the hand-frame. A second position signal was recorded from either an externally fixed, stationary transducer connected to the forearm, rather than the hand (shows movement at elbow only), or a transducer mounted on the forearm and connected to the hand (shows movement at wrist only). Position signals were scaled so that all stiffnesses were calculated as Newtons per millimetre of movement of the point on the arm where the perturbing force was applied (over the MCP joint). The signals were processed as previously described.

Subjects were instructed in the two tasks: (i) 'keep the elbow still and let the wrist follow the force', and (ii) 'keep the wrist still and let the elbow follow the force'. After considerable practice subjects performed a set of ten trials for each task. Before each trial subjects were required to hold a target force (5·9 N) and also to attain the same initial position. They did this by matching both the force target for the whole arm, and a position target for either the wrist or the elbow, on an oscilloscope display. This preliminary setting of the joints and exerted forces was necessary to enable measurement and averaging, but subjects found it complicated and difficult. We cannot be sure that the 'postural set' they used to attain the starting position was entirely compatible with the 'response set' we asked them to adopt immediately afterwards. The arm was then again perturbed by a slow ramp of the vibrator (5 mm or 1·5 N in 5 s, toward or away from the arm) starting a variable time after subjects indicated readiness. The first 3 s of the response, while subjects were unaware of the ramp, were recorded.

Stiffness of the whole arm and of the wrist or elbow was calculated from the force and appropriate position records averaged over five trials in each direction for each task.

RESULTS

Experiment 1

Colebatch & McCloskey (1987) showed that reflex stiffness at the elbow was task-dependent in human subjects. The present study showed that reflex stiffness of another joint, the wrist, could also be altered by altering the task. However, not all subjects succeeded in doing this. Of seventeen subjects who attempted to alter reflex stiffness at one joint, either during the performance of this experiment or during practice for expt 2, six were unsuccessful.

Of the eleven subjects who took part in expt 1, for eight, effective stiffness of the wrist was significantly less when subjects attempted to maintain force constant than when they attempted to maintain position constant. Examples for three subjects are shown on the left side of Fig. 2 (control). Force is plotted against position so that the slope of each plot represents the stiffness of the wrist. Each record comprises the average of five trials in the 'pull' direction (upper segment of each trace) and the average of five 'let go' trials (lower segment). Averaged trials of each subject performing the 'hold position' task are shown in traces *A* and 'hold force' in traces *B*. For each subject, stiffness while holding position (1·58, 2·28 and 1·36 N/mm) was greater than while holding force (0·24, 0·68 and 0·97 N/mm). For all successful subjects, the average stiffness while maintaining position was $1·49 \pm 0·43$ N/mm, and during force holding was $0·62 \pm 0·22$ N/mm. The remaining three subjects had differences that were not significant and so were not used further in the experiment. One successful subject chose not to continue.

To eliminate the possibility that joint stiffness was changed by co-contraction of agonists and antagonists, the extensors of the wrist were paralysed by anaesthetic block of the radial nerve. The responses of the same three subjects are shown on the right side of Fig. 2. Comparison of the slopes of traces *C* with *D* reveals that without extensors, stiffness during 'hold position' (1·43, 1·24 and 1·17 N/mm) was still greater than during 'hold force' (0·52, 0·59 and 0·43 N/mm).

Five of the six subjects whose extensors were anaesthetized retained the ability to change reflex stiffness to suit the task (Fig. 3). For the six subjects in whom the anaesthetic block was successful, average control values of wrist stiffness were $1·43 \pm 0·48$ N/mm (hold position) and $0·53 \pm 0·29$ N/mm (hold force). With the extensors anaesthetized, the values were $1·13 \pm 0·25$ N/mm (position) and $0·49 \pm 0·07$ N/mm (force). One subject was unable to alter the reflex response to perturbation after anaesthetic block of the extensor (Fig. 3, ■). However, prior to performance of the block subjects were asked to explain their strategies for

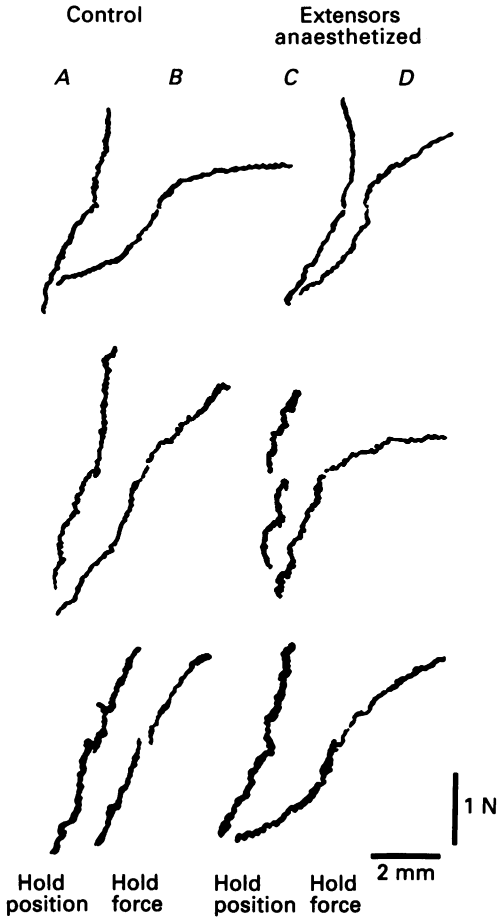

Fig. 2. Averaged plots of force against position during perturbations about the wrist for three subjects. The slope of each trace is the stiffness of the wrist. Each trace has two segments, each recorded over three seconds. The upper segments are the averages of responses to five 'pull' perturbations. The lower segments are the averages of five 'let goes'. Recording starts from the centre of the trace, with the arm in the set initial posture for both segments. When the arm was 'pulled', force increased and the hand was moved away from the body (a positive change of position). When the arm was 'let go', the reverse occurred. Breaks in the trace indicate slightly different starting positions. Traces A and B are the control trials, in which both the agonist flexors and antagonist extensors of the wrist were able to act. For trace A, subjects attempted to keep position constant while for trace B, subjects attempted to keep the tension constant. When the extensors of the wrist were anaesthetized, leaving only the flexors operative, all three subjects maintained a higher stiffness during the 'hold position' task (C) than during the 'hold force' task (D).

performing the tasks. This subject said that he maintained position by tensing the whole arm including the extensors of the wrist. That is, he increased stiffness of the arm by deliberate co-contraction. Thus it might be expected that he would be unable to maintain a high stiffness when co-contraction was prevented. As can be seen in Fig. 3, when the extensors were paralysed, the stiffness of his wrist during position holding fell to the same level as that achieved during the force holding task. Stiffness of the wrist during position holding was also reduced for some other subjects but in no other was the difference in stiffness between the position- and force-holding tasks entirely eliminated. Analysis of variance and *a posteriori* (Student–Newman–Keuls) com-

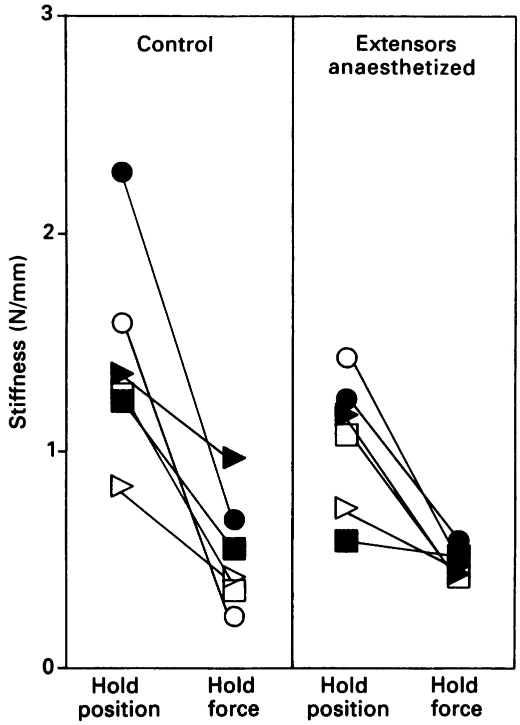

Fig. 3. Average stiffness of the wrist for all six subjects whose nerve to the extensors was successfully anaesthetized. Each subject is represented by a different symbol. The left box (control) shows the stiffness of the wrist with both the flexors and extensors able to act. Subjects were asked to perform two tasks. They were instructed to keep position constant, and in another set of trials to keep force constant. The right box shows the stiffness of the wrist of the same subjects performing the same two tasks when the extensors of the wrist were anaesthetized and so could not affect stiffness. All but one subject (■, see text) were able to alter the stiffness of the wrist when only the flexors were acting, as well as when agonists and antagonists were both available.

parison of stiffness for the two tasks, both with and without possible antagonist activity, showed stiffness during the maintenance of position in the control condition to be significantly greater than for the same task with the extensors anaesthetized ($P < 0{\cdot}05$). However, in both conditions, stiffness during the maintenance of position was greater than stiffness during the maintenance force ($P < 0{\cdot}01$). Therefore task-dependent changes in the stiffness about a joint are not solely the result of increased activation of motor units by co-contraction but are also due to alterations in the reflex response of the agonist muscle group.

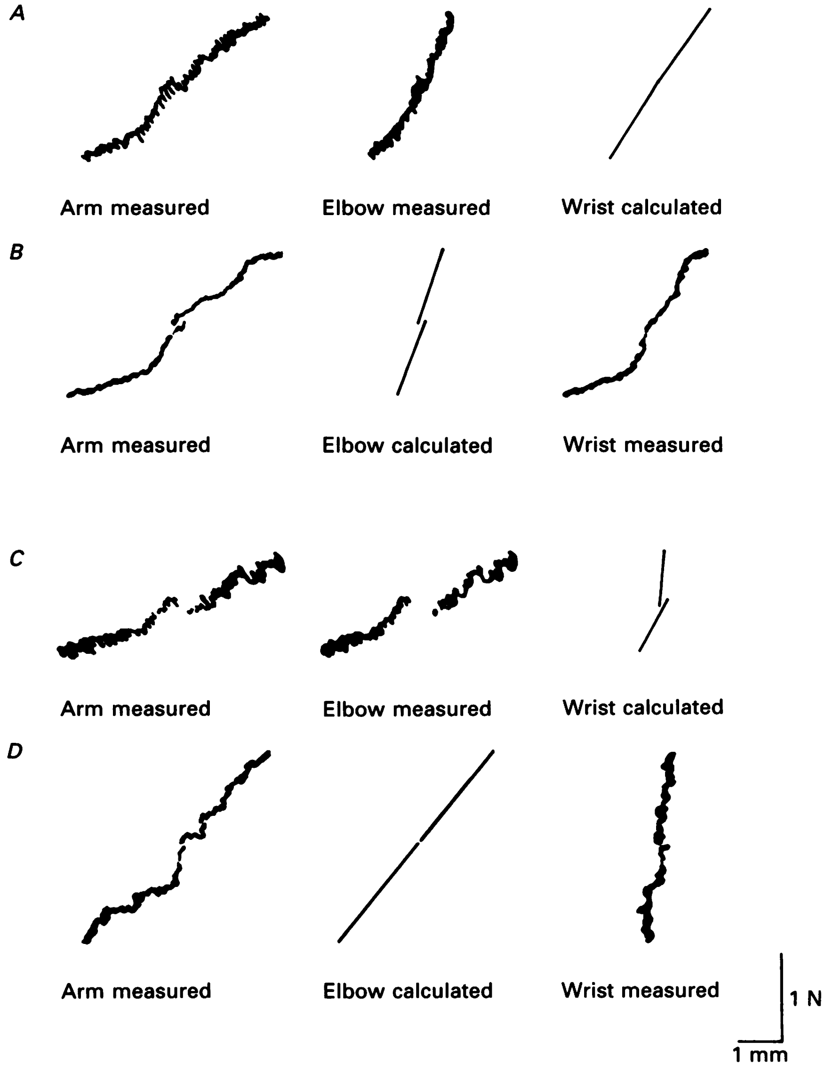

Fig. 4. Averaged records of one subject who altered independently stiffness about the wrist and stiffness about the elbow. Stiffness about the joints is shown by the slopes of the traces. Each section of the figure (*A*, *B*, *C*, *D*) has three records. The first shows the responses of the whole arm to the perturbations. The second is the response of the elbow and the last the response at the wrist. The response of the whole arm is the combination of responses at the elbow and wrist. Only two of the responses were measured in any set of trials, the third response being calculated from the other two. This subject took part in two experimental sessions in one of which (shown in *A* and *C*) the response of the elbow was measured along with that of the whole arm, and in the other of which (*B* and *D*) the response of the wrist was measured. The task being performed during the responses shown in *A* and *B* was to hold the elbow still while letting the wrist move. In *C* and *D*, the task was to hold the wrist still while allowing the elbow to move. Comparison of the slope of the elbow trace in *A* and *B* to that of the elbow in *C* and *D* reveals that the stiffness about the elbow was greater when the subject was instructed to hold the elbow still. Similarly, when the wrist was allowed to move (*A* and *B*), it was less stiff than when it was held still (*C* and *D*).

For all subjects, stiffness was calculated from a combination of the slope of the average 'pull' trials and the slope of the averaged 'let go' trials, as described in Methods. These slopes were obtained through linear regression of force on position. All averaged control and anaesthetized trials had regression coefficients greater than 0·85 (90% > 0·9). Those regressions that were further from linearity were spread among the subjects and among 'pull', 'let go', 'hold position', 'hold force', control and anaesthetized trials with no apparent pattern.

Experiment 2

Having found that reflex stiffness at one joint could be altered, we investigated the possibility that two joints could be controlled independently. This task proved very difficult for subjects to perform. Of an initial nine subjects, five were able to demonstrate the ability after considerable practice. They were able to decrease stiffness at the wrist while maintaining a high stiffness at the elbow, or could maintain a high stiffness at the wrist while allowing the elbow to move. Figure 4 shows the records from one subject. Force and position changes of the whole arm were measured, as were those of either the wrist or the elbow. Stiffness of the unmeasured joint was calculated from the other two values. In these force *vs.* position plots, the slope of the plot corresponds to the stiffness of the arm. Stiffness of the wrist was greater during the 'hold wrist still' task (1·66 N/mm) (Fig. 4*C*, *D*) than during the 'hold elbow still' task (0·56 N/mm) (Fig. 4*A*, *B*). Stiffness of the elbow was greater during 'hold elbow still' (0·75 N/mm) than during 'hold wrist still' (0·58 N/mm). Table 1 shows the mean stiffness for the five successful subjects, of the whole arm, the elbow and the wrist for the two tasks. Paired t tests showed significant differences between the tasks in stiffness both of the elbow ($P < 0.05$) and of the wrist ($P < 0.01$) while the stiffness of the whole arm remained unchanged ($0.5 < P < 0.9$).

TABLE 1. Stiffness (N/mm) of the whole arm, elbow and wrist during each of two tasks. Mean and standard error of the five subjects who demonstrated an ability to alter independently elbow and wrist stiffness are given

	Hold elbow still	Hold wrist still
Arm	0.34 ± 0.03	0.32 ± 0.04
Elbow	0.74 ± 0.11	0.42 ± 0.07
Wrist	0.86 ± 0.30	1.59 ± 0.19

Stiffness can also be expressed in angular units (Nm/rad) which are independent of the distance from the elbow to the point of application and measurement of force and position changes. Using the average length of 33·3 cm from elbow to MCP joint as the lever arm, stiffness at the elbow during the 'hold elbow still' task was 83 Nm/rad and for 'hold wrist still' (and let elbow move) was 64 Nm/rad. By comparison, Colebatch & McCloskey (1987) reported figures of 170 Nm/rad for maintaining position constant and 83 Nm/rad for maintaining force. The disparity between the studies probably reflects the different initial loads that subjects were asked to resist. Both mechanical and reflex components of muscle stiffness are known to increase with an increased initial load (Nichols & Houk, 1976; Hoffer &

Andreassen, 1981) and the initial torque required in the study by Colebatch and McCloskey was larger than that required here. In addition, the posture of the arm differed between the two studies so that different muscles may have been engaged.

DISCUSSION

A key feature of these experiments was the use of an elastic load (perturbation) that was not perceived by the subjects. Use of an elastic load allowed the possibility that subjects could resist the perturbation entirely successfully by holding the hand completely still or, when so instructed, allowed them the possibility of letting the hand move with the perturbation (Colebatch & McCloskey, 1987). By use of this type of perturbation, and the elimination of co-contraction, we have confirmed that subjects can alter the gain of their reflex response to stretch in a functionally appropriate direction by a change of volitional set. Thus, when subjects with anaesthetized wrist extensors attempted to keep position of the hand constant, the reflex stiffness of the wrist flexors was greater than when subjects attempted to hold force constant. In addition, some subjects were able to alter independently the stiffness of two adjacent joints. The elbow could be held stiff while the wrist was allowed to comply (move with the applied change in force), or the elbow could comply while the wrist resisted.

The initial response of a limb to a perturbation consists of effects due to mechanical properties of the limb, such as its mass, and the passive properties of the joint, connective tissues and muscle and tendons about the joint, as well as the intrinsic stiffness of the activated muscle fibres (Joyce, Rack & Ross, 1974). This is followed by reflex changes in muscle activation and then by voluntary muscle contraction. In the present experiments we measured these responses in terms of stiffness. This parameter was chosen for analytical and descriptive purposes and its use does not imply that stiffness was a physiologically specified or controlled variable.

The responses to perturbations recorded in this study depended mainly on the elastic component of intrinsic stiffness including 'short range stiffness' (Rack & Westbury, 1974), together with reflex stiffness. The effects dependent on acceleration (inertia) and velocity (viscous component of intrinsic muscle stiffness, Joyce *et al.* 1974) were minimized by the very slow onset and rate of change of the perturbation (Colebatch & McCloskey, 1987). The constant initial loading of the limb prevented any slack in tendons that might complicate the response, and while the elasticity of the tendons probably contributed to the recorded stiffness (Rack & Ross, 1984), this contribution should be the same for all trials and thus not affect the changes in stiffness observed with alterations of volitional set.

One possible source of changes in stiffness that was not controlled in this experiment is differential activation of the agonist muscles. The agonists here consisted of a group of muscles and if different muscles within the group, or different fibres within any of the muscles were activated to perform the two tasks this might result in a change of stiffness. This could occur if the intrinsic stiffness of the activated pools of fibres differed. However, as the initial load on the flexor group and the initial position of the wrist were kept constant, it is unlikely that different populations of motor units would be recruited.

Use of a slowly developing perturbation that was not initially perceived by the subject provided a 3 s interval in which the reflex behaviour could be studied. With a rapid stretch, the stimulus is almost immediately perceived and any response at a greater latency than the shortest possible reaction time must be excluded from a study of reflexes. Changes in longer latency reflex activity may not be identified as they can be submerged in the voluntary response (Houk, 1978). A slow, small stretch prolongs the time before the perturbation can be detected and so prolongs the time before it can be acted upon voluntarily. Furthermore, in the present study, any trial in which a perturbation was consciously perceived during the 3 s of recording was discarded, so that only responses occurring prior to perception remained.

Some of the sets of averaged trials show non-linearities (Fig. 2). There are differences in slope between 'pull' and 'let go' trials in some traces (trace *D*, middle panel). It is possible that there may be a real difference between loading and unloading responses, but the effect was not consistent over all subjects with most showing symmetrical trials. A consistent drift of the arm in one direction could also account for the asymmetry. The effect of a systematic drift on the calculated stiffness of the wrist is eliminated here by combining the slopes of responses to 'pull' and 'let go' perturbations (see Methods).

Despite reasonable correlations (coefficients > 0·85) for all linear regressions, there appears to be a period of high stiffness at the start of many of the 'hold force' trials. Stiffness then decreases with the increase in the perturbation (Fig. 2, top panel, trace *B* and *D*; bottom panel, trace *D*). This initial high stiffness may be a demonstration of short range stiffness which has been observed for small amplitude stretches and releases of contracting muscle (Joyce, Rack & Westbury, 1989; Rack & Westbury, 1974; Houk & Rymer, 1981). Short range stiffness is measured before the onset of a reflex response and has been attributed to the properties of muscle cross-bridges. A sudden 'yield' attributed to break-down of the cross-bridges is seen with larger amplitude changes of muscle length, particularly in the absence of intact reflex pathways. The reflex response to stretch appears to compensate for this yielding (Nichols & Houk, 1976).

In this study, the initial segment of the response to perturbation varied greatly between subjects and was not specifically analysed. The amplitudes of stretch and release seen during the segment were very small (< 0·4 % of the range of movement). This is smaller than the 1–2 % previously reported as the extent of short range stiffness (Rack & Westbury, 1974; Nichols & Houk, 1976; Houk & Rymer, 1981). However, this extent depends on the velocity of stretch as well as the initial load, and the velocity of stretch here is much slower than any previously used (Rack & Westbury, 1974). If the changes in stiffness demonstrated between 'hold position' and 'hold force' trials are, as we propose, due to a decrease in reflex gain, then it could be expected that the linearity of the response to perturbation would be compromised when the reflex response is no longer large enough to compensate for the yielding at the limits of short range stiffness.

Are the demonstrated changes in stiffness due to changes in reflex activity or to changes in co-contraction ? Feldman (1980, 1986) has argued that although the reflex response of a limb may be altered to suit a task, this is brought about by co-contraction of the agonist and antagonist muscle groups, not by any change in the gain of reflex activity. That is, for any given force output, the net joint torque can be maintained while stiffness about the joint is altered by changing the activation of opposing muscle groups. In control trials, we attempted to minimize co-contraction by loading the flexors with a constant force prior to onset of the perturbation. Later, to eliminate co-contraction completely, the nerve to the extensors was anaesthetized. In this situation subjects continued to demonstrate task-related differences in reflex stiffness. Furthermore, as the initial force loading the flexors, and the initial position of the arm were kept constant, the effects of different muscle lengths and of the initial level of motor unit recruitment were minimized. Thus, the observed changes in reflex stiffness were presumably mediated by changes in the gain of the reflex responses to perturbation.

However, even in our task that used a constant force, co-contraction appeared to play some role. Paralysis of the extensors of the wrist decreased stiffness of the wrist during both position holding and force holding tasks. Further, one subject lost his ability to 'hold position' (maintain a high stiffness) when the extensors were paralysed. It seems likely, therefore, that co-contraction plays a part in maintaining the stiffness of the intact limb, and it is probable that both co-contraction and changes in reflex gain act together to produce functional alterations in stiffness. The relative contributions may depend on the nature of the task (Loo & McCloskey, 1985; De Luca & Mambrito, 1987) and may vary from subject to subject.

Although we cannot rule out a contribution from co-contraction in the wrist–elbow task (Fig. 4) it is likely that the independent control of stiffness was mediated in part by changes in gain of the reflex responses to perturbation. If so, this provides evidence that the effect of volitional set is not a generalized excitation or inhibition of reflex activity but can be directed to a particular muscle group. The difficulty subjects had in learning to make the complementary changes in stiffness may indicate that the complicated task of reaching an identical starting posture when two joints were free to move (see Methods), required adoption of a postural or volitional 'set' which was difficult to alter immediately afterwards according to the requirements of the experiment. Alternatively, it may be that independent setting of the reflex activity about related joints is not a commonly performed task, or simply that we were unable to express the task in a more functionally relevant way.

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