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EFFECTS OF PRIOR INSTRUCTION AND ANAESTHESIA ON LONG-LATENCY RESPONSES TO STRETCH IN THE LONG FLEXOR OF THE HUMAN THUMB

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SUMMARY

1. Long-latency (40–80 ms) electromyographic (e.m.g.) responses of the contracting flexor pollicis longus to stretches applied at the thumb-tip, were studied in normal human subjects. Stretches were applied during four classes of contraction: (i) isometric 'hold', in which the subject held a steady isometric contraction; (ii) isometric tracking, in which the subject tracked a steadily rising force target; (iii) isotonic tracking, in which the subject flexed against a constant torque to track a position target; (iv) weight-lifting, in which the subject lifted a weight hung at one end of a lever by pressing the thumb-tip on the other end of the lever. The effects on the responses of prior instructions to 'resist' or to 'let go', and of local anaesthesia of the thumb, were studied.

2. The ability to modify the size of the long-latency e.m.g. response in accordance with prior instruction was variable. All subjects tested could do so during isometric holding contractions, but many could not do so during the other forms of contraction.

3. Local anaesthesia of the thumb significantly reduced the long-latency e.m.g. response in only some subjects, and abolished it in none. The reduction was most reliably seen for isometric force tracking contractions.

4. During thumb anaesthesia in different subjects, there was a significant correlation between the proportional increase in apparent heaviness of an object lifted by thumb flexion and the proportional reduction in the size of the long-latency e.m.g. response to muscle stretch.

INTRODUCTION

It is now well established that rapid stretch of a voluntarily contracting muscle evokes electromyographic (e.m.g.) responses at various latencies. The shortest-latency component corresponds to a tendon jerk, and has been called the M1 response (Tatton, Forner, Gerstein, Chambers & Liu, 1975). In some muscles, such as the digital flexors, this component is small and inconsistent. A component with a latency which is longer than the M1 response, but shorter than a conventionally measured voluntary reaction time, is the so-called long-latency response (Marsden, Merton & Morton, 1972*a*, *b*, 1976*a*, *b*), or M2 response (Tatton *et al.* 1975). The mechanism underlying this latter component has interested many: it has been said that it might represent a 'long-loop', possibly transcortical (Phillips, 1969) reflex, but other evidence has indicated that it may be based upon the discharges of group II spindle afferents (Matthews, 1984*a*, *b*). The possibility of such responses being based on a partitioning of bursts of spindle afferent input has also been raised (Hagbarth, Hagglund, Wallin & Young, 1981). It was not our intention in the present study to attempt to resolve these matters. Rather, the aim of the present experiments was to re-investigate, with an appreciable number of subjects, various matters on which the literature is at present contradictory.

In many muscles, the magnitude of the long-latency response can be modified according to the subject's pre-formed intention to 'resist' or to 'let go' in response to the stretch (Hammond, 1956, 1960; Newsom Davis & Sears, 1970; Evarts & Tanji, 1976; Iles, 1977; Evarts & Granit, 1976; Tatton, Bawa, Bruce & Lee, 1978; Colebatch, Gandevia, McCloskey & Potter, 1979). Some of these modifications have been said to be modifications of fast, voluntary reactions, rather than of reflex responses (Marsden, Rothwell & Day, 1983). Marsden, Merton & Morton (1971, 1972*a*, *b*, 1973, 1975, 1976*a*, *b*, *c*, 1977) carried out an extensive series of experiments on long-latency responses to stretch of the contracting flexor of the terminal joint of the thumb, flexor pollicis longus. In all of these studies the authors were the experimental subjects. They reported that long-latency responses in the thumb could *not* be influenced by a subject's volitional 'set', and indeed, they took this finding as evidence for the reflex, rather than voluntary, nature of the response (Marsden *et al.* 1976*a*). In this paper they noted, however, that the rapid isotonic contractions, within which they introduced their stretches of the thumb flexor, were unlike the steady isometric contractions within which Hammond (1956, 1960) had imposed stretches when he had described an influence of volitional 'set'. They thus implied that the nature of the muscular contraction being performed might determine whether or not volitional 'set' could influence the size of long-latency response. Subsequently, Marsden, Merton, Morton, Adam & Hallett (1978), and Rothwell, Traub & Marsden (1980), reported that later components of the long-latency e.m.g. response to thumb stretch *could* be influenced by volitional 'set', but did not take up the question of why the earlier findings had been to the contrary. Subsequently, Day, Rothwell & Marsden (1983) noted that the influence of 'set' was small for the thumb, in comparison with its influence on the elbow extensor, triceps.

Marsden *et al.* (1971) also reported that in the thumb '...the stretch reflex is...abolished or, at any rate, greatly reduced' by thumb anaesthesia. They subsequently confirmed this report (Marsden *et al.* 1973, 1975, 1976*a*, 1977). Later they noted that the effect of anaesthesia became less potent when tested repeatedly in the same subject over a period of years (e.g. Marsden *et al.* 1977). It was proposed that anaesthesia acted by turning down the 'gain' of a reflex loop based on intramuscular stretch receptors (Marsden *et al.* 1972*a*), or by removing a source of 'gating' facilitation to the action of muscle spindles, or by 'co-operating at a cortical level' with inputs from muscle spindles to permit stretch reflexes to occur (Marsden *et al.* 1977). Nevertheless, it was also noted that the result in the thumb might mean that the long-latency responses are not based upon intramuscular receptors, and might instead be generated by cutaneous or joint receptors (Marsden *et al.* 1976*a*). Apparently analogous long-latency responses in other muscles, however, are elicited by excitation of intramuscular receptors, rather than joint or cutaneous receptors. This has been demonstrated in experiments which showed that local anaesthetic or ischaemic block of joint or cutaneous receptors does not reduce the long-latency responses to stretch of the flexors of the big toe (Marsden *et al.* 1977), or wrist (Bawa & McKenzie, 1981), or of reflexes from infraspinatus or pectoralis major (Marsden *et al.* 1975, 1977).

In 1977 Gandevia & McCloskey studied the increase caused by thumb anaesthesia in apparent heaviness of objects lifted by flexion of the thumb. Their study had been inspired by the reports by Marsden *et al.* (1977) that thumb anaesthesia abolished long-latency stretch responses, and Gandevia & McCloskey interpreted the increases in subjective heaviness as due to the increased voluntary 'effort' needed to compensate for an anaesthesia-induced loss of reflex assistance to contraction. This interpretation was criticized by Marsden, Rothwell & Traub (1979), who claimed that anaesthesia does *not* abolish the long-latency responses to muscle stretch in the thumb, but reduces them, on average, by only about 30%, and in some subjects not at all. Marsden *et al.* (1979) did not, however, discuss the apparent conflict between their findings and the earlier ones of Marsden *et al.* (1977). Subsequently, in experiments reported briefly by Potter & McCloskey (1979), and experiments on two subjects by Matthews (1984*a*), anaesthetizing the thumb was found to have no effect, or only a small effect, on long-latency responses to stretch.

The present study was undertaken to attempt to resolve the conflicting findings, outlined above, on the influences of volitional 'set' and thumb anaesthesia on long-latency responses to stretch of the contracting thumb flexor. Various forms of contraction were studied. The work has been reported in abstract form (Loo & McCloskey, 1981).

METHODS

Experiments were performed on twenty-six normal subjects of both sexes, aged 19–32. The authors were not subjects. Not all subjects performed all tests. The flexor pollicis longus of the right thumb was studied in all subjects. All but three of the subjects were right-handed. Subjects were given time to familiarize themselves with the experimental procedures on the day of the experiment, but no special or extended training was given. For each experiment the subject was seated at a table on which the right forearm rested. The fingers of the right hand were wrapped loosely around a vertical rod projecting from the level of the table top. At the top of this rod was a metal T piece of adjustable height upon which the proximal phalanx of the thumb rested, leaving the terminal phalanx projecting beyond, and free to move in a vertical plane. The interphalangeal joint of the thumb was flexed 10–35 deg from its fully extended position, according to the subject's preference. A horizontal bar above the proximal phalanx, or adhesive tape around it, was used to hold the proximal phalanx on the T piece on which it rested; this method of immobilization did not obstruct the blood supply to the thumb and was not uncomfortable. A dual-beam oscilloscope was placed before the subject at eye level; displayed on this were a target beam, and a beam registering the tension exerted in an isometric contraction, or the position of the thumb during an isotonic contraction.

The thumb was anaesthetized in some subjects after informed consent had been obtained in writing. Digital nerve block was performed by the injection of 1–2·5 ml 2% lignocaine (without adrenaline) at both sides of the base of the thumb (Gandevia & McCloskey, 1977). Anaesthesia was confirmed to touch, pressure and pain before observations were commenced, and was repeatedly confirmed during the experiment. Anaesthesia lasted for 45 min–2 h. Observations were discontinued as soon as anaesthesia became incomplete.

Types of contraction. External forces were applied to stretch the flexor of the terminal joint of the thumb in four separate series of experiments. In each series a different form of muscular contraction of the thumb was in progress at the application of stretch. These forms of contraction were: (i) an isometric 'hold', in which the subject held a steady isometric force by thumb flexion, (ii) isometric tracking, in which the subject tracked a force target (see below) by increasing the force of isometric flexion of the thumb, (iii) isotonic tracking, in which the thumb was flexed against a constant torque to track a position target, and (iv) weight-lifting, in which the subject lifted a weight hung at one end of a 'see-saw' device (Gandevia & McCloskey, 1977), by flexing the distal phalanx so as to press on the other end.

In the isometric tasks, subjects pressed the ball of the thumb against a flat circular (2 cm diameter) brass disk set on the end of a rod, the position of which was controlled by a large electromagnetic vibrator (Advanced Dynamics, AVN 300) operating under position feed-back. Strain gauges attached to the shaft of the vibrator measured the force between it and the thumb-tip, and this signal was displayed to the subject on one beam of the oscilloscope before him. In the isometric holding task subjects were required to exert a constant pre-set force of between 2 and 5N to align the tension signal and the target beam. In the isometric tracking task the tension signal was offset on the screen by a ramp voltage which deflected it through 8 cm in 1 s if no alteration in exerted tension occurred. The target beam remained stationary. In order to hold the tension signal on target through this period the subject had to increase the force exerted by thumb flexion from its starting level to 15N in the 1 s period. Because the ramp of force required in the tracking task caused the signal of force output to remain fixed on the oscilloscope screen, this method minimized the subject's anticipation of arrival of an imposed perturbation (see below) by reference to the grid of the oscilloscope. Each displacement of the signal of tension in such tracking tasks was preceded by 1–2 s by a spoken warning ('ready') from an experimenter.

For the isotonic tracking task the thumb-pad pressed against a brass bar. This rotated the shaft of a brushless DC-torque motor (Aeroflex TQ 52) which was mounted co-axially with the terminal joint of the thumb. A co-axial potentiometer registered joint angle, and provided a signal for display on the oscilloscope to the subject. The thumb was required to exert a force of 2–5N to remain stationary against the opposing torque from the motor. After a spoken warning from the experimenter, the target beam on the oscilloscope was displaced in such a way as to require an isotonic flexion of the thumb through 20 deg in 1 s, at constant angular velocity, to maintain alignment of the position signal and the target.

Both forms of tracking task involved quite rapid muscular contractions. This was because we wished to study similar contractions to those studied in the thumb by others. Thus, both our isometric and isotonic tracking tasks were of similar duration to those previously described. In our experiments, the commencement of tracking was determined by an experimenter, whereas Marsden *et al.* (1976*a*) usually allowed the subject to decide the moment of commencement. Otherwise, conditions here were similar to those used by Marsden *et al.* (e.g. 1976*a*). It was confirmed for both tracking tasks used here that tracking did occur: this was done by altering the rate or extent of progress of the target within occasional trials, and demonstrating clear modifications of the contractions in progress in response to this.

In the weight-lifting task the thumb depressed one end of a 'see-saw' to lift a weight of 500 g attached equidistant from the fulcrum at the other end. This weight was attached to the fulcrum by a string that was pulled tight by approximately 10–20 deg of thumb flexion: the weight was then lifted from its support. The subjects were told to lift the weight and put it down again repeatedly, 'as if judging its heaviness'. They chose their own frequency and speed of lifting. In this form of contraction no target was set, and no visual feed-back of position or force was given.

Stretch. All experiments were set up so as to make the occurrence and timing of imposed stretches unpredictable. Random control runs without stretches were introduced or, in the isometric holding tasks, the timing of imposed stretches was varied deliberately. These steps were taken to ensure that fast, voluntary responses to predictable stimuli did not superimpose on the reflex responses under study (Rothwell *et al.* 1980). That these steps were successful in this regard was shown by the absence of progressive shifts in behaviour throughout experimental runs, as might have occurred, for example, if subjects were learning to detect some clue about the timing of the stretch.

In the isometric tasks stretch of the contracting thumb flexor was achieved by driving back the shaft of the electromagnetic vibrator. A rate of stretch was chosen for each subject which elicited clear, but submaximal long-latency e.m.g. responses, with no responses at tendon jerk latency: typically, the thumb-tip was driven back through 3–10 deg over 30–100 ms. For the simple holding contractions, stretches were applied at random intervals (4–10 s) by an experimenter pressing a silent button out of sight of the subject. The isometric tracking tasks were performed in sets of eight. Again, there were 4–10 s periods between individual contractions. In four of the eight contractions a stretch was applied, as described above, 550 ms after the tracking task commenced; in the other four, randomly intermixed, the tracking task proceeded to completion without interruption.

In the isotonic contractions, thumb stretch was applied by suddenly increasing the current in the torque motor by an amount sufficient to drive the thumb-tip back through 5–10 deg within 70–100 ms. Here, again, trials were performed in sets of eight: four unimpeded contractions randomly intermixed with four trials in which stretch was applied 550 ms after tracking commenced. Individual trials were 4–10 s apart.

During weight-lifting, stretch of the contracting thumb flexor was achieved by using the DC-torque motor, which was mounted co-axially with the beam of the 'see-saw' device. The torque motor was triggered on randomly chosen trials, when the thumb was just beginning to lift the weight from its support. This action of the torque motor drove the thumb back, deposited the weight on its support and then continued on, allowing the attachment of the weight to the beam to fall slack. The thumb-tip was pushed back 5–20 deg in 20–60 ms.

Data collection and analysis. E.m.g. activity was recorded with surface electrodes placed over the belly of flexor pollicis longus, following the method of Marsden *et al.* (1976*a*). The earth electrode was a sheet of metal taped to the arm just above the elbow. E.m.g. activity was recorded for 250 ms during each trial, 50 ms before the stretch arrived and 200 ms afterwards.

The e.m.g. activity was amplified usually by a factor of 1000 or 2000, then filtered with a band width of 100 Hz–2 KHz. The signal was then integrated (Neurolog NL703), either with a time constant of 2 ms, or of 200 ms. The 2 ms time constant gave essentially a rectified, minimally smoothed, record of e.m.g. The 200 ms time constant gave an approximation of a true integral of activity through the 250 ms recording period. The integrator was earthed until the moment recording commenced.

Trials with and without stretch of the thumb flexor were averaged separately. The raw e.m.g. or the integrated and amplified e.m.g. from each trial and their averages (Neurolog NL300) were displayed on an oscilloscope and plotted on a pen recorder, both out of sight of the subject.

The averaged e.m.g. integrals (200 ms time constant) recorded on the pen recorder were used for quantitative measurements in arbitrary units. The reflex size was estimated by measuring the height of the averaged e.m.g. integral 80 ms after the start of the ramp stretch, and subtracting from this the averaged e.m.g. integral at the same time from the trials in which no stretches were applied. In flexor pollicis longus, the long-latency response has a latency of 40–60 ms (Marsden *et al.* 1971; Brown, Rack & Ross, 1982; Matthews, 1984*a*). The arbitrary time 80 ms was chosen because it was less than the latency generally accepted for commencement of voluntary activity: voluntary reaction times for our subjects to a light tap on the thumb-tip were usually about 100 ms. We did not reliably see the two components of long-latency response described by Marsden *et al.* (1978), and we found no evidence of the changes we report here occurring, preferentially, in an early or late component of the response. No 'scaling' of the e.m.g. records of the kind described by Marsden *et al.* (e.g. 1976*a*), was performed. Sets of trials were excluded from analysis if the averages of both integrated e.m.g. prior to stretch, and either the position or force record (depending on the contraction under study), did not superimpose in control trials and trials in which stretches were applied. It should be noted that this requirement applied to all sets of comparable trials, including those made with and without anaesthesia. As subjects tend to co-contract the thumb flexor and extensor during anaesthesia (Marsden *et al.* 1979), it was necessary to train subjects not to do this; this was fairly easily done in trial periods of 5–10 min in which the subjects were permitted to see their e.m.g. and force/position traces on an oscilloscope, and adjust their contractions to avoid co-contraction.

Reflex size and background activity were measured when comparing conditions before and after anaesthesia, or following instructions to 'resist' or 'let go'. Student's *t* tests (two-tailed) were used to determine if the reflex size or background activity were significantly different ($P < 0.05$). At least forty trials (ten sets of four trials) were used in each condition, for comparison.

RESULTS

'Resist' vs. 'let go'

Subjects were tested for their ability to modify the size of the long-latency response to stretch of the contracting, long flexor of the thumb. Before each set of trials they were instructed either to 'resist' strongly and quickly, or to 'let go' as soon as possible, if a perturbation was applied. Control trials in which no perturbation was applied were used for comparison.

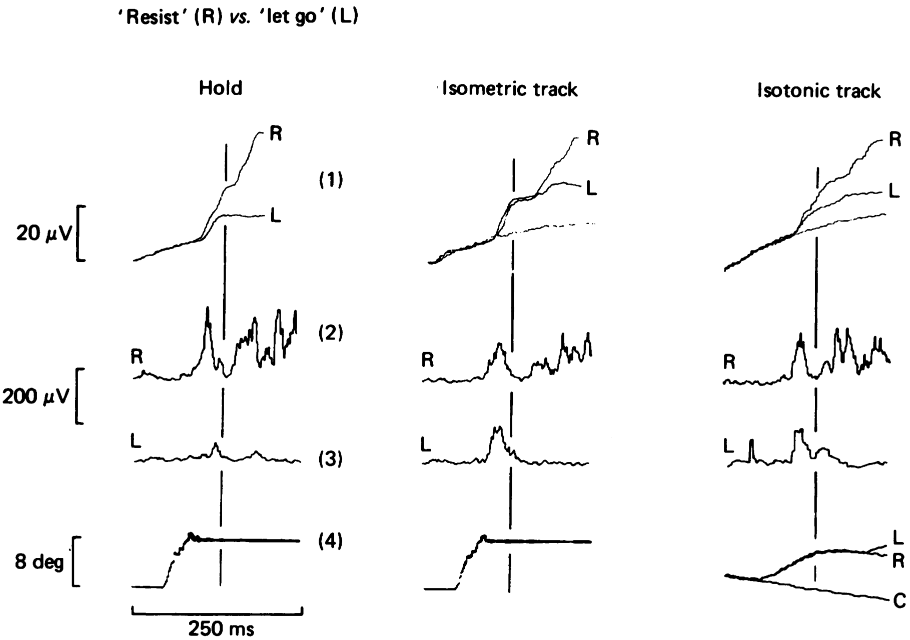

Fig. 1. This shows results from one subject performing isometric hold (left column), isometric force tracking (middle column) and isotonic position tracking (right column) tasks with an unanaesthetized thumb. In each column, from above downwards, the traces show: (1) integrated (200 ms time constant) and averaged e.m.g. for 'resist' (R) and 'let go' (L) trials; for 'isometric track' and isotonic track' experiments, the control e.m.g. (no stretch) is also shown (not labelled); each trace is the average of four trials; note that the 200 ms time constant does not give a true integral of e.m.g. activity, but only an approximation of it (a 'leaky' integral) (the downward curvature seen in the control periods, and evident at the ends of 'let go' trials, is because of this); (2) integrated (2 ms time constant) and averaged (average of four trials) e.m.g. for 'resist' (R) trials; (3) integrated (2 ms time constant) and averaged (average of four trials) e.m.g. for 'let go' (L) trials. (Because the experimental arrangement permitted recording and averaging of e.m.g. with only one time constant of integration at a time, the trials averaged in the lower pairs of records were from a series conducted immediately after those averaged for the upper traces.) (4) Position trace showing angular excursion of thumb.

Fig. 1 shows typical records from a subject in whom stretches were applied during isometric 'hold', isometric tracking, and isotonic tracking contractions. The recordings show e.m.g. activity 'integrated' using the 200 ms time constant (approximating true integration) and at 2 ms time constant (essentially a rectified and minimally smoothed record of the activity). The vertical lines on the records are at 80 ms from commencement of stretch, the time before which e.m.g. activity was taken to include the long-latency response (see Methods). Features of the records shown in Fig. 1 which were characteristic of all records were: (i) the absence of e.m.g. activity at tendon jerk latency (the rate and extent of stretch were set, as described, to achieve this), (ii) the superimposition of integrated e.m.g. activity (200 ms time constant) in the period up to the start of the long-latency responses, for control trials and trials in which stretches were applied, and (iii) the superimposition of the position records up to commencement of stretch in the isotonic tracking series, for control and test trials.

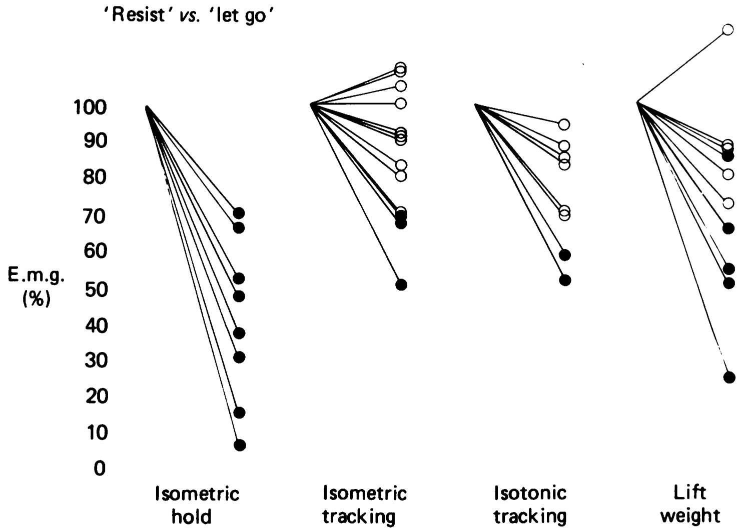

Fig. 2. Summary of results from all subjects tested for their ability to alter the magnitude of the long-latency e.m.g. response to stretch of the long flexor of the unanaesthetized thumb according to their volitional 'set'. Results for the four categories of muscular contraction studied are shown. For each subject the mean size of the long-latency e.m.g. response when the prior instruction was to 'resist', is set as 100 %, and its mean size when the prior instruction was to 'let go' is plotted as a circle: ●, significant changes ($P < 0.05$); ○, data in which no significant difference between the two conditions was demonstrated. Points for individual subjects are joined.

Fig. 2 summarizes the performances of all subjects tested for their ability to modify long-latency responses according to prior instruction to 'resist' or to 'let go'. It can be seen that all subjects tested could significantly alter the long-latency response to stretches imposed during the isometric holding task. The mean reduction in e.m.g. activity at 80 ms from the start of stretching was 28–95 % when the prior instruction was 'let go' rather than 'resist'.

The subjects were less able to alter the responses according to prior instruction, for stretches imposed during other forms of contraction (Fig. 2). For isometric tracking, only three of thirteen subjects tested gave significantly smaller e.m.g. responses (by 32–52 %) when told to 'let go' rather than 'resist'. With isotonic tracking (the form of contraction for which Marsden *et al.* (1976*a*) reported an absence of influence of prior instruction), only two of eight subjects could modify the responses significantly. The responses of these two were reduced by 42 and 48 % when the instruction was 'let go' rather than 'resist'. For stretches imposed during the lifting of a weight, five of the ten subjects tested could modify their e.m.g. responses significantly, the responses being reduced by 12–75 %, when the instruction was 'let go' rather than 'resist'. Not all subjects performed all tests, so it was difficult to test the consistency of individual subjects across the tests. However, no marked inconsistencies were noted. All subjects who showed significant reductions of long-latency responses in the two tracking tasks (the types of contraction in which instruction-dependent control was least frequently observed) were also able to control the response similarly in the isometric hold and weight-lifting tasks when tested on these.

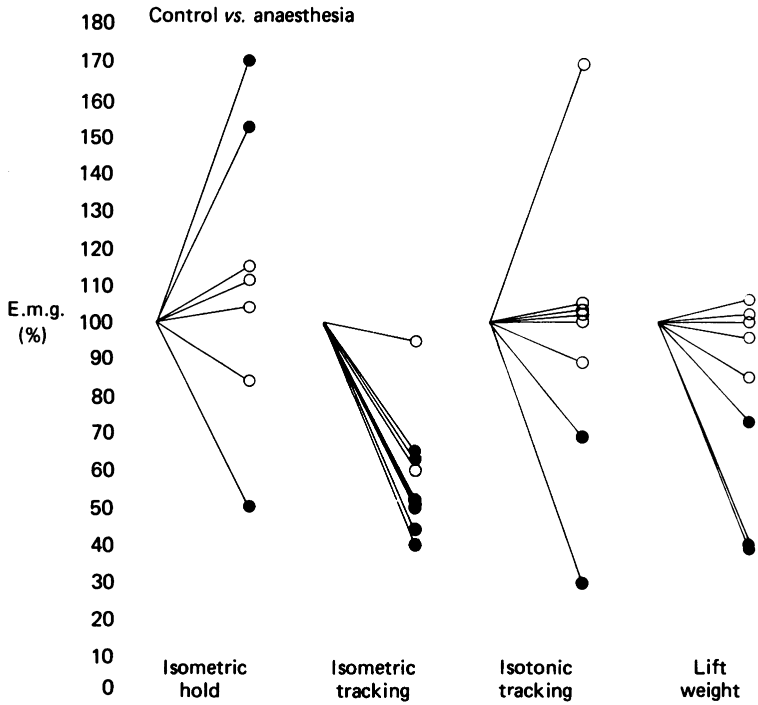

Fig. 3. Summary of results from all subjects tested for the effects of local anaesthesia of the thumb to alter the magnitude of the long-latency e.m.g. response to stretch of its long flexor. Results for the four categories of muscular contraction studied are shown. For each subject the mean size of the long-latency e.m.g. response in the unanaesthetized thumb is set as 100 %, and its mean size during anaesthesia is plotted as a circle: ●, significant changes ($P < 0{\cdot}05$); ○, data in which no significant difference between the two conditions was demonstrated. Points for individual subjects are joined. All subjects were given the instruction to 'resist' all perturbations.

Anaesthesia

Anaesthesia of the thumb had inconsistent effects on the magnitude of long-latency responses to stretches imposed during the contractions. In all of these tests the subjects were given the instruction to 'resist' any imposed stretch strongly and promptly. The results are summarized in Fig. 3.

For stretches imposed during isometric holding contractions, anaesthesia significantly depressed the long-latency response in only one of the seven subjects tested.

In an essentially similar series, Marsden, Rothwell & Traub (1979) found anaesthesia reduced the response by an average of 30 %, although the effect was absent, as here, in some subjects. In the present series, however, two of the seven subjects tested had a significantly enhanced long-latency e.m.g. response during anaesthesia.

In the isometric tracking task, thumb anaesthesia was associated with a significant reduction in long-latency response of 35–62 % in six of eight subjects. In the isotonic tracking task, however, significant reduction of the response occurred in only two

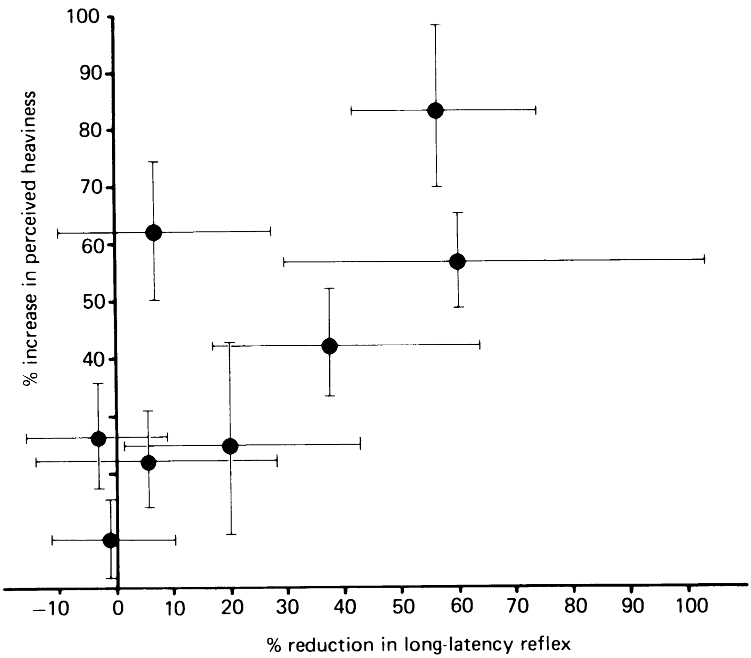

Fig. 4. This shows the percentage increase caused by thumb anaesthesia in the perceived heaviness of an object lifted by flexion of the tip of the thumb, plotted against the percentage reduction, caused by thumb anaesthesia, in the long-latency e.m.g. response to stretch of the long flexor of the thumb. Each point gives the mean (and S.E. of mean) for an individual subject. There is a significant ($P < 0{\cdot}05$) positive correlation of the data: subjects in whom thumb anaesthesia most reduced the long-latency e.m.g. response experienced a greater increase in the apparent heaviness of an object lifted by the thumb.

of the eight subjects tested (by 33 and 72 %). It should be noted that this is the experimental condition for which Marsden, Merton & Morton (1971) reported that 'the stretch reflex is... abolished or... greatly reduced', in Dr Marsden and Dr Merton. For stretches imposed during the lifting of a weight, anaesthesia was associated with a significant reduction of long-latency response in three of eight subjects (by 37, 58 and 62 %). Again, not all subjects performed all tests, but inconsistent behaviour of individual subjects from test to test was not apparent.

The subjects whose long-latency responses to stretch were tested during weight-lifting contractions were also required to estimate the heaviness of an object (500 g) lifted by thumb flexion before and after the thumb was anaesthetized. This was done by the method of Gandevia & McCloskey (1977), a simple weight-matching task. There was a variable increase in apparent heaviness of the object during anaesthesia, a phenomenon reported and discussed by Gandevia & McCloskey (1977), Marsden *et al.* (1979) and Gandevia, McCloskey & Potter (1980). For the subjects studied here there was a significant correlation between the proportional increase in apparent heaviness and the proportional *reduction* in the size of the long-latency e.m.g. response to muscle stretch (Fig. 4).

DISCUSSION

The major purpose of the present study was to check two matters which had been left in doubt following the series of investigations by Marsden and co-workers (see References) on long-latency e.m.g. responses to stretch of the long flexor of the thumb. These were whether or not the size of the long-latency responses can be modified according to the instructions given to a subject prior to a stretch, and whether or not anaesthesia of the thumb reliably abolishes or attenuates the responses. In our experiments stretches were imposed during four different types of contraction: isometric holding, isometric tracking, isotonic tracking and weight-lifting.

Only for stretches imposed during isometric holding contractions could subjects reliably modify the size of long-latency responses according to prior instruction and so, presumably, to their volitional 'set'. In this respect the thumb is like other muscles, where a similar phenomenon has often been described (see Introduction). In the other forms of thumb contraction, which are possibly more complex, or require greater concentration, only a minority of subjects could modify the long-latency responses according to prior instruction. This may help to explain why, in their two subjects, Marsden *et al.* (1976*a*) failed to find an influence of prior instruction for stretches imposed during contractions similar to our 'isotonic tracking' ones, while they and others did find such an influence during isometric holding tasks (Marsden *et al.* 1979; Potter & McCloskey, 1979; Rothwell *et al.* 1980).

Anaesthesia of the thumb did not abolish the long-latency e.m.g. response in any of our subjects for any of the forms of contraction studied. In only a minority of subjects did it significantly attenuate the response, and this occurred most frequently for stretches imposed within the isometric tracking task. As noted previously, the original claims regarding the effects of thumb anaesthesia made by Marsden, Merton & Morton (1971, 1973, 1976*a*, 1977) had required modification following the observation of Marsden, Rothwell & Traub (1979) that such effects were variable and sometimes absent. Thus, it would seem unwise to propose a significant and consistent role for afferent impulses from the skin and joint of the thumb in producing, or co-operating with impulses from muscle afferents to produce the long-latency e.m.g. response to muscle stretch.

It is of interest, nevertheless, that a significant correlation exists between the increase in apparent heaviness of an object lifted by flexing an anaesthetized thumb, and the decrease (if any) in the long-latency e.m.g. response in that thumb (Fig. 4). Because it is now clear that anaesthesia does not *abolish* the long-latency response, we feel it would be unwise to persist with Gandevia & McCloskey's (1977) hypothesis that a loss of reflex *accounts* for the increased heaviness, although the correlation demonstrated here suggests it may contribute to it. Here, the calculations performed by Marsden *et al.* (1979) are pertinent, and our conclusion is in agreement with the calculations (but not the conclusions) in that report, and with the conclusions of Gandevia *et al.* (1980).

While the present investigation draws attention to differences in behaviour of long-latency e.m.g. responses to stretches imposed in different forms of contraction, it should be noted that only very rapid 'tracking' contractions were studied. This is because we sought to resolve questions arising from other studies which used similarly rapid contractions. For the same reason the stretches we imposed were large, although it could well be that proprioceptive reflexes behave quite differently when the perturbations which evoke them are smaller and, perhaps, more 'natural' (e.g. Evarts, 1981).

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