J. Physiol. (1979), 294, pp. 303–315
With 8 text-figures
Printed in Great Britain

EFFECT OF THUMB ANAESTHESIA ON WEIGHT PERCEPTION, MUSCLE ACTIVITY AND THE STRETCH REFLEX IN MAN

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(*Received 5 January 1979*)

SUMMARY

1. We have confirmed the results of Gandevia & McCloskey (1977) on the effect of thumb anaesthesia on perception of weights lifted by the thumb. Weights lifted by flexion feel heavier and weights lifted by extension feel lighter.
2. The change in size of the long-latency stretch reflex in flexor pollicis longus or extensor pollicis longus after thumb anaesthesia cannot explain the effect on weight perception by removal or augmentation of the background servo assistance to muscular contraction.
3. During smooth thumb flexion, thumb anaesthesia increases e.m.g. activity in flexor pollicis longus and extensor pollicis longus for any given opposing torque.
4. During smooth thumb extension the opposite occurs: e.m.g. activity in both extensor and flexor pollicis longus decreases.
5. Clamping the thumb at the proximal phalanx to limit movement solely to the interphalangeal joint reduces or abolishes the effect of anaesthesia on both weight perception and e.m.g. activity during both flexion or extension tasks.
6. Gandevia & McCloskey's findings on the distorting effects of thumb anaesthesia on weight perception cannot be used to support the hypothesis of an efferent monitoring system of the sense of effort. Our results emphasize the close functional relationship between cutaneous and joint afferent information and motor control.

INTRODUCTION

Recently, Gandevia & McCloskey (1977) have shown that anaesthesia of the thumb alters the subject's perception of heaviness of objects lifted by thumb movements. For example, they found that weights felt heavier after anaesthesia when lifted by thumb flexion, but lighter after anaesthesia when lifted by thumb extension. Gandevia & McCloskey suggested that these changes in perception might be due to alterations in reflex load compensation, citing the experiments of Marsden, Merton & Morton (1977) who had shown that thumb anaesthesia can abolish the long-latency stretch reflex in flexor pollicis longus. Loss of the stretch reflex after anaesthesia would decrease the servo assistance provided to central motoneurones, thereby necessitating a larger voluntary motor command to support the same weight, which implies that weight perception is estimated by monitoring the voluntary outflow from the brain to the muscle. However, this interpretation depends upon the assumption that anaesthesia causes no alteration in the anterior horn cell discharge to the thumb muscles lifting the weight. Marsden *et al.* (1977) noted that thumb anaesthesia led to an increase in flexor pollicis longus electromyogram (e.m.g.) activity during thumb flexion against a constant torque. Therefore, we set out to elucidate whether Gandevia & McCloskey's results could be explained by anaesthesia distorting the distribution of muscle activity.

We have confirmed Gandevia & McCloskey's findings that a weight lifted by thumb flexion feels heavier after thumb anaesthesia, and that a weight lifted by thumb extension feels lighter. But these perceptual illusions reflect corresponding changes in muscle e.m.g. activity because thumb anaesthesia disturbs the normal pattern of agonist and antagonist action.

METHODS

Our subjects were eleven unpaid normal volunteers and included two of the authors (M.T. and J.C.R.).

Weight matching

We repeated the experiments of Gandevia & McCloskey (1977) in which the subject lifted weights by flexing each thumb against a see-saw lever, from the other end of which hung a light bucket (out of sight) containing the weights. The subject lifted a reference weight (700 g) by flexion of his left (reference) thumb and he attempted to match it with weights presented to his right (indicator) thumb. The weights were varied by a random amount (50–250 g in 50 g divisions) in the right-hand bucket by the experimenter, who added or subtracted weights according to the subject's instruction. Ten weight matches were made and the average weight lifted by the right side was assumed to give an objective indication of the perceived heaviness of the reference weight. The subject then had a 10 min rest, after which the left thumb was anaesthetized and the weight matching process repeated.

In a subsidiary experiment, the proximal phalanx of both thumbs was clamped during the weight matching task, thus restricting movement to the interphalangeal joint.

In the weight matching trials with thumb extension only 500 g were put in the reference bucket. The bucket was run over a pulley so that the weight could be lifted by elevation of the other end of the lever.

Anaesthesia

The reference thumb was anaesthetized by digital nerve block using 2 ml. 2 % lignocaine without adrenaline, injected bilaterally 0·5 cm distal to the base of the digit. A rubber band was wound lightly round the base of the thumb before the lignocaine injection, and was released when the thumb had been rendered anaesthetic for two minutes. Anaesthesia lasted about 2 hr.

In three subjects we investigated whether cutaneous anaesthesia alone could distort the normal pattern of e.m.g. activity in flexor pollicis longus and extensor pollicis longus in the thumb flexion task. For this purpose 1 ml. 2 % lignocaine was injected subcutaneously into the pad of the thumb. This was a painful procedure and required about ten separate insertions of the hypodermic needle. Anaesthesia lasted about 2 hr.

Tracking and measurement of e.m.g.

Thumb flexion. The apparatus used was described by Marsden, Merton & Morton (1976). The thumb pad bore on a crank arm, which was carried on the spindle of a low inertia electric motor (Printed Motors Ltd, type G9M4H), with the spindle approximately co-axial with the interphalangeal joint. The movement of the crank of the arm deflected the lower beam of a Tektronix D10 oscilloscope by about 1 cm for 2° of rotation. The subject had to match the lower beam with an upper beam which moved from left to right across the screen at about 10°/sec every 15 sec.

E.m.g. activity was recorded between 1 cm diameter silver–silver chloride disk electrodes placed over the belly of flexor pollicis longus. Recordings from extensor pollicis longus were made via a pair of intramuscular 3/1000 inch diameter platinum iridium wire electrodes coated with Trimel. In six subjects, surface electrodes were also placed over the thenar eminence to give a measure of synergistic activity. The e.m.g. was pre-amplified by a Devices 3160 pre-amplifier with a time constant of 20 msec, low pass filtered to attenuate the signal by 3 db at 25 kHz and was then amplified by a Devices 3120 amplifier. The signal was full wave rectified and integrated by a Devices Signal Processor, type 4010.

The output from the potentiometer, which measured the angular position of the motor, was used to actuate a Schmidt Trigger when the thumb had flexed about 5°. This trigger was used both to reset the integrators and to activate a PDP12 computer. The computer was used to collect the rectified and integrated e.m.g. over a 1 sec epoch and average the result of fifteen separate trials at each torque studied. The change in the integral of the e.m.g. between the start and the end of the one second recording period was used as a measure of muscle activity. In absolute terms the integrated electromyogram could be calibrated in μV.sec, but since comparisons were not made between subjects the arbitrary units of measurement on the computer visual display unit were used (the programme AV used for recording the experiments was written by Mr H. B. Morton).

The subjects were asked to execute a series of smooth thumb flexions against a range of constant torques offered by the motor (from 0·04 to 0·22 Nm). This range was chosen to span the force required to lift the standard weight used in the weight matching task, and was presented in ascending order with a 2 min rest between each torque. As with the weight matching trials, the tracking task was performed with the proximal phalanx both clamped and unclamped.

When the subject had completed the tracking task, he repeated the task at two different torques at each end of the range to ensure that the results were reproducible and that fatigue had not taken place.

Thumb extension. In this task the polarity of the motor was reversed and the crank arm pressed against the surface of the thumb nail. Subjects found controlled extension more difficult than the flexion task, but all were able to track smoothly after about ten trial runs. The procedure was then the same as for thumb flexion, except that the range of torques was reduced (0·04–0·12 Nm) to allow for the relative weakness of the extensor muscle.

Stretch reflex

Stretch reflexes were elicited from flexor pollicis longus (seven subjects) or extensor pollicis longus (four subjects) as agonists, both before and after anaesthesia. During the thumb flexion task, the standing torque in the motor was 0·08 Nm, and this was increased suddenly to 0·18 Nm so as to stretch flexor pollicis longus at random during the movement. For thumb extension, the standing torque was 0·06 Nm, increasing suddenly to 0·14 Nm randomly during the task. E.m.g activity was recorded for 50 msec before and 200 msec after the stretch, and twenty-four or thirty-two responses were averaged. One half of all trials were controls in which there was no change in the applied torque.

Analysis of data

All statistical analysis was done on raw data, although for the purposes of illustration percentage changes are usually shown. In the weight matching experiments, an unpaired two-sided Student's t test of the ten matches made as a control and the ten matches made when anaesthetic was carried out to assess the significance of changes in perceived heaviness in individuals. Analysis of the whole group of subjects was made using a paired Student's t test of the mean data. Changes in the amount of e.m.g. activity were analysed using a paired Student's t test on the results obtained at the reference torque before and after anaesthesia.

RESULTS

Weight matching

We have represented the results in the same manner as Gandevia & McCloskey (1977) with the weight lifted by the indicator thumb, after anaesthesia of the reference thumb, being expressed as a percentage of the control weight matched before anaesthesia. We have confirmed Gandevia & McCloskey's original results. All nine subjects lifted a heavier weight with their indicator thumb after the reference thumb had been anaesthetized (mean increase 34 %) (Fig. 1*A*). However, when both thumbs were clamped at the proximal phalanx, anaesthesia of the reference thumb did not cause an increase in the weight lifted by the indicator thumb (mean increase only 6 % in seven subjects).

During thumb extension our results with the unclamped thumb again agreed with the observations of Gandevia & McCloskey. After reference thumb anaesthesia, the mean weight lifted by extension of the indicator thumb in ten subjects fell (mean decrease 37 %) (Fig. 1*B*). Nevertheless, when the experiment was repeated with both proximal phalanges clamped, there was on average only a 15 % fall in the weight lifted by the indicator thumb after anaesthesia (nine subjects).

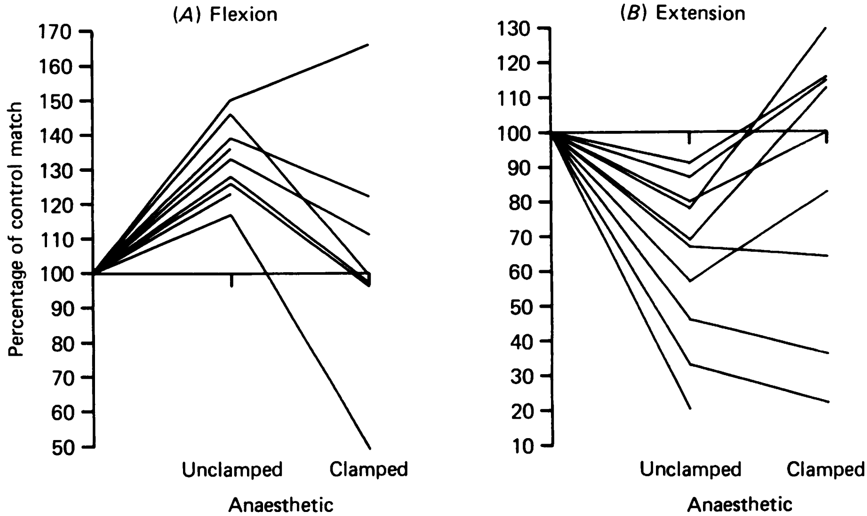

Fig. 1. The effect of anaesthesia on the estimation of weights lifted by either flexion (*A*) or extension (*B*) of the thumb. Results are expressed as a percentage of control estimates with the thumb intact. Each line joins three points for a single subject. The change in weight perception after anaesthesia (as a percentage of the control) is shown with the thumb unclamped and clamped for each subject. In *A*, the reference weight of 700 g was lifted by thumb flexion. When unclamped, all subjects perceived the weight as heavier (paired *t* test, $P < 0{\cdot}0005$). When the thumb was clamped, only two subjects still felt the weight as significantly heavier ($P < 0{\cdot}05$) but the rest did not and, on average, there was no difference from control estimates ($P > 0{\cdot}05$). In *B* the reference weight of 500 g was lifted by thumb extension. When unclamped, all the subjects perceived the weight as lighter after anaesthesia (paired *t* test, $P < 0{\cdot}005$). When clamped, only four subjects had a significant ($P < 0{\cdot}05$) decrease in weight perception and the group as a whole showed no change ($P > 0{\cdot}05$).

E.m.g. during tracking task

Fig. 2 shows the rise in the value of the integrated e.m.g. of flexor pollicis longus after one second of thumb flexion against a range of torques in a typical subject. The amount of e.m.g. activity recorded from the active muscle (measured as described in Methods) was linearly related to the torque exerted (cf. Bigland & Lippold, 1952). At any given torque there was an increase in the level of e.m.g. activity after the thumb had been anaesthetized. The increase in integrated e.m.g. at 0·1 Nm torque for all subjects after anaesthesia is shown in Fig. 3*A* as a percentage of the control level before anaesthesia at the same torque. The value of 0·1 Nm was chosen for display since this was the force exerted by the thumb in the weight matching flexion task. In all eight subjects there was an increase in flexor pollicis longus activity after anaesthesia (mean increase 44 %). As with weight matching, thumb anaesthesia produced much less distortion of long flexor activity when the proximal phalanx was clamped (mean increase 17 %). Coincident with this rise in flexor activity after anaesthesia, there was also an increase in the amount of extensor pollicis longus activity (mean increase 148 % in six subjects when unclamped) (Fig. 3*B*).

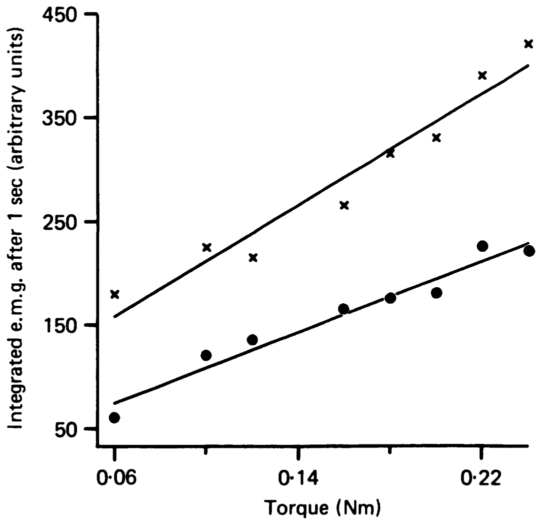

Fig. 2. Relationship between e.m.g. and torque in a single subject during a 10° isotonic thumb flexion. The rectified e.m.g. from flexor pollicis longus was integrated over a 1 sec period during thumb flexion, and the increase measured in arbitrary units. The increase in e.m.g. averaged for fifteen movements (ordinate) is plotted for each opposing torque supplied by the motor (abscissa). ●—●, unanaesthetized thumb unclamped; ×—×, anaesthetized thumb unclamped.

Anaesthesia of the thumb also altered the e.m.g. activity of the thenar muscles during thumb flexion. The extent to which these muscles were employed varied from individual to individual, and the relationship between the integrated thenar muscle e.m.g. activity and torque was not linear. However, in four of six subjects studied, there was a considerable reduction in thenar e.m.g. after anaesthesia. Thus, thumb anaesthesia appears to change the relationship between agonist and synergist as well as between agonist and antagonist.

The effect of thumb anaesthesia on extensor pollicis longus e.m.g. activity in the thumb extension task is shown for one subject in Fig. 4. It can be seen that contrary to the behaviour of the flexor pollicis longus on the thumb flexion task, when the long extensor was used as an agonist, the integrated e.m.g. *vs.* torque relationship decreased after the thumb was anaesthetized. The percentage change in extensor pollicis longus e.m.g. at 0·06 Nm torque, which is equivalent to the 500 g reference weight lifted in the weight matching extension task, is shown for six subjects in Fig. 5. The mean fall in integrated e.m.g. was 33 %. As with weight matching,

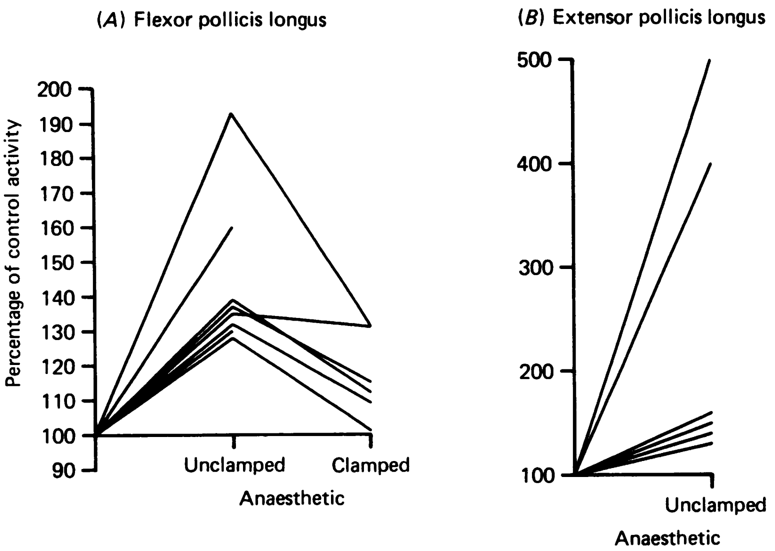

Fig. 3. Changes in e.m.g. after thumb anaesthesia in flexor pollicis longus (*A*) and extensor pollicis longus (*B*) during smooth flexion of the thumb. Integrated e.m.g. was measured as described in the legend to Fig. 2. The increase at 0·1 Nm torque with the thumb anaesthetized is expressed on the ordinate as a percentage of the activity in the same mode (clamped or unclamped) when not anaesthetized. Each line joints three points for a single subject. In *A* the e.m.g. activity in the agonist increased by 44 % after anaesthesia in eight subjects when unclamped (paired *t* test, $P < 0{\cdot}0005$). When clamped the mean increase was only 17 % ($P < 0{\cdot}005$). In *B* the activity in the antagonist increased by 148 % after anaesthesia in six subjects when unclamped (paired *t* testing of these data is inappropriate because the distribution is not normal: Wilcoxon's signed rank test gives $P < 0{\cdot}05$).

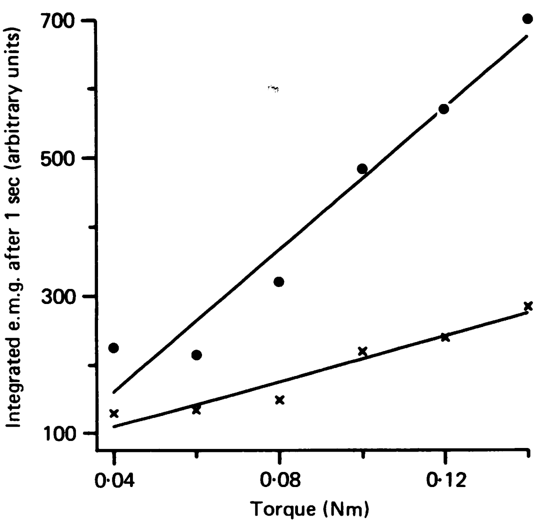

Fig. 4. Relationship between e.m.g. in extensor pollicis longus and torque in a single subject during a 10° isotonic thumb extension. The data are expressed as in Fig. 2. ●—●, unanaesthetized thumb unclamped; ×—×, anaesthetized thumb unclamped.

clamping the distal phalanx reduced the magnitude of the change in muscular activity caused by anaesthesia (mean decrease only 17 %). The change in antagonist muscle activity after anaesthesia was not as clear as in the thumb flexion task. During thumb extension, flexor pollicis longus was used as a brake to smooth the movement produced by the contraction of the long thumb extensor. The level of activity in the long flexor depended on the accuracy and strategy used to track, which varied from subject to subject. However, for five subjects in whom repeatable results were obtained, flexor pollicis longus activity decreased by an average of 13 % after anaesthesia when the thumb was not clamped.

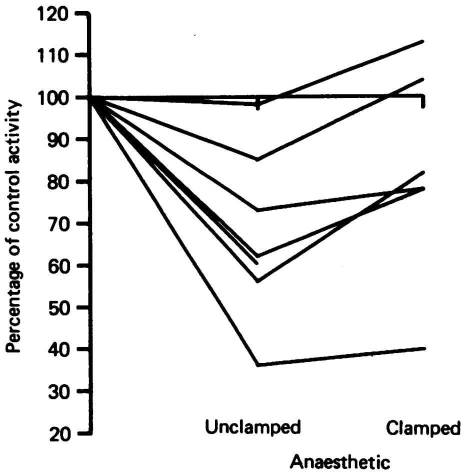

Fig. 5. Changes in e.m.g. of extensor pollicis longus after anaesthesia during smooth isotonic extension of the thumb. Muscle activity is expressed as in Fig. 3, as percentage changes over unanaesthetized levels during the same task. The mean decrease after anaesthesia in seven subjects when unclamped was 33 % (paired t test $P < 0{\cdot}01$), but when clamped was 17 % (paired t test $P > 0{\cdot}05$).

Thumb pad anaesthesia

It could be argued that the rise in muscular activity in the thumb flexion task and the change in weight perception after anaesthesia were due to the mechanical effect of the lignocaine injected at the base of the thumb. The thumb was swollen for some time after the injection and this might have limited movement at the interphalangeal joint. To exclude this possibility, we anaesthetized the pad of the thumb alone in three subjects and studied thumb flexion (Fig. 6). All three experienced an increased sense of heaviness. In addition, clamping of the proximal phalanx diminished the distorting effect of anaesthesia in the tracking task and in the weight matching task. This result suggests that anaesthesia of the thumb pad alone could lead to distortion of the long flexor e.m.g. and weight perception in the flexion task. However, we cannot rule out the possibility of spread of some anaesthetic to the interphalangeal joint capsule, although appreciation of passive movement at the joint was unaffected, even with the thumb relaxed.

Stretch reflexes

The stretch reflex in flexor pollicis longus when used as an agonist during thumb flexion was examined in seven subjects (five of whom had never undertaken the task before). The results for one subject are shown in Fig. 7. Anaesthesia in this subject did not alter the stretch reflex but did cause an increase in the e.m.g. activity of the long thumb flexor, an increase comparable to the increased perception of heaviness when lifting weights by thumb flexion. The size of the stretch reflex was

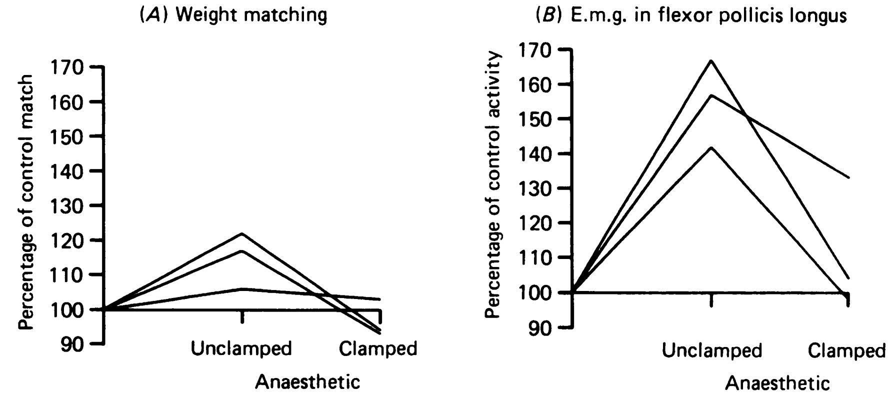

Fig. 6. The effect of thumb pad anaesthesia on weight perception and e.m.g. in three subjects. In *A* the results of weight matching are presented as in Fig. 1. The weight felt heavier when the thumb was unclamped (an increase of 18 %), but no different when the thumb was clamped. In the same session, the subjects also performed a series of smooth thumb flexions before and after anaesthesia, and the changes in e.m.g. in flexor pollicis longus are shown in *B*. Anaesthesia increased e.m.g. activity by 55 % with the thumb unclamped and by 12 % when clamped.

expressed as the activity in the electrically integrated e.m.g. between 25 and 80 msec after the stretch, as a percentage of the activity in the same interval during control trials when no stretch was given. The size of the stretch reflex before and after anaesthesia is shown in the Table. On average, the stretch reflex decreased by 30 % after anaesthesia, but in only one subject was it dramatically reduced, and in two (who were practised in the task) it was not altered.

On the basis of the observed effect of anaesthesia on the stretch reflex in flexor pollicis longus in individual subjects, we have calculated the expected change in weight perception. In subjects M.T., B.D., C.R. and L.V., the effect of anaesthesia was quite insufficient to explain the observed increase in perceived heaviness. In the two remaining subjects, D.R. and J.M., the observed perceptual changes could only be explained if the stretch reflex contributed over 25 % of the force of contraction.

Since anaesthesia decreased the perceived heaviness of weights lifted by thumb extension, we looked at the effect of anaesthesia on the stretch reflex in extensor pollicis longus during thumb extension. In only one of four subjects was there an increase in the size of the stretch reflex in the long extensor after anaesthesia, but this was not large enough to explain the observed change in weight perception (see Table 1). In the other three subjects, the reflex size decreased rather than increased.

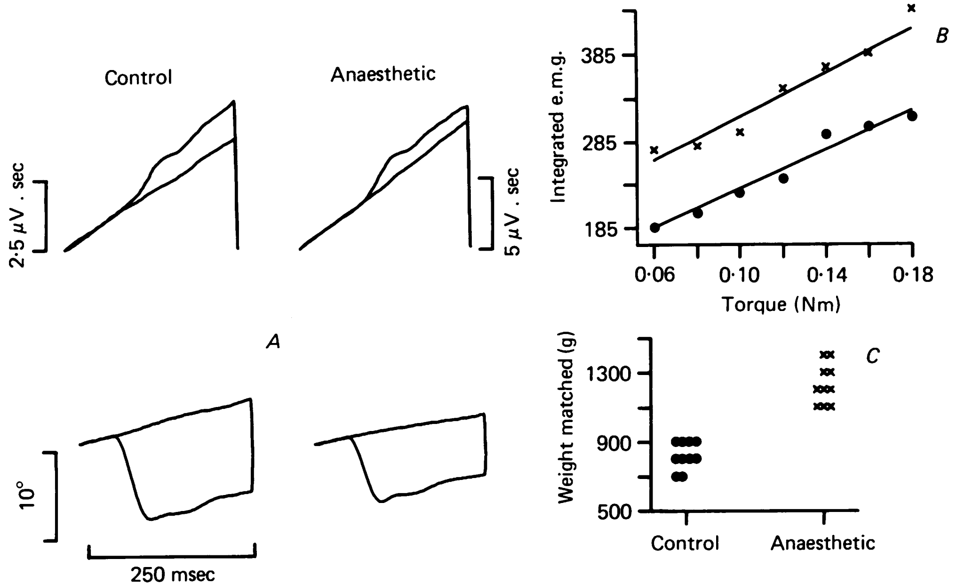

Fig. 7. Effect of anaesthesia on the stretch reflex (*A*) and e.m.g. (*B*) in flexor pollicis longus and on weight perception (*C*) during thumb flexion in a single subject (B.D.). The upper two traces in *A* are integrated e.m.g.s from surface electrodes scaled to have the same slope (note the different calibration markers); the lower traces are records of angular displacement of the terminal phalanx of the thumb. Each trace is the average of thirty-two trials, the anaesthetized trials being performed last. A control record with no perturbation is shown as well as the response to stretch of flexor pollicis longus. The upper, diverging, trace in the integrated e.m.g. is the response to stretch; the divergence occurs with a latency of approximately 45 msec after the perturbation. In absolute terms, it is larger when anaesthetic, but the scaling of the traces shows that it constitutes the same proportional increase over background activity (see Marsden *et al.* 1976). The smaller displacement record during stretch of the anaesthetized thumb is a reflexion of the stiffer system caused, in part, by the extra muscular activity around the joint. In *B*, the corresponding results of uninterrupted smooth thumb flexion are shown as in Fig. 2. × — ×, thumb anaesthetized; ●—●, control, without anaesthesia. In *C* the ten actual weights matched by the indicator thumb to a reference 700 g lifted by thumb flexion are shown. The average weight matched with the thumb intact (●) was 820 g, rising to 1370 g when anaesthetized (×) (unpaired *t* test: $P < 0{\cdot}001$), an increase of 67 %.

TABLE 1. Changes in stretch reflex size and in weight perception with thumb anaesthesia. In columns 2 and 3 the size of the stretch reflex between 25 and 80 msec after the stretch has been estimated from integrated e.m.g. records such as those shown in Fig. 8. The increase in activity is expressed as a percentage change from the control e.m.g. activity in the same period. Column 2 shows stretch reflex size with the thumb intact and column 3 the size when the thumb was anaesthetized. The changes in percentage size of the stretch reflex are shown in column 4

		Stretch reflex size		
	Subject	Non-anaes.	Anaes.	% change in stretch reflex
Flexion	M.T.	128	103	−20
	B.D.	79	87	+9
	C.R.	250	250	0
	D.R.	66	31	−52
	J.M.	253	26	−90
	C.T.	66	49	−26
	L.V.	90	60	−33
Extension	M.T.	74	34	−47
	J.C.R.	464	492	+6
	C.R.	41	3	−92
	P.D.R.	28	13	−53

Forefinger anaesthesia

Gandevia & McCloskey (1977) found that anaesthesia of the forefinger of the lifting hand increased the sense of heaviness in thumb flexion tasks. Stimulating the forefinger had the opposite effect and made weights feel lighter. We have not been able to find any changes in flexor pollicis longus e.m.g. activity after anaesthesia or electrical stimulation of the forefinger. Nor have such manoeuvres altered the stretch reflex in the long flexor during thumb flexion (Fig. 8). In fact, in the subject illustrated, the stretch reflex in flexor pollicis longus was slightly larger during forefinger anaesthesia which would be predicted to cause a decrease, rather than an increase in thumb weight perception.

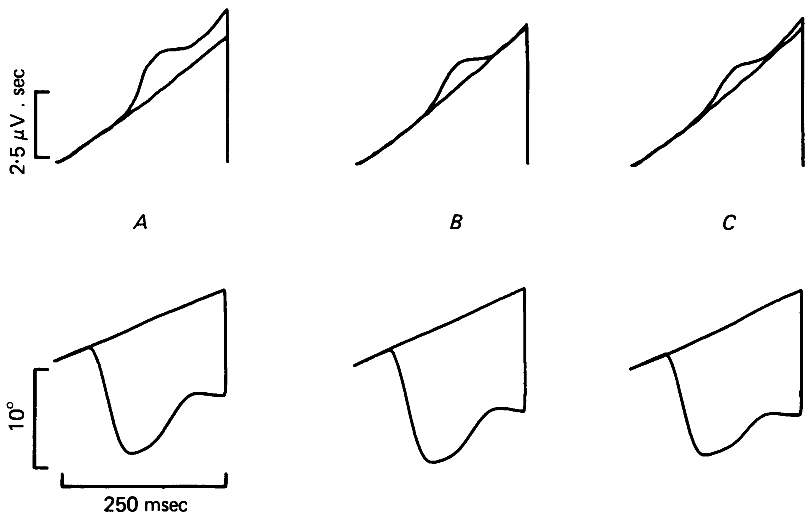

Fig. 8. Stretch reflex in flexor pollicis longus during electrical stimulation or anaesthesia of the forefinger of the same hand. The upper traces are the integrated e.m.g.; the lower traces the angular displacement of the terminal phalanx of the thumb as in Fig. 7*A*. The traces are averages of thirty-two trials each. Those in *A* were done first with the forefinger rendered anaesthetic by application of a rubber band around the proximal phalanx for 1 hr. The records in *B* and *C* were performed 15 min after recovery from anaesthesia. In *B*, the forefinger was completely normal. In *C*, it was electrically stimulated with 200 μsec pulses of 55 V at 45 Hz through ring electrodes round the proximal phalanx. This produced a sensation of pressure along the whole length of the digit, but was not painful. The finger was only stimulated while the thumb was tracking, for a period of approximately 2 sec, and not during rests between trials. The computed size of the stretch reflex between 25 and 85 msec after the perturbation (see text) was 230, 179, 163 % of control in *A*, *B* and *C*, respectively.

DISCUSSION

Our results confirm Gandevia & McCloskey's (1977) observations that thumb anaesthesia changes the perception of weights lifted by thumb flexion or extension. However, these perceptual illusions are not due, as they suggested, to concurrent changes in the stretch reflex of the active muscle. Anaesthesia of the thumb may make weights lifted by thumb flexion feel heavier without necessarily altering the stretch reflex in flexor pollicis longus, and it may make weights lifted by thumb extension feel lighter, but it never increases the stretch reflex in extensor pollicis longus.

Such perceptual illusions are, however, accompanied by corresponding changes in the degree of muscle activation as detected by surface e.m.g. measurement. Thus the increased heaviness perceived on thumb flexion after anaesthesia is accompanied by increased activity in flexor pollicis longus, while the decrease in heaviness on thumb extension is accompanied by a decrease in extensor pollicis longus activity. The sense of heaviness thus is linked directly to the degree of activation of the agonist muscle.

These changes in e.m.g. activity produced by thumb anaesthesia were not due to any systematic change in electrode impedance in the course of the experiments. In three subjects the flexor tracking task was carried out in the same session as the extensor task; the e.m.g. increased in the former but decreased in the latter in both the agonist and the antagonist. In addition, anaesthesia of the forefinger did not alter flexor pollicus longus e.m.g. activity in the flexor task, while anaesthesia of the thumb decreased flexor pollicis brevis e.m.g. activity at the same time as increasing flexor pollicis longus activity in the flexor task. The differences in results obtained in these various tasks also makes it most unlikely that alterations in e.m.g. activity after thumb anaesthesia were due to changes in the degree of synchronization of the motor units such as to alter the summed action potentials recorded by surface electrodes.

Since the perceptual illusions of heaviness are accompanied by corresponding changes in e.m.g. activity in the active muscle, the illusions themselves do not prove conscious awareness of changes in central command signals. Whether or not man is aware of corticospinal motor discharge by some form of 'sense of effort' must be decided on the basis of other evidence.

The changes in muscle activation of the prime mover caused by thumb anaesthesia are associated with corresponding changes in activation of the antagonist muscle. Thus, after thumb anaesthesia, the increase in activity in flexor pollicis longus on thumb flexion is associated with a concurrent increase in activity in extensor pollicis longus, while the decrease in activation of extensor pollicis longus on thumb extension is accompanied by a corresponding decrease in flexor pollicis longus e.m.g. Indeed, the changes in contraction of the prime mover after anaesthesia are necessary to maintain the same force of contraction required to lift the weight in the face of the changes in activity of the antagonist. Anaesthesia increases antagonist contraction on thumb flexion, so flexor pollicis longus is activated more to lift the weight, which now feels heavier. The reverse occurs with thumb extension. Anaesthesia of the thumb distorts the normal balance of agonist–antagonist muscle action.

Anaesthesia of the pad of the thumb sufficient to abolish cutaneous sensation without affecting appreciation of joint position has effects similar to those of anaesthesia of the whole thumb. Sensory information from the skin of the pad of the thumb therefore appears to regulate the balance of contraction between the muscles responsible for moving the distal phalanx of the thumb. This effect seems most specific for the skin of the thumb, for anaesthesia of other fingers does not greatly alter activity in flexor and extensor pollicis longus. Although Gandevia & McCloskey (1977) found that anaesthesia of the first finger (but not the other fingers) did alter perception of weights lifted by thumb flexion, the effects were small and we have not found finger anaesthesia to alter contraction of flexor and extensor pollicis longus in such a task. We do not know how this distortion of muscular activity is brought about after thumb anaesthesia. However, the findings of Marsden *et al.* (1977) of the effect of thumb anaesthesia on the flexor pollicis longus long-latency stretch reflex have underlined the possible importance of cutaneous and joint afferent input in more subtle motor function. In particular, the experiments of Lewis & Porter (1974) have shown that cutaneous anaesthesia of the wrist in monkeys increases the pyramidal cell discharge associated with movement of the hand.

Information from the thumb itself is not always required for the correct balance of activation of flexor and extensor pollicis longus required to flex the terminal phalanx. Thus, the effects of anaesthesia on muscle activation and weight perception during thumb flexion are reversed by clamping the proximal phalanx of the thumb. Why clamping should restore the behaviour of the anaesthetized thumb towards normal is not clear. Clamping prevents contraction of flexor and extensor pollicis longus from bending the proximal metocarpo-phalangeal joint of the thumb. With the thumb free, the effects of contraction of these muscles to cause thumb flexion must be judged by changes in pressure on the thumb pad, changes in muscle length, and change in angles of both the terminal interphalangeal joint and the proximal metacarpo-phalangeal joint. Furthermore, with the thumb free, changes in length and contraction of flexor and extensor pollicis brevis become important. The computation of this complicated mass of information obviously is simplified by clamping the proximal phalanx of the thumb, which eliminates movement at the proximal joint and also the effects of changes in short thumb muscles. In this simpler situation with the thumb clamped, cutaneous information from the pad of the thumb appears less essential for apportioning the balance of contraction between agonist and antagonist.

In conclusion, information from the thumb, probably predominantly from the skin of the pad, is required to determine the correct innervation of flexor and extensor pollicis longus to execute flexion and extension of the terminal phalanx of the freely mobile thumb. Loss of this information, as by anaesthesia, causes a faulty balance of innervation of the agonist and antagonist. As a result, errors in the perception of the heaviness of weights lifted by thumb movement occur. The change in the feeling of heaviness reflects the change in the degree of activation of the agonist required to lift the weight, which itself reflects the change in degree of activation of the antagonist caused by the anaesthesia. Obviously there is an intricate functional connexion between the sense organs of the human thumb and the muscles that move it.

We should like to thank Mr H. C. Bertoya and Dr B. L. Day for expert technical assistance during the course of these experiments. This work was supported by the Medical Research Council.

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