Journal of Physiology (1991), **442**, *pp.* 585–599
With 7 *figures*
Printed in Great Britain

INDEPENDENT DIGIT CONTROL: FAILURE TO PARTITION PERCEIVED HEAVINESS OF WEIGHTS LIFTED BY DIGITS OF THE HUMAN HAND

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(*Received 1 November 1990*)

SUMMARY

1. A weight-matching task was used to investigate the ability to estimate heaviness when weight lifting was isolated to the extrinsic flexor muscles (or portions thereof) that act on the digits of the hand.

2. Subjects matched a *reference* weight (200 g) lifted by a digit on the right with a *variable* weight lifted by the left thumb; a *concurrent* weight was simultaneously lifted by a digit on the right (reference) side. The reference and concurrent weights were lifted either by the same muscle (digital portions of flexor digitorum profundus), or anatomically separate but functionally related muscles (flexor digitorum profundus and flexor pollicis longus). Anaesthesia of the radial nerve and/or posturing of the hand was used to eliminate any small forces generated by co-contraction of the extensor muscles of the digits.

3. When the concurrent weight was equal to or greater than the reference weight, the perceived heaviness of the *reference* weight increased significantly from control trials (in which no concurrent weight was lifted). Although perceived heaviness of the reference weight increased progressively as the concurrent weight increased, reproducibility (expressed as the coefficient of variation) did not deteriorate when a weight was lifted concurrently. These findings were qualitatively similar when the reference and concurrent weights were lifted by two digital portions of flexor digitorum profundus or when the weights were lifted by flexion of the thumb and index finger. Also, anaesthesia of the digits which lifted the reference and concurrent weights did not alter the changes in perceived heaviness.

4. Perceived heaviness of the reference weight lifted by flexor digitorum profundus did not change when subjects lifted the concurrent weight with a remote muscle group (ankle dorsiflexors).

5. This study shows that signals of heaviness are systematically overestimated whenever more than one portion of the extrinsic muscles which flex the different digits are simultaneously active. Given that estimates of heaviness are biased by the central motor command, one explanation is that when the total motor drive

increases, the central nervous system is unable to partition precisely the destination of motor commands to functionally related 'muscles'.

INTRODUCTION

The literature on motor control often refers to the ability of primates to move their fingers independently. However, finger movement is produced by intrinsic muscles acting on single fingers together with extrinsic muscles with multiple tendons acting on the fingers. Independent finger action may necessitate selective control of digital portions of the extrinsic muscles. If present, such selective control for movement of single fingers could be achieved by focal inputs descending to whole or parts of the relevant motoneurone pool. One major implication of the concept that the digits are controlled independently was examined in the present study, namely the perception of forces generated by the long flexor muscles acting on the distal phalanges of the digits.

Estimation of force or heaviness is biased by the central motor command rather than by peripheral signals related to the tension generated in the muscle. The evidence for this derives largely from the observation that perceived heaviness increases when a muscle is experimentally weakened with curare (Gandevia & McCloskey, 1977*a*, *c*), or by muscle fatigue (McCloskey, Ebeling & Goodwin, 1974; Gandevia & McCloskey, 1978; Jones, 1983) or it operates on an unfavourable part of its force–length curve (Cafarelli & Bigland-Ritchie, 1979). Perceived heaviness also increases if the motoneurone pool is inhibited by muscle spindle input from the antagonists (McCloskey *et al.* 1974) or by cutaneous afferents (Aniss, Gandevia & Milne, 1988; see also Gandevia & McCloskey, 1977*b*). In all of these studies, the peripheral signals related to muscle tension should not have changed. Thus, these judgements are believed to reflect signals related to centrally generated motor commands, possibly involving the motor cortex (Gandevia, 1982; for reviews see McCloskey, 1981; Gandevia, 1987; Cafarelli, 1988; Jones, 1988).

The present study was designed to assess whether perceived heaviness could be determined for each of the digits of the hand independently when two different portions of flexor digitorum profundus contracted or when anatomically distinct but functionally related muscles of the hand contracted (i.e. flexor digitorum profundus and flexor pollicis longus). Throughout the text, we refer to a 'muscle' in conventional anatomical terms, although the central nervous system can command movement via different regions of some muscles such as the long flexors and extensors of the digits (Gandevia, 1989). The specialization of particular compartments within muscles is currently the subject of debate (Windhorst, Hamm & Stuart, 1989). Preliminary accounts of some findings have been published (Kilbreath & Gandevia, 1990*a*, *b*).

METHODS

Subjects were procured for each of the experiments from a group of thirty-nine volunteers. Although not informed of the exact hypothesis being tested, subjects were informed of the method. Additionally, informed written consent was given prior to experiments involving anaesthesia (see below). The experimental procedures were approved by the local ethics committee.

Experimental procedure

Subjects were required to match a weight lifted with one digit of the right hand to a weight lifted by flexion at the interphalangeal joint of the left thumb. The weight lifted by the right hand was the *reference* weight and, unknown to the subject, did not change during an experiment. The weight lifted by the left thumb was the *variable* weight and was adjusted according to the subjects' instructions. Additionally, on the right (or reference side) subjects simultaneously lifted a weight with a different digit (termed the *concurrent* weight) on some trials. The matching combinations are grouped into lifting combinations involving (i) the same muscle, i.e. flexor digitorum profundus, (ii) anatomically distinct muscles that act on the digits, i.e. flexor pollicis longus and flexor digitorum profundus, and (iii) a remote muscle group. The number of subjects participating in any specific experiment, i.e. lifting combination, is given below.

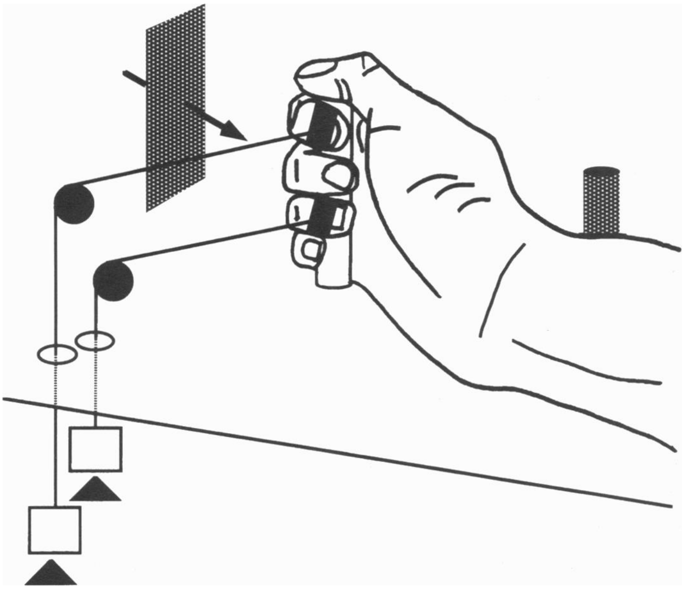

Fig. 1. The experimental set-up used when flexor digitorum profundus lifted the reference weight and the concurrent weight. The middle phalanges of the fingers were held against the vertical rod by an adjustable stabilizing bar, indicated by the arrow. This limited flexion at the distal interphalangeal joint to flexor digitorum profundus and prevented effective co-contraction of the extensor muscles.

Lifting combinations with flexor digitorum profundus. The three lifting combinations in which flexor digitorum profundus lifted the reference weight and the concurrent weight were as follows: reference weight lifted by index and concurrent weight lifted by the middle finger (sixteen subjects completed this combination, i.e. $n = 16$), vice versa ($n = 13$), and the reference weight lifted by the index and the concurrent weight lifted by the ring finger ($n = 10$). In all three combinations the reference weight was 200 g, and the concurrent weights were 100, 200 and 300 g.

The reference and concurrent weights were lifted by flexion at the distal interphalangeal joint. At this joint, flexor digitorum profundus is the sole flexor. Figure 1 illustrates the position of the subject's right hand for the lifting task. Subjects sat with their forearms and hands resting on a table. The fingers of the right hand lightly grasped a vertical rod. Another vertical rod maintained the wrist at approximately 20 deg extension. An adjustable, stabilizing bar held the middle phalanges of the digits against the distal rod and thereby prevented extension at the proximal interphalangeal joints. The hand posture was necessary to disengage completely the extensor mechanism and prevent any torque produced by co-contraction of the extensor muscles from counteracting the torque which had to be developed by flexor digitorum profundus (Marsden, Rothwell & Traub, 1979; Gandevia, McCloskey & Potter, 1980; see also Gandevia & McCloskey, 1976; Matthews & Miles, 1988). Small plastic rings were placed around the distal phalanges of the index, middle, and/or ring fingers, depending on the experimental condition. Lines from these rings ran over pulleys to light trays holding the weights.

Perceived heaviness of weights lifted by the fingers can be significantly influenced by cutaneous afferents innervating the fingers (Gandevia & McCloskey, 1977*b*; Marsden *et al.* 1979; Aniss *et al.* 1988). Thus, to examine whether the changes in perceived heaviness which occurred when the hand was fully sentient were dependent upon activation of cutaneous and joint afferents during the lift, the three experimental combinations were repeated on each subject on separate days with the fingers used to lift the reference and the concurrent weights anaesthetized. Lidocaine (1%; 3–4 ml/finger) was injected adjacent to the digital nerves of the relevant fingers at the base of the proximal phalanx. A rubber band was placed loosely just distal to the metacarpophalangeal joint and this ensured that the digital block remained clinically complete for the duration of each experiment. Ten subjects completed index and middle finger combinations with anaesthetic and nine subjects completed the index and ring finger combination. The present study was not designed to investigate whether subjects' estimates of perceived heaviness (when no anaesthesia was present) would be altered by the presence of digital anaesthesia; an increase in perceived heaviness has been previously documented with digital anaesthesia (e.g. Gandevia & McCloskey, 1977*b*, *c*; Marsden *et al.* 1979).

Lifting combinations with the flexors of the index and thumb (flexor digitorum profundus and flexor pollicis longus). Two lifting combinations used these anatomically distinct muscles: the reference weight lifted by flexion at the distal interphalangeal joint of the index and the concurrent weight lifted by flexion at the interphalangeal joint of the thumb, using flexor pollicis longus ($n = 8$), and vice versa ($n = 8$). The reference weight in both combinations was 200 g and the concurrent weights were 100, 200 and 300 g. The method for lifting with the index finger was the same as outlined above. To lift with flexor pollicis longus, the interphalangeal joint of the thumb was supported on an adjustable T-bar on top of the vertical rod lightly grasped by the fingers. The thumb's distal phalanx rested on the end of a lever. A light tray containing the weights was supported from the other end of the lever.

While potential co-contraction of the extensor mechanism for the index finger was mechanically prevented by the hand posture adopted, an additional step was required when lifting with the thumb to eliminate any possible co-contraction of extensor pollicis longus. To eliminate the action of extensor muscles arising in the forearm, the radial nerve was localized by percutaneous electrical stimulation over the spiral groove and then blocked with lidocaine (2% with adrenaline; 6–8 ml). The blocks developed over 15–30 min and remained clinically complete to sensory and motor testing for 2–7 h.

Lifting combination with a remote muscle group. To determine whether the changes in perceived heaviness were non-specific, i.e. they occurred when any two 'muscles' were active, one combination used a muscle group remote from the hand to lift the concurrent weight. The reference weight of 200 g was lifted by the long finger flexor of the index finger with the concurrent weight (2·15 or 4·3 kg for female or male subjects respectively) lifted by the ankle dorsiflexors ($n = 6$). The weights lifted by the ankle dorsiflexors were chosen to exceed 15% of the maximum voluntary torque (Adams, Gandevia & Skuse, 1990).

Lifting protocol

For all matching tasks, the *variable* weight was lifted by flexion at the interphalangeal joint of the thumb. The position of the thumb was the same as that described above. Each experimental session included a control condition in which subjects matched the reference weight lifted by one digit on the right with the variable weight on the left. In other conditions, subjects matched the reference weight while concurrently lifting a weight with another digit on the reference side. There were ten trials per condition. Subjects were instructed to make the weights feel the same by requesting an increase or decrease in the variable weight after lifting the weights simultaneously a maximum of three times. Also, they were instructed that they were not limited in the number of times they could request an increase or decrease in the weights, and that the addition or subtraction could overshoot their estimate so they were not confined to changing weights in one direction only. Subjects were given no information on the strategies to estimate heaviness, or the velocity at which to lift the weights. When the subject reported that the variable weight felt the same as the reference weight, the next trial commenced. The initial variable weight could range from 2·5 to 300% of the reference weight and the minimum amount by which the weight was changed was 5 g. The subjects could not see the weights which were supported externally on stands between lifts. Subjects were not informed when the weight lifted concurrently with the reference weight was changed. Subjects completed all of the trials per condition in a block, with the order of conditions randomized between subjects.

Effect of fatigue upon estimation

The effect of fatiguing the muscle that lifted the concurrent weight was investigated in six subjects. Subjects completed ten trials in which they matched a reference weight of 200 g lifted by the index while concurrently lifting 300 g with the ring finger. Once the subject reported the reference and variable weights to be equal in the final control trial, the subject immediately lifted 1·5 kg by flexion of the distal joint of the ring finger and supported it for 60 s. The reference weight, lifted by the index, was supported externally (and not by the subject) while the ring finger lifted the 1·5 kg. After 60 s, subjects immediately commenced the next match of the reference weight while concurrently lifting the usual 300 g with the ring finger. The latter procedure was repeated until subjects had completed ten trials.

Electromyographic recordings

Electromyographic (EMG) activity was recorded in two subjects in three sessions while they lifted weights equal to or greater than those used in the weight-matching tasks. Intramuscular electrodes, consisting of pairs of stainless-steel wires (50 μm diameter) with 1–2 mm of insulation removed, were used. In two sessions, EMG was recorded simultaneously from different portions of flexor digitorum profundus while in another, it was recorded from the lateral index portion of flexor digitorum profundus and from flexor pollicis longus. Activity was amplified, filtered (53 Hz–3 kHz) and stored on tape.

Data analysis

The raw estimates of perceived heaviness from *each* experiment, i.e. lifting combination, were subjected to two-way analysis of variance (ANOVA) to determine the effect on perceived heaviness when another digit in the same hand concurrently lifted a weight, after the variation between subjects had been eliminated. Statistical variability between subjects is highly significant (e.g. Gandevia & Kilbreath, 1990); in all of the present experiments subject variability was also significant ($P < 0{\cdot}01$). As it was not the intent to study inter-subject variation, this aspect will not be further addressed. Two-way ANOVA was similarly used to investigate the effect on the subject's reproducibility of estimates when another digit was concurrently active. Reproducibility of weight matching for repeated trials (sometimes referred to as the accuracy) has been defined as the coefficient of variation determined from the subject's estimates (Gandevia & Kilbreath, 1990; see also Newell, Carlton & Hancock, 1984). For the study of fatigue, we analysed fatigue trials numbered one to five and six to ten separately. Duncan's multiple-range test was used if the ANOVA revealed a significant effect when lifting the concurrent weight. Statistical significance was set at $P < 0{\cdot}05$.

RESULTS

The present study examined the ability of subjects to assess independently the perceived heaviness of weights lifted by one digit when a neighbouring digit was concurrently active. This required subjects to lift weights of 100–300 g by flexion at the distal joints of the digits. In control electromyographic recordings we documented that such weights could be lifted with minimal co-contraction of adjacent digits (Fig. 2). Throughout the present studies we eliminated any torque generated by antagonist extensor muscles: this was done with a hand posture which disengaged these muscles or with a complete block of the radial nerve above the elbow. Similar results were obtained in preliminary studies in which the actions of antagonist muscles were not eliminated.

Lifting combinations with flexor digitorum profundus

The first three experiments limited lifting of the reference weight and the concurrent weight to flexor digitorum profundus. In all three combinations used to lift the reference and concurrent weights, i.e. index and middle, middle and index, index and ring fingers, the mean estimates of perceived heaviness of the reference weight increased when a weight was concurrently lifted by another finger (Fig. 3). Each combination of the grouped data, analysed with a separate two-way ANOVA, was highly significant ($P < 0{\cdot}01$; see Table 1). Duncan's multiple-range test revealed that the estimates were significantly different from the control condition in all combinations when 200 and 300 g were concurrently lifted with the reference weight and for two of the three combinations when the lowest of the concurrent weights (100 g) was lifted. When the index lifted the reference weight and the middle finger concurrently lifted 100 g, the estimate of perceived heaviness did not vary significantly from the control condition.

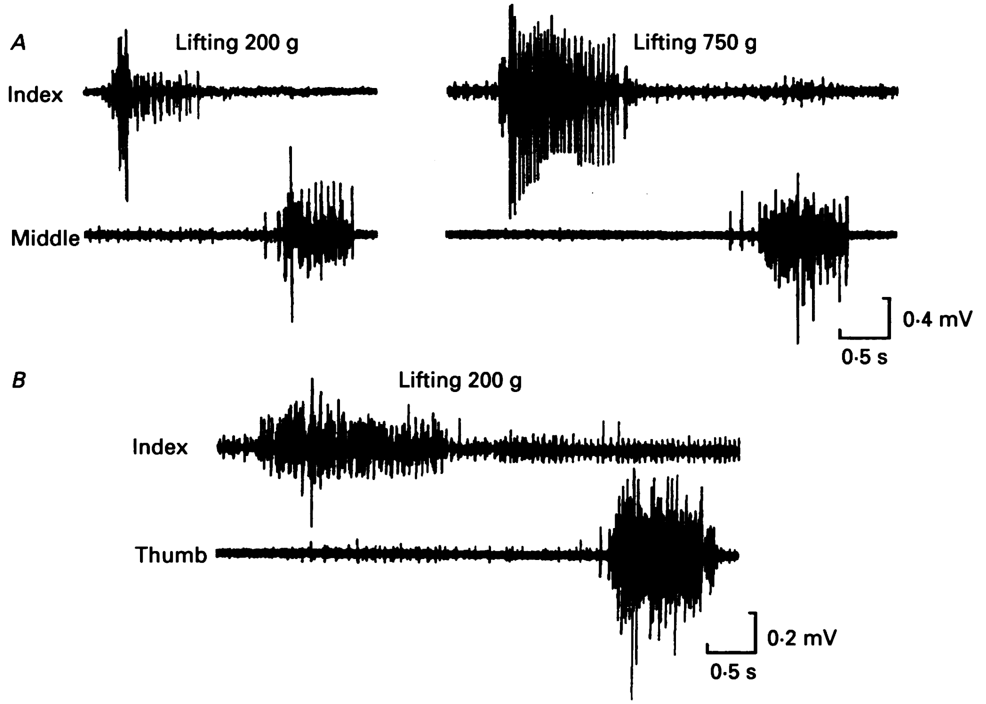

Fig. 2. EMG recordings from one subject. *A*, two pairs of electrodes inserted into flexor digitorum profundus. One pair selectively recorded activity when the index flexed and a more medial pair recorded activity when the middle digit flexed. *B*, one pair of electrodes inserted into the lateral (index) portion of flexor digitorum profundus and one pair into flexor pollicis longus. For both combinations, there was minimal co-activation of the adjacent muscle when weights of 200 g were lifted. Some co-activation probably occurred when 750 g was lifted with the middle finger portion of flexor digitorum profundus (top right traces).

When fingers used to lift the reference and concurrent weights were anaesthetized, we found similar trends to those when they were not anaesthetized. As shown in Fig. 3*B*, the mean estimates of perceived heaviness increased when the concurrent weight increased. All three combinations with the fingers anaesthetized were also highly significant (ANOVA, $P < 0{\cdot}01$; see Table 1): perceived heaviness increased significantly above control levels when 200 or 300 g was concurrently lifted.

Reproducibility of the estimates, measured as the coefficient of variation (see Methods), was not affected by lifting a concurrent weight. Reproducibility did not deteriorate, although the mean estimates progressively increased. For example, when the middle digit lifted the reference weight and the index lifted the concurrent weight ($n = 13$), the mean coefficient of variation (±S.D.) for the control condition and when 300 g was concurrently lifted was 12·5 (±2·7) % and 12·1 (±4·8) % respectively. When the fingers were anaesthetized, the coefficients of variation for the control trials were slightly but significantly greater ($P < 0{\cdot}05$); they did not increase when a concurrent weight was lifted. Following anaesthesia of the fingers

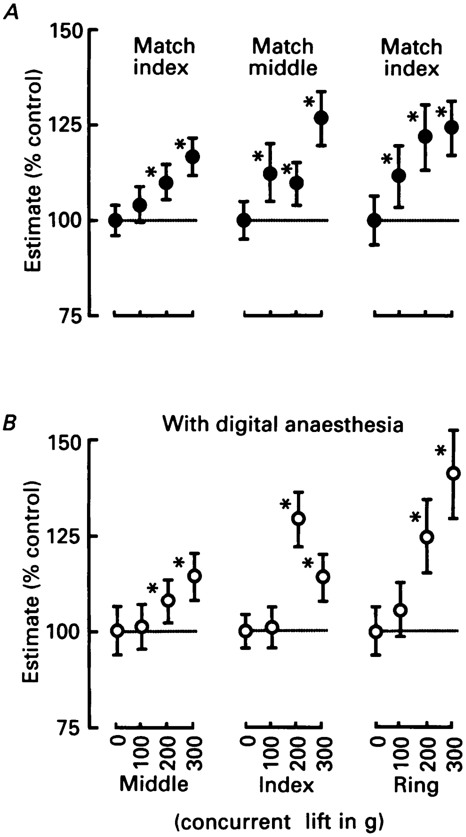

Fig. 3. Results from the three lifting combinations in which flexor digitorum profundus lifted the reference weight and the concurrent weight. Data obtained when the fingers were unanaesthetized (*A*) and when they were anaesthetized (*B*). Mean (±S.E.M.) values of the group data, normalized to the mean value for the estimate of heaviness of the reference weight under control conditions (i.e. no concurrent weights lifted), are shown. See text for the number of subjects that participated in each combination. The finger that lifted the reference weight (200 g) is indicated at the top of the panel, and the finger that lifted the concurrent weight at the bottom. In this and subsequent figures, a significant difference from a control condition (no concurrent weight lifted) is indicated by an asterisk ($P < 0{\cdot}05$).

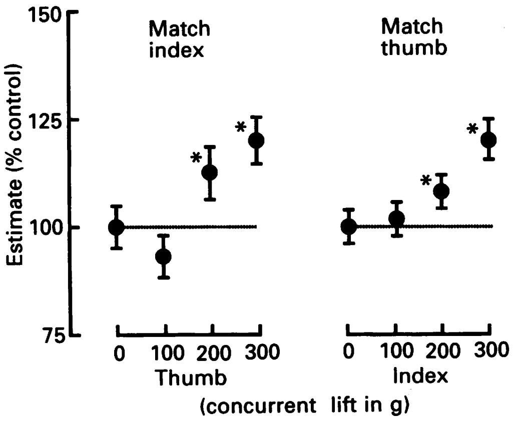

Fig. 4. Mean (±S.E.M.) values are shown for the lifting combinations in which flexor digitorum profundus (index portion) and flexor pollicis longus lifted the reference weight (200 g) and the concurrent weight. Same format as in Fig. 3. Eight subjects participated in each combination. Perceived heaviness increased significantly above the control level when weights of 200 and 300 g were lifted concurrently.

TABLE 1. *F*-ratio and *P* value for each combination of digits for the matching weight and the concurrently lifted weight. The one combination which was not statistically significant occurred when the reference weight was lifted by the index and the concurrent weight lifted by ankle dorsiflexors (foot).

Matching weight	Concurrent weight	Digital anaesthesia	*F* (d.f.)	*P*
Index	Middle	–	17·99 (3, 45)	0·001
Middle	Index	–	42·13 (3, 36)	0·001
Index	Ring	–	27·73 (3, 27)	0·001
Index	Middle	+	8·50 (3, 27)	0·001
Middle	Index	+	29·33 (3, 27)	0·001
Index	Ring	+	58·10 (3, 24)	0·001
Index	Thumb	–	29·99 (3, 21)	0·001
Thumb	Index	–	37·03 (3, 21)	0·001
Index	Ring	– (fatigue)	34·52 (2, 10)	0·001
Index	Foot	–	0·15 (1, 5)	n.s.

that lifted the reference weight (middle finger) and concurrent weight (index finger; $n = 10$), the mean coefficients of variation (±S.D.) were 21·1 (±12·7) % and 23·4 (±9·1) % for the control condition and when subjects concurrently lifted 300 g respectively.

Lifting combinations with the flexors of the index and thumb (flexor digitorum profundus and flexor pollicis longus)

When flexor digitorum profundus and flexor pollicis longus were used to lift the reference weight and the concurrent weight, the results were qualitatively the same as when parts of flexor digitorum profundus lifted them (Fig. 4). Perceived heaviness increased significantly with concurrent weights of 200 and 300 g (ANOVA, $P < 0·01$; see Table 1). However, when the subjects matched the weight lifted by the index, the group mean estimate of the reference weight decreased slightly (but not significantly) when 100 g was concurrently lifted by the thumb. Reproducibility in estimation of the perceived heaviness of the reference weight did not deteriorate when a weight was concurrently lifted by an anatomically distinct muscle. To indicate the scatter of observations, data from an individual who did both combinations of lifting with flexor digitorum profundus and flexor pollicis longus are shown in Fig. 5.

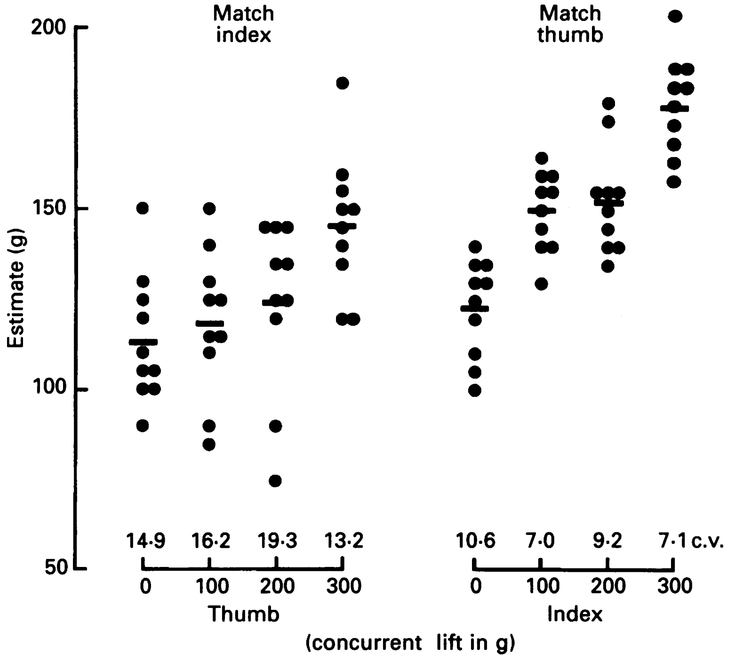

Fig. 5. Data from a single subject for two studies in which flexor digitorum profundus and flexor pollicus longus lifted the reference and concurrent weights. The subject's radial nerve was anaesthetized for each study. On the left, the reference weight (200 g) was lifted by the index and the concurrent weight was lifted by the thumb, and on the right, the converse. The coefficient of variation for each condition is shown on the horizontal axis. The mean estimates, indicated by the horizontal bars, increase when a weight is concurrently lifted.

When a muscle group remote from the hand lifted the concurrent weight, the increase in perceived heaviness documented for the other muscle combinations was absent (Fig. 6; see Table 1). Thus there was no significant difference in estimates between the control condition and when the concurrent weight was lifted with the ankle dorsiflexors.

Effect of fatigue of the muscle lifting the concurrent weight

Studies were undertaken to determine whether the estimate of heaviness of the reference weight was influenced by a signal directly related to tension in the muscle lifting the concurrent weight or by the motor command required to lift it. The reference weight (200 g) and concurrent weight (300 g) were lifted by the index and ring portions of flexor digitorum profundus respectively. The ring finger flexor was fatigued selectively and progressively (see Methods). Perceived heaviness of the reference weight lifted by the index increased as the long flexor of the ring finger fatigued (Fig. 7). While the same reference and concurrent weights were lifted in all trials, there was a significant increase in perceived heaviness of the reference weight in the first five fatigue trials, with a further significant increase in the last five estimates ($P < 0{\cdot}01$; see Table 1).

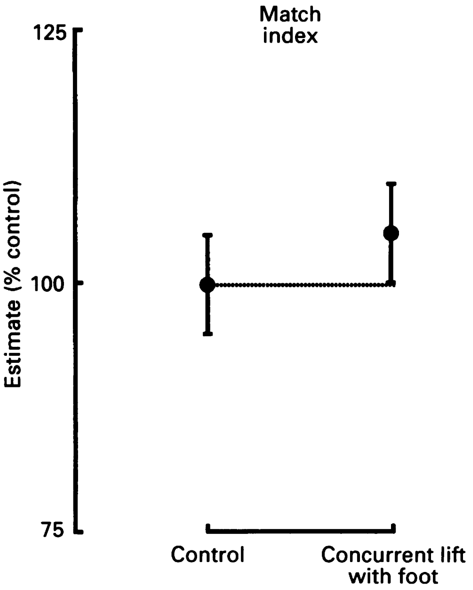

Fig. 6. Results when the concurrent weight was lifted by a remote muscle group (ankle dorsiflexors). Mean (±S.E.M.) values for the group data ($n = 6$), normalized to the mean value for the control condition, are shown. There was no significant difference between the control condition and when a weight was concurrently lifted by the ankle dorsiflexors.

DISCUSSION

Our major finding is that the perceived heaviness of a weight lifted by one long flexor of a digit in the hand increases when the long flexor of an adjacent digit concurrently lifts a weight. The magnitude of this error increases progressively with the size of the concurrently lifted weight and reaches approximately 20% when the two weights are equal. Perceived heaviness of the reference weight also increases when the muscle involved with the concurrent lift is fatigued. The increase in perceived heaviness when a weight is concurrently lifted is not evident when the concurrent weight is lifted by a remote muscle group in the leg and is therefore unlikely to represent an illusion arising when any two muscle groups contract simultaneously. Further support for this conclusion is that the reproducibility in estimation of perceived heaviness is unaffected by the concurrent lifts. The increase in perceived heaviness associated with concurrent lifting with the digits of the hand occurs not only when two digital portions of flexor digitorum profundus lift the weights, but also when the functionally related flexor pollicis longus and the index portion of flexor digitorum profundus contract. The latter finding is significant because of previous studies showing that the nett reflex input from cutaneous and joint mechanoreceptors in the index facilitates operation of flexor pollicis longus (thereby leading to a reduction in perceived heaviness of a weight it supports), and the converse, the input from the thumb facilitates operation of the long flexors of the index (Gandevia & McCloskey, 1977*b*). The mechanisms underlying this facilitation presumably involve both short- and long-latency reflexes (e.g. Marsden, Merton & Morton, 1976; Loo & McCloskey, 1985). However, the results obtained with complete digital anaesthesia show that the phenomenon documented here can occur independently of any tonic or phasic input arising in the digits. A second finding documented formally in this study is that the reproducibility of weight estimation was slightly but significantly reduced when the digits involved in the lift were anaesthetized.

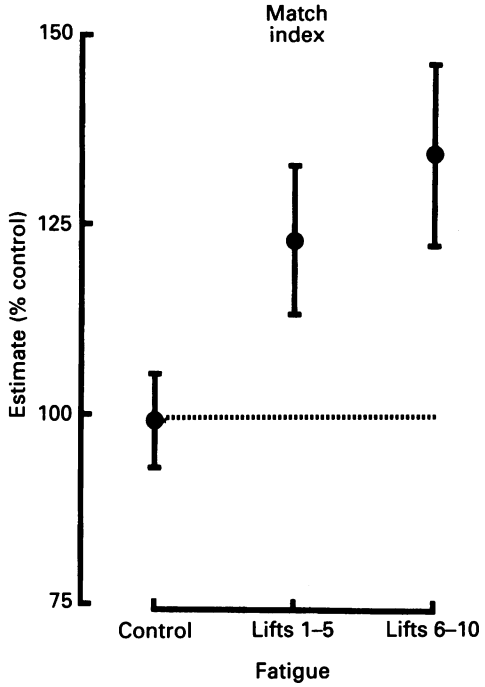

Fig. 7. Results when the muscle that lifted the concurrent but not the reference weight was fatigued. Results are normalized to the mean value for the estimate of heaviness of the reference weight under the control condition, i.e. match 200 g lifted by the index while concurrently lifting 300 g with the ring finger. Means ± S.E.M. ($n = 6$) are plotted. Perceived heaviness of the reference weight increased as the muscle used to lift the concurrent weight progressively fatigued (see Methods). The mean estimate of each combination is significantly different from the mean of the other two combinations.

Three explanations can be advanced to explain the increase in perceived heaviness of a reference weight when a weight is concurrently lifted by another digit. The first is based on a 'mechanical' interaction between the distal tendons of flexor digitorum profundus. While there are forces transmitted from one digital portion of flexor digitorum profundus to another (particularly among the medial three digits) this is unlikely to explain the effect because a comparable change in perceived heaviness occurred for muscles with anatomically distinct tendons (flexor pollicis longus and the index portion of flexor digitorum profundus), and the effect was of similar magnitude when non-adjacent portions of flexor digitorum profundus (to index and ring finger) contracted. Furthermore, such an explanation would probably lead to a reduction in perceived heaviness (rather than the observed increase) if force were 'passively' transmitted from the tendon of the concurrently active muscle into the one involved in lifting the reference weight. An additional potentially confounding mechanical effect was eliminated in all the studies conducted here: the mechanical pull from any antagonist co-contraction was prevented by the specific posture of the hand and/or by complete anaesthesia of the radial nerve above the elbow.

The second explanation which could explain the increase in perceived heaviness is derived from the evidence that perceived heaviness is biased by a signal related to the level of centrally generated motor command or effort required for the lift (for review see McCloskey, 1981; Gandevia, 1987; Cafarelli, 1988; Jones, 1988). It is known from anatomical and electrophysiological studies that the corticofugal output to a motoneurone pool shows some divergence. This divergence is least apparent for single intrinsic hand muscles and more marked for muscles within the forearm acting on the wrist and digits, i.e. a single motor cortical cell with corticomotoneuronal connections facilitates, on average, two to three agonist muscles in the forearm (Cheney & Fetz, 1985; Kasser & Cheney, 1985; see also Buys, Lemon, Mantel & Muir, 1986). In addition, Gandevia & Rothwell (1987) showed that, for single intrinsic but not extrinsic muscles of the hand, subjects could learn to direct differentially liminal motor commands which were subthreshold for activation of the motoneurone pool. However, subjects can grade forces with comparable reproducibility for a range of muscle groups in the upper limb (Gandevia & Kilbreath, 1990), so that inability to focus liminal motor commands on extrinsic hand muscles could reflect the anatomical divergence described above. With this second explanation, the central nervous system may be unable to determine precisely the destination of the increased total motor drive which is necessary when a concurrent weight is lifted. Thus, for example, when weights are simultaneously lifted by flexion of the index and thumb, the motor command to the thumb is perceived to be increased (erroneously) because the destination of the corticofugal outputs to the thumb and index cannot be completely separated. Such an explanation could deal easily with the progressive increase in the perceived heaviness with the size of the concurrently lifted weight, and with the increase during fatigue of the muscle lifting the concurrent weight. Another manifestation of this 'divergence' seen in everyday activities may be the inability to flex one digit rapidly without also involving an adjacent digit.

A third explanation is that the increase in perceived heaviness during a concurrent contraction may reflect a change in apparent 'excitability' of the motoneurone pool. When lifting with a single muscle (first dorsal interosseous), cutaneous reflexes which produce documented oligosynaptic inhibition (or facilitation) of the motoneurones recruited to lift the weight were associated with graded increases (or decreases) in perceived heaviness (Aniss *et al.* 1988). Although the changes in perceived heaviness described here occurred during digital anaesthesia and during inactivation of the antagonists, the nett reflex effects produced by muscle spindle endings and Golgi tendon organ afferents will be difficult to predict during the concurrent lift. If the nett effect were inhibition (or disfacilitation due to muscle spindle unloading) of the motoneurones involved in the reference lift, then the results could be explained. Such 'inhibition' would need to be gradable with contraction strength and to be more evident with muscle fatigue when reflex inhibition or disfacilitation occurs (Bigland-Ritchie, Dawson, Johansson & Lippold, 1986; Hagbarth, Kunesch, Nordin, Schmidt & Wallin, 1986; Gandevia, Macefield, Burke & McKenzie, 1990). Such an organization of the peripheral reflex machinery is clearly possible given the complexity of interneuronal circuits (for review see Baldissera, Hultborn & Illert, 1981; Fournier & Pierrot-Deseilligny, 1989), but may not provide the full explanation. Furthermore, an effectively inhibitory interaction between close synergists active together would have to be reconciled with evidence for group Ia facilitation between muscles acting on the fingers and wrist (Clough, Kernell & Phillips, 1968; Panizza, Lelli & Hallett, 1989; Fritz, Illert, de la Motte, Reeh & Saggau, 1989).

This work was supported by the National Health and Medical Research Council of Australia. The authors are grateful to Professors D. Burke and D. I. McCloskey for comments on the manuscript.

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