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ACCURATE REPOSITIONING OF THE HUMAN THUMB AGAINST UNPREDICTABLE DYNAMIC LOADS IS DEPENDENT UPON PERIPHERAL FEED-BACK

BY B. L. DAY AND C. D. MARSDEN

From the University Department of Neurology, Institute of Psychiatry, and King's College Hospital Medical School, de Crespigny Park, London SE5 8AF

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SUMMARY

1. The strategy of accurate movement of the human thumb has been studied in nine subjects. An open-loop hypothesis, which states that a new final position is defined by re-setting the agonist/antagonist spring constants, was tested.

2. Subjects were trained to flex the top joint of the thumb rapidly through 20 deg in about a third of a second from a fixed starting position against a load. Occasionally, and unpredictably, the viscous friction of the load was altered prior to it's being moved. The spring hypothesis predicts that such a change in load should have no effect on final position accuracy.

3. Under normal conditions no final position error developed when the viscous friction was increased. A small overshoot occurred when the viscous friction was decreased.

4. The electromyogram recorded from surface electrodes over the belly of flexor pollicis longus in the forearm revealed an increase in activity in response to an increase in viscous friction and a decrease in activity when the viscous friction was reduced.

5. When the joint and cutaneous afferents from the thumb were anaesthetized, the e.m.g. response to a change in viscous friction was severely attenuated and consistent final position errors developed.

6. Even though the compensatory open-loop muscle properties went some way towards maintaining accuracy, the change in final position error that occurred as a result of thumb anaesthesia correlated well ($r = 0{\cdot}84$) with the amount of muscle e.m.g. response that was lost.

7. The latency of the e.m.g. response to a change in viscous friction was compared to that of a voluntary response by asking the subject to push down or let go upon perception of the load change. Approximately the first 100 ms of the e.m.g. response was unaffected by the voluntary intervention of the subject.

8. We conclude that the spring hypothesis does not explain human thumb movement. It is argued that the long-latency stretch reflex machinery is responsible for some automatic compensation for unexpected interference with movement.

INTRODUCTION

The neural mechanism by which a limb is moved accurately to a new location in space is not known. From observations on head and arm movements in monkeys (Bizzi, Polit & Morasso, 1976; Polit & Bizzi, 1979), Bizzi proposed an open-loop hypothesis of movement control in which final position is defined by setting the spring constants of agonist and antagonist muscles.

Bizzi *et al.* (1976) trained vestibulectomized monkeys to make stereotyped head movements, without visual guidance, in response to a visual signal. Occasionally a torque load was applied to the head at the beginning and throughout a head movement, and was removed when the movement was completed. The crucial observations were (1) no final position error developed after the removal of the torque load, when compared to an unperturbed movement, and (2) deafferentation of the neck, which abolished all e.m.g. responses to the torque change, did not decrease the accuracy of head positioning. Polit & Bizzi (1979) later examined movements of the elbow in monkeys and found that the accuracy of the final position of the arm was independent of the initial limb position in normal and in de-afferentated animals. More recently Kelso & Holt (1980) performed similar experiments during finger positioning tests in man and claimed to have obtained comparable results. That is, mid-course perturbations during rapid finger positioning to a learnt target location did not affect accuracy. When afferent feed-back was interfered with by abolishing joint and cutaneous afferent information from the hand, the small constant error that did develop was considered insignificant by the authors.

The implication of these data is that the final steady-state position of the head or limb is coded in the α-motoneuronal discharge to the agonist and antagonist muscles, independent of feed-back from the moving part. Bizzi pointed out that this would give the moving part the qualities of a spring, whose parameters of spring stiffness and rest length are independently defined by contraction of agonist and antagonist muscles. Movement to a new position then becomes a matter of re-setting agonist/antagonist activities as if to change the rest length of the spring, which would determine a unique final position regardless of initial limb position or any transient external force changes.

The aim of the present experiments was to test the 'open-loop spring' hypothesis as a mechanism for accurate limb positioning in man. The method used was to train subjects to rapidly flex the interphalangeal joint of the thumb through 20 deg from a fixed starting position against a load. The load consisted of the inertia of a motor/potentiometer/lever arrangement, a small constant torque acting to extend the thumb, and viscous friction, most of which was artificially produced by the motor in a velocity feed-back configuration. The viscous friction acted as a force to oppose dynamic changes in position (proportional to velocity) but not in response to static position changes. A spring trying to return to its rest length against a viscous friction load will do so regardless of the magnitude of viscous friction that it is working against. A prediction arising from the 'open-loop spring' hypothesis is that unpredictable changes in viscous friction of the load, although affecting movement trajectory, will have no effect on final thumb position accuracy, even if no change in agonist or antagonist muscle activity occurs.

A preliminary report of our findings was given to the Physiological Society in March 1981 (Day & Marsden, 1981).

METHODS

The experiment was performed on nine volunteers whose ages ranged from 21 to 29 years. Each subject was seated with his right arm semi-pronated on a padded board; the proximal phalanx of the right thumb was clamped, allowing free movement of the distal phalanx. The subject wrapped the fingers around the vertical stem of the clamp. The pad of the thumb rested lightly on a lever which was prevented from over-extending the thumb by a mechanical stop. The lever was attached to the output shaft of a servo-controlled torque motor, the shaft of which was aligned so as to rotate on the same axis as that of the interphalangeal joint of the thumb (Fig. 1). Flexion of the thumb in a vertical plane, therefore, caused the lever to move down and the motor to rotate, the amount of rotation being transduced by a potentiometer. About 3 deg of thumb extension from the rest position, which was with the top joint of the thumb flexed by about 10 deg, caused the thumb-nail to depress a microswitch mounted about the thumb. The motor, clamp and thumb were covered to prevent the subject obtaining direct visual clues of movement. The subject faced a cathode-ray oscilloscope (c.r.o.) upon which two 1 inch vertical lines were generated one below the other. Horizontal movement of the bottom line was controlled by the output from the potentiometer attached to the motor, to present a visual display of lever position. The top line was used as a target. The e.m.g. of flexor pollicis longus, the sole flexor of the distal phalanx of the thumb, was recorded using surface electrodes placed over the belly of the muscle in the forearm. The raw e.m.g. was filtered (−3 db at 80 Hz, 2·5 kHz), rectified and smoothed (time constant 0·003 s). Lever velocity was obtained by differentiating the lever position signal (cut-off frequency 72 Hz to reduce high frequency noise). The experiment was controlled and data stored using a PDP 12 computer (sampling frequency 250 Hz).

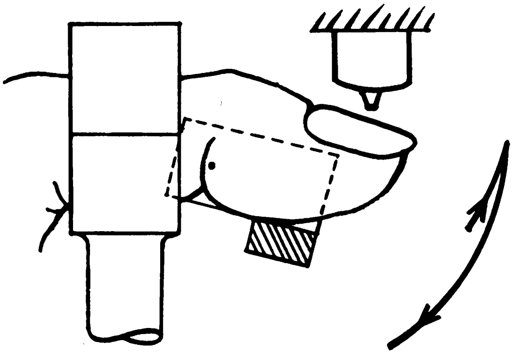

Fig. 1. Thumb arrangement. A microswitch is mounted above the thumb-nail to provide a trigger pulse when depressed and released by an extension–flexion movement of the thumb. The lever, on which the thumb presses, is attached to the output shaft of a d.c. torque motor.

The load took the form of a fixed inertia (motor, potentiometer, lever) and a small constant torque (0·02 Nm) opposing thumb flexion which ensured that the lever remained in contact with the thumb during the movement. To this was added a variable viscous friction controlled by the torque motor. This was implemented by having a negative velocity feed-back loop in the motor controller circuit, the amount of viscous friction being altered by changing the gain of the velocity feed-back. The effect of changing the viscous friction of the load on the trajectory of movement of the lever produced by a real spring is shown in Fig. 2. The control value of viscous friction was set at 0·0042 Nm rad^{-1} s. The three test values were 0·0084, 0·0056 and 0·0028 Nm rad^{-1} s representing a large increase, a small increase and a small decrease respectively, all of which could be perceived as changes in load by the subjects. The viscous friction was designed to act unidirectionally (i.e. during thumb flexion). This meant that when the thumb was returned to its rest position following a flexion movement, the lever, under the action of the constant torque, rapidly returned to the mechanical stop and its return velocity was unaffected by the magnitude of the viscous friction acting in the opposite direction.

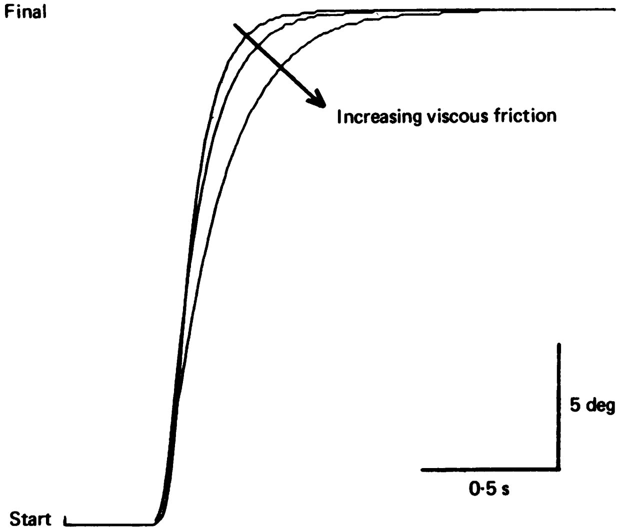

Fig. 2. Movement trajectory of the thumb lever alone (without the thumb) when released from a fixed starting position under the action of a stretched spring. The final equilibrium position was independent of the value of the viscous friction of the load, which took the values 4·2, 5·6 and $8{\cdot}4 \times 10^{-3}$ Nm rad^{-1} s.

To perfect the movement required, each subject carried out at least 256 thumb flexions to the demanded end position with the viscous friction set at the control value. This was done by setting the target line on the c.r.o. to a position which was equivalent to a thumb flexion of 20 deg from the rest position. When ready the subject initially extended the thumb to depress the microswitch with the thumb-nail. This was followed by a swift flexion movement through 20 deg in about 300 ms. As the thumb started to flex the microswitch was released, which acted as a trigger to simultaneously start data collection and to blank the c.r.o. for 1 s thus depriving the subject of current visual information concerning the movement. After 1 s from the trigger point the data collection was complete and the traces representing lever and target position returned to the c.r.o. This enabled the subject to assess the accuracy of the movement that had just been completed. After observing the degree of success the subject returned the thumb to the rest position ready for the next movement. It was usual for the subject, on returning the thumb to the rest position, to go straight into thumb extension and hence the next movement, thus establishing a rhythm. After each thirty-two runs four averages ($n = 8$) of lever position and velocity were superimposed and displayed to the subject on a screen. The subject was then urged to reduce variability in terms of accuracy and trajectory by trying to get the four traces to ideally lie on top of each other in future attempts. Also, the subjects were told to change the speed of movement, if necessary, so that the movement duration (time for velocity trace to return to zero) was about a third of a second.

The test session followed the training session after a short break. The subjects were informed that occasionally and unpredictably the load on the lever might change. They were instructed that it was essential to maintain accuracy throughout the experiment whether they detected the load changes or not. As before, they were given visual knowledge of results after each flexion movement.

A test run was defined as one during which there was either an increase or decrease in viscous friction. The control runs were grouped according to their temporal relationship with the test run; control 1 was the run preceding the test run. Control 2 was the run immediately following the test run and control 3 was the run following control 2. A variable and unpredictable number of control runs were interspersed between control 3 and control 1 (the probability of n control runs being interspersed is given by the formula, $P_n = 3^n/4^{n+1}$). These extra control runs were not recorded.

The runs were organized in blocks of thirty-two consisting of eight test runs, all with the same change in viscous friction, plus eight of each of the three control runs. Only the average of each eight runs was recorded. This was followed by three more blocks of thirty-two runs still using the same viscous friction change; the same procedure was then applied to the other two changes in viscous friction. Therefore, during this test session each subject performed 384 movements which were recorded, plus an indeterminate and variable number of extra control runs which were not recorded.

Either some hours later on the same day, or on the day following, each subject returned for the second test session. This was preceded by a practice session which allowed them to get used to the control loading conditions again. When ready, the subject's thumb was anaesthetized by injecting 4 ml of 2 % xylocaine as a ring block. This effectively anaesthetized cutaneous and joint receptors in the thumb whilst leaving the muscle receptors in the forearm intact. More practice runs followed to allow the subject to get used to the lack of sensation. Most subjects initially found it more difficult to move the thumb after anaesthesia and had to be encouraged to try and match the speed of movement before the anaesthetic. However, once the movement pattern was re-established it was maintained throughout. The test procedure used before the anaesthetic block was then repeated.

Four variables were measured: (1) accuracy, as defined by the mean final position of the lever during the control runs subtracted from that during the test runs; (2) movement duration, which was measured from the velocity record and defined as the time taken for the velocity trace to pass from zero and back to zero again; (3) flexor e.m.g. modification, which was quantified by integrating the filtered rectified smoothed e.m.g. over the 1 s period for the test runs, subtracting that for the control runs, and expressing it as a percentage of the control run value; (4) peak force ratio, which was indirectly measured from records of motor current and represents the value of the maximum force generated by the thumb on the lever during the test runs divided by that generated during the control runs.

Statistical analysis was carried out using the non-parametric Wilcoxon's signed rank test for paired differences.

RESULTS

Before assessing the effect of unexpectedly altering the viscous friction of the load on the accuracy of limb positioning, the effect on subsequent control runs was evaluated. Comparison of the final position (position after 1 s from start of movement) of the thumb during control 2 (the run after the test) with control 1 (the run before the test) revealed no consistent change under normal conditions, but after the local anaesthetic ring block of the thumb there was a consistent effect (Table 1). Following anaesthesia subjects overshot in control runs after a run with an increase in viscous friction, and undershot after runs in which viscous friction was reduced. This corruption of control runs by the presence of the test run was dealt with by comparing the test performance with that of control 1 only, controls 2 and 3 being discarded.

The outcome of unpredictably changing the viscous friction of the load prior to the subject moving it is illustrated for one subject in Fig. 3, before and after thumb anaesthesia. In this subject, under normal conditions, the effect of the viscous friction change was to alter the trajectory of the thumb whilst barely affecting final accuracy. In addition, the flexor e.m.g. showed increases in activity when the viscous friction was increased and a reduction in activity when it was decreased (the initial part of

TABLE 1. Effect of load change on control run accuracy

Viscous friction (× control value)	2·0	1·3	0·7
Normal (deg)	0·2 (0·2 ± 0·1)	0·1 (0·1 ± 0·1)	0·0 (−0·1 ± 0·1)
Anaesthetized (deg)	1·1** (1·1 ± 0·2)	0·5** (0·8 ± 0·3)	−0·4* (−0·4 ± 0·2)

Median (mean ± S.E. of the mean) values of thumb final position during control 1 subtracted from that during control 2 ($n = 9$).

* $P < 0·05$; ** $P < 0·01$ (Wilcoxon's signed rank test). Viscous friction during the conrol runs was $4·2 \times 10^{-3}$ Nm rad^{-1} s.

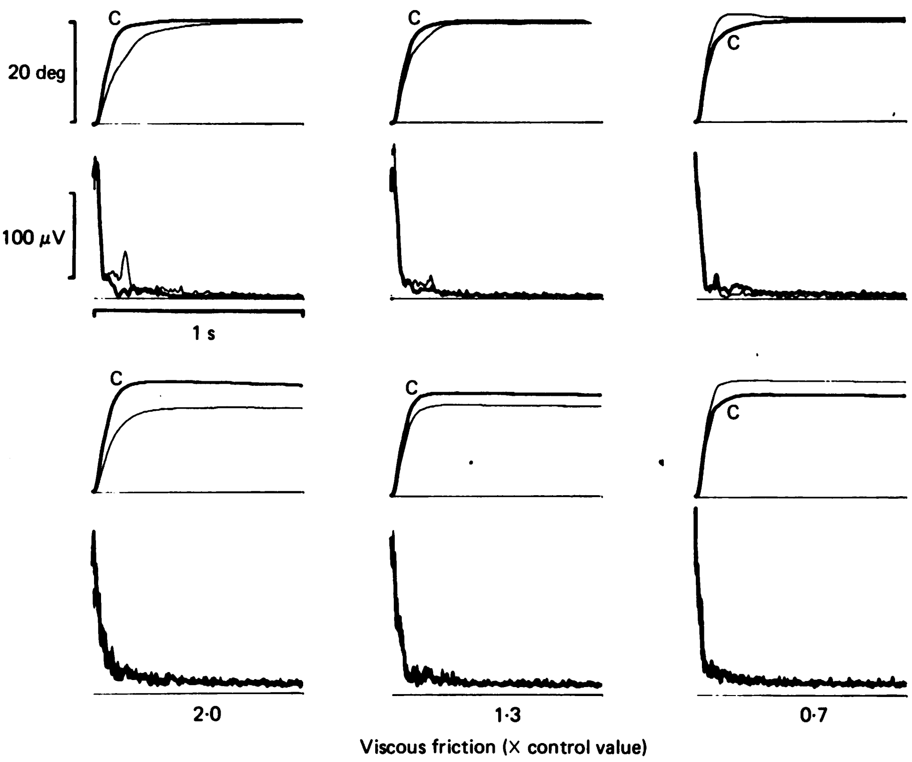

Fig. 3. Response of one subject to unpredictable changes in viscous friction of the load. The traces show the effect of three sizes of viscous friction change, both with sensation intact and after anaesthesia of the thumb. The control runs (control 1) are denoted both by the thicker lines and by C in the position traces. From above down are shown (*a*) thumb position (flexion produced an upward deflexion), and (*b*) the smoothed rectified e.m.g. from the long thumb flexor in the control 1 and test runs. Each trace represents the mean of thirty-two runs. The upper set of panels is from the intact thumb, the lower set of panels is after ring block of the thumb with local anaesthetic such as to abolish sensation. The left-hand series of records is for a larger increase in viscous friction, the middle series for a smaller increase and the right-hand series is for a reduction in viscous friction. The control value of viscous friction was set at $4·2 \times 10^{-3}$ Nm rad^{-1} s.

the flexor e.m.g. burst was not recorded, since it was movement of the thumb that triggered the data collection). During thumb anaesthesia the e.m.g. responses were drastically reduced, and thumb final position accuracy suffered. The thumb undershot when the viscous friction was increased and overshot when it was decreased.

These results were typical of those of all nine subjects. The mean final position error, compared to control 1, is shown in Fig. 4 for all subjects under all three conditions of load change, before and after anaesthesia. With sensation intact, increasing the viscious friction had no consistent effect on the accuracy of thumb positioning. Decreasing the viscous friction produced a small consistent overshoot. After anaesthesia, which effectively abolished afferent input from joint and cutaneous sources, the constant error under all three load change conditions increased. The magnitude and direction of the error was related to the size and direction of the change in viscous friction.

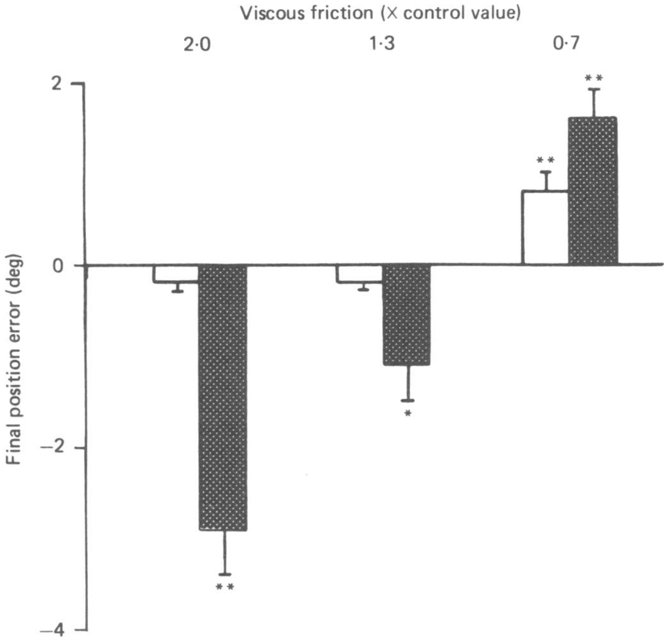

Fig. 4. The group mean (±S.E. of the mean) final position error during thumb flexion (test – control 1 for thirty-two runs) for all nine subjects for the three viscous friction changes, before (open columns) and after (filled columns) thumb anaesthesia. Values calculated from final position during control 1 subtracted from that during the test run ($n = 9$). A positional undershoot is shown by bars below the baseline, an overshoot by bars above the baseline. * $P < 0{\cdot}05$; ** $P < 0{\cdot}01$ (Wilcoxon's signed rank test).

The mean modification in thumb flexor e.m.g. resulting from the unpredictable changes in viscous friction is shown in Fig. 5 for all subjects for the three load changes, before and after thumb anaesthesia. With sensation intact, there was a consistent e.m.g. response during all three changes of viscous friction. The size of e.m.g. response was dependent upon the magnitude and direction of the viscous friction change.

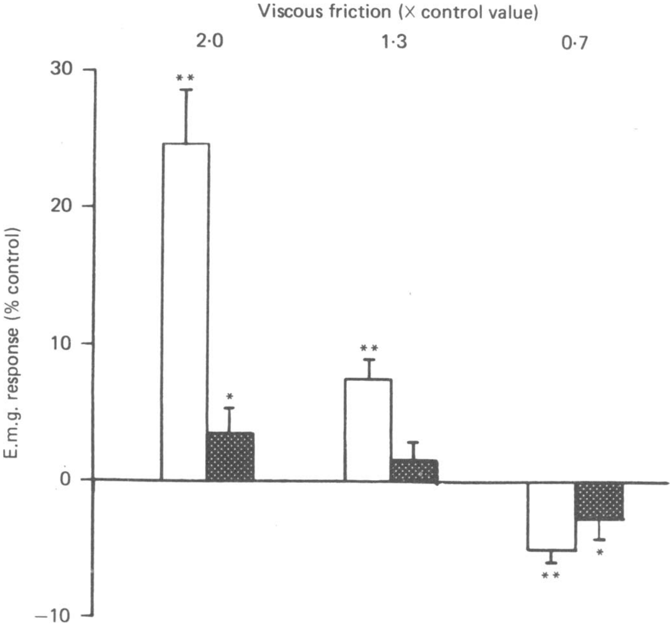

Fig. 5. The group mean (±S.E. of the mean) e.m.g. response of the long thumb flexor (test − control 1 for thirty-two runs) to the three viscous friction changes in all nine subjects, before (open columns) and after (filled columns) thumb anaesthesia. Values calculated as e.m.g. activity in the test run, measured over a 1 s period, minus that in the control 1 run, and expressed as a percentage of that in control 1 run. An increase in e.m.g. is shown as bars above the base line, and a decrease as bars below the base line. * $P < 0.05$; ** $P < 0.01$ (Wilcoxon's signed rank test).

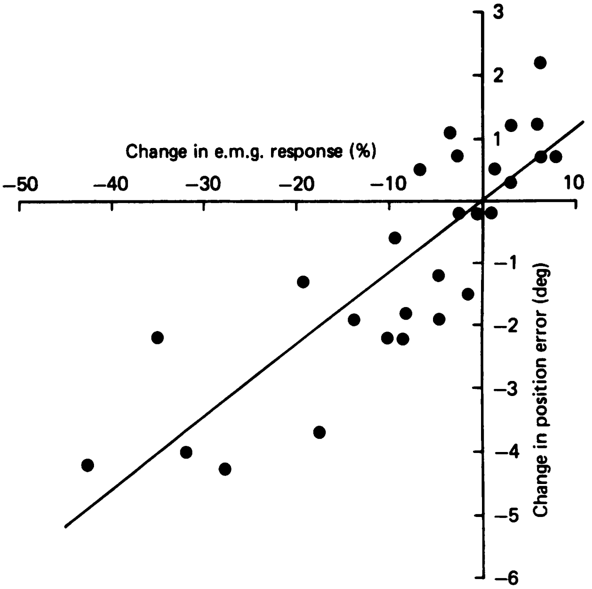

Fig. 6. Mean change in e.m.g. response of long thumb flexor plotted against mean change in final position error as a result of thumb anaesthesia for each of the nine subjects, and for the three viscous friction changes. Linear regression analysis yielded the equation $y = 0.01 + 0.12\,x$ ($r = 0.84$; $P < 0.001$).

Thumb anaesthesia drastically reduced the magnitude of the e.m.g. response to the test runs.

To investigate whether the decrease in accuracy after thumb anaesthesia was due to the failure of an appropriate muscle response, as indicated by alteration of the e.m.g. response to the test runs after anaesthesia, a scatter diagram composed of the mean data from each subject for each load change was plotted (Fig. 6). The change in e.m.g. response after anaesthesia is plotted on the abscissa; this was calculated by obtaining the percentage e.m.g. modification (see Methods) with sensation intact and subtracting it from the percentage e.m.g. modification after anaesthesia. Similarly, the change in accuracy after anaesthesia is plotted on the ordinate; this was calculated by subtracting the final thumb position error with sensation intact from that after thumb anaesthesia. These data, when subjected to linear regression analysis, yielded a regression line with a slope of 0·12 ± 0·01 (S.E. of the mean) and a correlation coefficient of 0·84. The loss in accuracy of compensation for unpredictable alterations in viscous friction after thumb anaesthesia therefore was well correlated with the loss of the muscle's response to such changes.

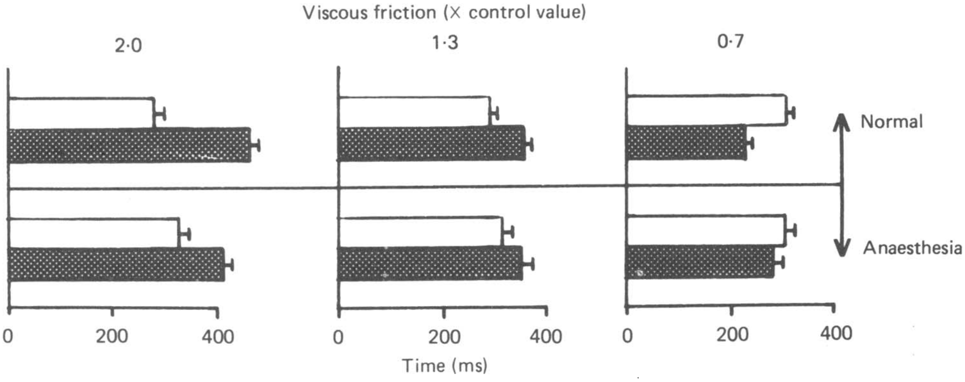

Fig. 7. Summary of thumb flexion movement duration data for the nine subjects for each of the three changes in viscous friction, before (top) and after (bottom) thumb anaesthesia. Shown are the group mean ± S.E. of the mean for control 1 runs (open columns) and for test runs (filled columns). The movement duration during control 1 runs differed from that during the test runs ($P < 0.01$; Wilcoxon's signed rank test) for all conditions.

The movement duration data is summarized in Fig. 7. With sensation intact, the effect of the viscous friction change was to reliably extend or shorten the movement duration depending upon the direction of the load change. With the thumb anaesthetized the effect persisted, but was less marked. By subtracting the mean movement duration during the control runs from that obtained during the test runs, the change before and after the anaesthetic could be compared. After thumb anaesthesia the introduction of a change in viscous friction had less effect on movement duration than under normal conditions for the larger increase ($P < 0.01$) and the decrease ($P < 0.05$) in viscous friction.

The effect of changing the viscous friction of the load on the maximum force exerted by the thumb on the lever during the flexion movement is given by the peak force ratio. The mean peak force ratio differed from unity ($P < 0.001$) for all sizes of load change and took the values of 1·23, 1·11 and 0·88 for the large increase, small increase and decrease in viscous friction respectively. The mean time of occurrence of the peak force after the start of the movement ranged from 60 to 91 ms for all conditions. Anaesthesia of the thumb had no effect on the magnitude or timing of this phenomenon. These data demonstrate that the thumb responded to the load change by developing an appropriate increase or decrease in peak force according to the direction and size of the changes in viscous friction. Fig. 8 shows an example from one subject of how the force (as indicated by the motor current), and flexor e.m.g. changed during control and test movements. Fig. 8 verifies that the motor current profiles for both the test and control runs were unaffected by thumb anaesthesia, at least for the period up to the time of generation of the peak force. After this time, as the motor current declined, with an intact thumb a burst of increased activity was seen in the e.m.g. record and the mechanical consequences of this burst were easily identified in the motor current record representing an increase in force generated by the thumb. With the thumb anaesthetized both these electrical and mechanical events were not apparent.

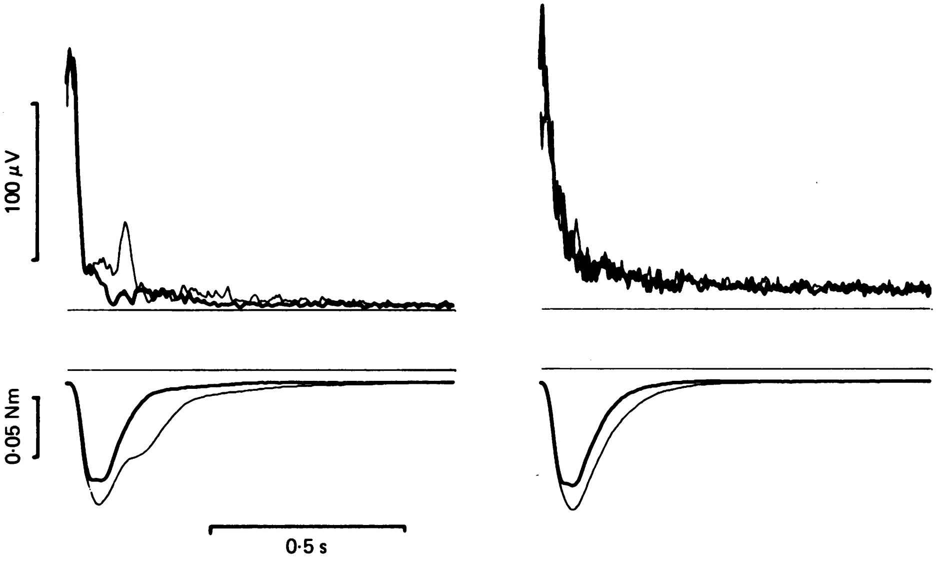

Fig. 8. Effect of an unexpected change in viscous friction (from $4{\cdot}2 \times 10^{-3}$ to $8{\cdot}4 \times 10^{-3}$ Nm rad^{-1} s) on the filtered rectified smoothed e.m.g. from the long thumb flexor (top) and motor torque (bottom), before (left) and after (right) thumb anaesthesia. In the absence of an e.m.g. response after anaesthesia, the muscle properties alone produce a different force profile, as reflected in the motor torque records, in response to an alteration in limb trajectory (right). A downward deflexion of the motor torque trace indicates a force acting to extend the thumb. The control 1 runs are denoted by the thicker lines. Each trace is the average of thirty-two runs.

TABLE 2. Latencies of e.m.g. response and voluntary reaction to changes in load

Viscous friction (× control value)	First burst (ms)	Push down (ms)	Let go (ms)
5·5	92 (±10)	208 (±8)	174 (±28)
3·8	89 (±3)	236 (±32)	202 (±20)
3·2	94 (±8)	314 (±98)	191 (±23)

Mean (±S.E. of the mean) latencies to onset of initial e.m.g. compensation (first burst), and to the changes in e.m.g. activity produced by the subject's voluntary intent to flex the thumb hard (push down) or relax the thumb (let go) as soon as the change in load was perceived, are shown ($n = 4$). The control value of viscous friction was set at $7{\cdot}5 \times 10^{-4}$ Nm rad^{-1} s.

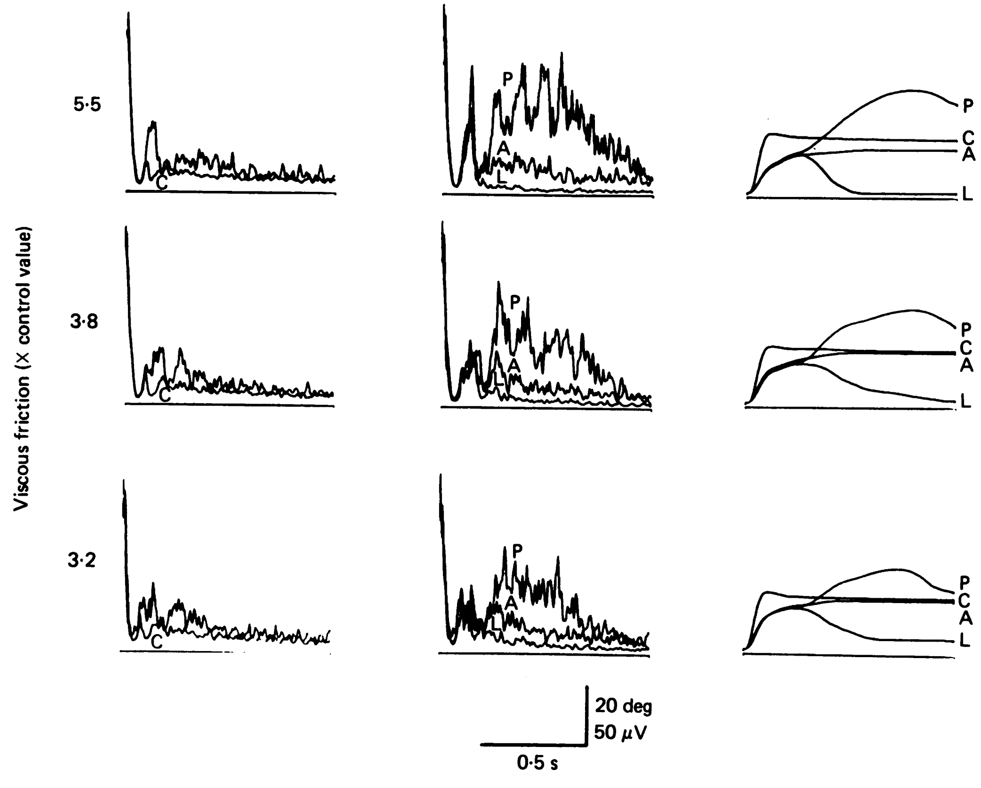

Fig. 9. Voluntary reactions to perception of the change in viscous friction of the load. Shown are the mean responses ($n = 16$) for three sizes of viscous friction change, the control value of viscous friction being set at $7{\cdot}6 \times 10^{-4}$ Nm rad^{-1} s. The left-hand series of traces show the filtered, rectified, smoothed e.m.g. during the control 1 (C) runs and the test runs. The middle series shows the filtered, rectified, smoothed e.m.g. for test runs only with the addition of the subject being asked to either push down hard (P), or relax and let go (L), or maintain accuracy (A) as soon as the change in viscous friction is perceived. The right-hand series shows the thumb lever position under all four conditions.

In a separate series of experiments on four subjects (three of whom had participated in the experiment described above), the average latency of the e.m.g. response to a change in viscous friction of the load together with the average latency of a voluntary response to the load change were evaluated. In order to facilitate latency measurements the e.m.g. response was accentuated by using different values of viscous friction to those used previously. The value of viscous friction used during the control runs was $7{\cdot}6 \times 10^{-4}$ Nm rad^{-1} s, and the three test values were 5·5, 3·8 and 3·2 times this value. Test runs were administered randomly with control runs (one test run to three control runs). The experimental protocol was the same as before, but the subjects were asked to comply with the instructions to either (1) maintain accuracy, or (2) press down as hard as possible, or (3) relax the thumb and let go, as soon as they felt the load to have changed from its control value. Each subject performed forty-eight control runs and sixteen test runs at each of the three changes in viscous friction and for each of the three instructions. The mean latencies from all four subjects are presented in Table 2. Approximately the first 100 ms of the e.m.g. response to the load change could not be altered by the subject producing a voluntary response upon perception of the change in load. The only measurements to be substantially affected by decreasing the size of the load change were the mean and standard error of the latency to 'push down'. However, this was due to the contribution from the one subject who had not participated in the earlier experiment and whose latency to 'push down' was substantially increased as the load changes became smaller and hence more difficult to detect. The results from one subject are presented in Fig. 9 and illustrate how the first major e.m.g. burst, which appears in response to the load change, occurs too early to be modified by a voluntary updating of the motor command to the thumb flexor muscle.

DISCUSSION

The principal aim of these experiments was to test the hypothesis that accurate limb positioning is attained in an open-loop fashion, with positional accuracy being maintained by the C.N.S. regarding the limb as a spring, the parameters of which it controls (Bizzi *et al.* 1976; Polit & Bizzi, 1979; Kelso & Holt, 1980). A movement of the limb to a specified position would then involve a central re-setting of agonist and antagonist muscle activities as if to specify a new spring rest length. Whilst it is true that a stationary limb has spring-like properties (Polit & Bizzi, 1979), the question has been whether the C.N.S. uses these properties to compute motor commands to accurately reposition a limb without the need of afferent feed-back. The results presented here, however, show that this is not the sole mechanism that is used, at least for rapid movements of the human thumb. A stretched spring returning to its rest length will always do so regardless of the magnitude of viscous friction acting. The deterioration in accuracy of final position of the thumb in the face of unpredictable alterations in viscous friction after thumb anaesthesia demonstrates that the system is not programmed as a simple open-loop spring (Figs. 3 and 4).

The reason why abolishing joint and cutaneous afferent input coincides with a loss in accuracy may be explained by the motor modifications that were observed in the e.m.g. recorded from flexor pollicis longus (f.p.l.). When the viscous friction of the lever was changed the thumb trajectory was altered and, with sensation intact, the motor output to the thumb flexor was modified appropriately. After thumb anaesthesia the magnitude of this e.m.g. modification was reduced. In fact, the extent to which the e.m.g. response was affected by the anaesthetic correlated well with the magnitude of the loss in accuracy. This suggests that the e.m.g. response provided effective compensation for unpredictable changes in viscous friction, thereby helping to drive the limb to the intended end position. In other words, the system controlling thumb final position in these experiments was a closed-loop system. The control system, however, although providing adequate compensation for increases in viscous friction, was less effective when the viscous friction was reduced. This was demonstrated by the observation that a small but consistent overshoot developed in the intact thumb when the viscous friction was unexpectedly decreased.

In addition to the closed-loop compensation provided by the change in motor outflow to f.p.l., the muscle properties alone were responsible for a significant amount of positional compensation. The thumb generated a different force profile in response to the load change even after anaesthesia when the e.m.g. response was abolished (Fig. 8). This difference was reflected in the peak force ratio and in the movement duration data both of which were shown to be a function of the magnitude and direction of the load change. Therefore, for a given pattern of motor excitation, deviation from the control limb trajectory caused the muscle to generate a force profile which differed in magnitude and duration from that of the control. These changes were such as to compensate partially for the unpredictable alteration in viscous friction and to help preserve positional accuracy. The well-known force–velocity and force–length relationships of skeletal muscle (Hill, 1938; Wilkie, 1950) go some way towards explaining this behaviour. Partridge (1965, 1966, 1967) observed and analysed the complex dynamic behaviour of isolated cat skeletal muscle and found it to have similar positional compensatory properties to those described here. He found that when the motor nerve was stimulated by a sinusoidally modulated pulse rate and the muscle was allowed to move an inertial load, the muscle shortened and lengthened in response to the changing stimulus. The important finding was that the amplitude of the movement of the load was independent of both the magnitude of the inertial load and the modulation frequency over a remarkable range. It was as if the muscle itself had an internal feed-back loop directing the size of force generation in response to load movement. As Partridge (1966) pointed out, nerve pulse rate defines load position more exactly than muscle force.

The question remains as to the mechanisms underlying the compensatory e.m.g. response. The change in viscous friction of the load, although not causing the flexor muscle to be stretched externally at any time during the movement, did alter the trajectory of the thumb from that anticipated by the subject. Therefore, there occurred a mis-match between the afferent signal that was expected as a result of the movement and that which was actually received by the C.N.S. In fact, the most likely way the subject could tell that a change in viscous friction had occurred was to be conscious of such a mis-match. Although subjects could reliably detect the large increases in viscous friction, and to some extent also could perceive the smaller load changes, the e.m.g. compensatory response took place well before any conscious voluntary reaction to the change in viscous friction could be executed. This implies that at least the first 100 ms of the e.m.g. compensatory response is automatic.

The e.m.g. response described here can be likened to the long-latency halt response described by Marsden, Merton & Morton (1972) as due to operation of the long-latency stretch reflex machinery. The comparison is supported by the similarity of behaviour of the two responses to thumb anaesthesia, both being severely reduced by abolishing joint and cutaneous afferent input (Marsden, Merton & Morton, 1977; Marsden, Rothwell & Traub, 1979). Marsden *et al.* (1972) explained the brisk response of the long thumb flexor to halting thumb flexion as due to muscle spindle discharge occurring, not as a result of muscle stretch, but as a consequence of a mis-match between extrafusal and intrafusal muscle lengths caused by halting the movement. Co-activation of α- and γ-motoneurones to drive thumb flexion would cause contraction not only of the extrafusal muscle fibres to produce this movement, but also of the intrafusal fibres, which would not be affected by the halt. A change in viscous friction which alters the movement trajectory would have a similar, but graded, effect depending upon the magnitude of the load change. Such a change in spindle discharge could then be used to reflexly alter the motor outflow to the flexor muscle in an appropriate manner.

Marsden, Merton & Morton (1976) examined the operation of the stretch reflex machinery in the long thumb flexor in a manner somewhat analogous to the present experiments. They wished to study the earliest time a subject could alter his motor outflow when faced with one or two constant torque loads unpredictably. The arrangement was to ask a subject to flex his thumb against a lever held by a constant torque provided by the torque motor against a backstop. The size of the load was varied randomly, but the subject could not estimate the load until his thumb had hit the lever and lifted it clear of the backstop. Under these circumstances Marsden *et al.* (1976) found that e.m.g. activity in the long thumb flexor altered to compensate for a new load after a latency of some 60–85 ms from the time the lever moved to the onset of the e.m.g. difference. This interval is very comparable to the range of mean latencies for the e.m.g. modification produced to overcome the largest increase in viscous friction for four subjects (80–120 ms).

From all these data we believe that a large part of the compensation for unpredictable changes in dynamic load introduced by variations in viscous friction during human thumb flexion is achieved accurately and automatically by operation of the long latency stretch reflex machinery, which provides true servo assistance to movement in these circumstances.

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