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ACCURACY OF WEIGHT ESTIMATION FOR WEIGHTS LIFTED BY PROXIMAL AND DISTAL MUSCLES OF THE HUMAN UPPER LIMB

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SUMMARY

1. It is well established that tactile acuity is greater over digits than over the proximal parts of the upper limb and that the corticospinal projection is especially dense for distal muscles. To determine whether the acuity for judgements of forces exerted by distal muscles differed from that for proximal muscles, a weight-matching task was used with first dorsal interosseous, flexor pollicis longus and elbow flexors.

2. Reference weights equivalent to approximately 3% (light) and 15% (heavy) of the maximal voluntary contraction were lifted by one muscle group on the left. They were matched with a variable weight, lifted by the same group, on the right.

3. In naive subjects, the coefficient of variation for repeated estimates of perceived heaviness was significantly lower for proximal than distal muscles. Measured in this way, 'accuracy' (i.e. reproducibility of the estimates) was not greater for the intrinsic muscles of the hand. This result could not be explained by the way in which the weights were supported by the index finger. When the data were expressed as the relative difference between the reference and the matched weight, each muscle group behaved similarly.

4. For a particular muscle, accuracy was greater when the heavy rather than the light weights were lifted.

5. Given that estimates of forces and heaviness are biased by signals of central motor command (McCloskey, 1981; Gandevia, 1987; Cafarelli, 1988; Jones, 1988), these signals could be graded no more finely for distal than proximal muscles. Furthermore, relative accuracy was greater for forces at the high rather than the low end of the comfortable 'matching' range of force for a particular muscle.

INTRODUCTION

Traditionally, the highly skilled actions of the hand have been thought to require finer control of movements than for actions of the forearm or upper arm. For example, when discussing the difference between muscles of the arm and the hand, De Luca, LeFever, McCue & Xenakis (1982, p. 124) wrote that 'the function of the first dorsal interosseous is to produce small, accurate movements of the index finger, requiring fine force gradation.... Since the deltoid is used primarily for generating large, powerful contractions, finely controlled firing-rate activity is unnecessary during normal voluntary effort.' The underlying assumption has been that the perceptual and motor control of the hand is 'specialized'. This assumption would appear to be supported by a study on single motor unit recruitment involving muscle of the hand and forearm (Gandevia & Rothwell, 1987). Subjects could learn to direct subthreshold motor commands (in the absence of peripheral feedback) to single motor units of extremely low threshold in the intrinsic hand muscles, but not in the more proximal muscles of the forearm. Furthermore, the distal muscles of the primate upper limb receive relatively dense corticospinal projections compared to more proximal muscles (e.g. Liddell & Phillips, 1950; Phillips & Porter, 1964). While the hand clearly shows greater tactile acuity than proximal areas of skin, there is no evidence that this 'distal acuity' occurs for the sensation of muscle force or heaviness. The latter sensations are biased by signals of centrally generated motor commands (or effort) rather than being simply signals of achieved force from cutaneous, joint or muscle afferents (reviews: McCloskey, 1981; Gandevia, 1987; Cafarelli, 1988; Jones, 1988).

The size principle of motoneuron recruitment (Henneman, 1957; review: Henneman & Mendell, 1981) should also influence the ability to grade muscular force. Muscle force is increased by recruitment of new motor units and by rate modulation of motor units already recruited. As the recruitment of low-threshold units can be finely graded, especially for intrinsic hand muscles (Milner-Brown, Stein & Yemm, 1973; Stephens & Usherwood, 1977; Dengler, Stein & Thomas, 1988; see also Gandevia & Rothwell, 1987) it might be predicted that accuracy of force judgements is greater for low forces.

The ability to match forces or weights may be considered in terms of accuracy and precision, accuracy reflecting the reproducibility of the estimates, and precision the approximation to the absolute force or weight. Using these measurements of performance, the present study investigated firstly, whether the ability to estimate weights lifted by distal muscles is greater than for either proximal or a combination of proximal muscles and distal muscles, and secondly, whether the ability is greater when relatively low forces are generated. A preliminary account of some findings has been published (Kilbreath & Gandevia, 1989).

METHODS

Subjects

Sixteen volunteer subjects (fifteen females, one male) participated in the study. Their ages ranged from 20 to 55. Subjects were unaware of the hypothesis being tested and they had not previously participated in experiments involving force- or weight-matching tasks. The procedures have been approved by the local ethics committee.

Experimental procedure

In the main study, four lifting tasks were used. In the first three, the lifts were performed by the following muscles: (i) first dorsal interosseous (FDI), (ii) flexor pollicis longus (FPL) and (iii) the elbow flexors (EF). The fourth task was a 'composite' task which required activity in many upper limb muscles. The matching task required the subject to lift the weights simultaneously on the left and right sides. A 'reference' weight was lifted on the left side and a 'variable' (or matching) weight on the right. The subjects lifted the weights from about one-third into the available joint range through to the end of the active range for FDI, FPL and EF. The subjects were asked to make the weights 'feel the same' by requesting an increase or decrease in the weight on the right side.

Subjects were not limited to reporting that the weights felt the same within a specified number of adjustments to the variable weight and they were not confined to requesting a change in weights in only one direction (the addition or subtraction of weights could 'overshoot' their perceived heaviness of the reference weight). Subjects were not instructed in the number of times they were permitted to lift each set of weights prior to making a decision. However, subjects tended to lift

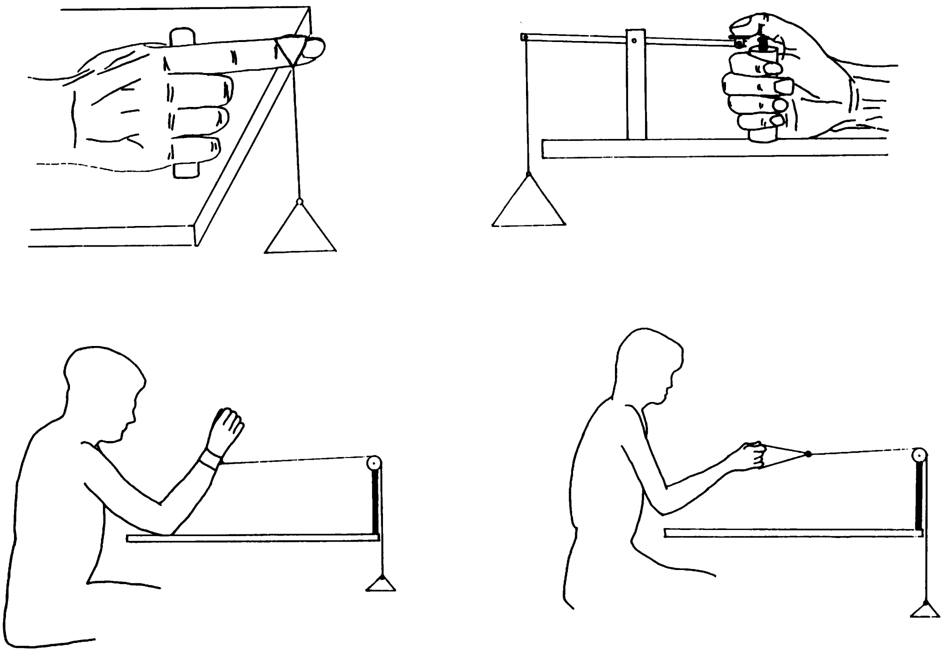

Fig. 1. Diagrammatic representation of the four lifting tasks. Subjects simultaneously lifted a reference weight on the left side and a variable weight on the right. Upper left: lifting with FDI. Weight is supported by a narrow band on the distal phalanx. Upper right: lifting with FPL. Movement is isolated to flexion of the terminal phalanx of the thumb using a stabilizing bar. Lower left: lifting with the EF. Lower right: lifting with proximal and distal muscles (i.e. the composite task). Subjects were required to lift the weight by holding a pre-shaped band across the proximal phalanges. Parts of the figure adapted from Aniss *et al.* (1988) and Gandevia & McCloskey (1978).

them two to four times before they decided whether the variable weight felt the same, heavier, or lighter than the reference weight. No further information was given on the type of strategy to use (e.g. angular velocity used to lift the weights) or the way in which the weights were to feel 'the same'. Between lifts and while the weights were being changed, the weights were supported externally. Each trial was completed when the subject perceived that the left side was equal to the right side. Approximately half the trials started with the variable weight heavier than the reference weight, and half with the variable weight lighter. Subjects were also unaware that the reference weight did not usually change during a sequence of trials.

The initial weight lifted on the right side ranged from 5% to 250% of the reference weight. For all matching tasks, the variable weight was changed by a minimum of 5% of the reference weight. Thus, if the reference weight for lifting with EF was 550 g, the variable weight was adjusted by a minimum of 28 g. All adjustments were made in multiples of 5% of the reference weight. In each session of the main study, one of the four tasks was studied in which a subject completed fifteen trials with a relatively heavy reference weight and fifteen trials with a relatively light reference weight. The reference weights were standardized such that the light and heavy weights represented approximately 3 and 15% of the maximal isometric force for each muscle group respectively. These values were taken from normal torques (for males and females) from this laboratory (Colebatch & Gandevia, 1989). Thus, the light weights lifted for FDI, FPL and EF were 75, 140 and 550 g respectively for the female subjects and 125, 240 and 1040 g for the male subject. The heavy weights lifted for FDI, FPL and EF were 275, 640 and 2650 g respectively for the female subjects and 625, 1040 and 4640 g for the male subject. To minimize any systematic effect from muscle fatigue, the four lifting tasks were performed on different days. The order of the lifting tasks and the sequence of high and low reference weights were randomized. After ten lifting trials, a subject rested for 2–3 min to prevent fatigue. During the tasks, the subjects were unable to see the weights being used.

The four lifting tasks are depicted diagrammatically in Fig. 1. To isolate FDI, the subject was seated with forearms resting on a table. All fingers except the index finger lightly grasped a 10 mm wide vertical rod; the index finger was maintained in an extended position. Small bands of 25 mm width were placed just proximal to the nail bed of the index digit from which an inextensible line was suspended. Attached to the line was a light weight bucket into which weights could be placed. Lifting weights using this technique involves the agonist (FDI) with minimal co-contraction of the antagonist (palmar adductor muscle) (Aniss, Gandevia & Milne, 1988).

For weights lifted by FPL, subjects rested with their forearms on the table and lightly grasped a vertical rod with all digits except their thumb (Fig. 1). To isolate the lifting movement to flexion at the interphalangeal joint of the thumb, and thereby the FPL, the joint rested on a cross-bar. The distal phalanx rested on the end of a lever. From the other end of the lever an inextensible string supported a light bucket containing the weights.

To assess EF, subjects sat with only their elbows resting on the table (Fig. 1). Subjects were positioned such that the elbow passed through its mid-range, and the forearm was perpendicular to the table as weights were lifted. Cuffs 60 mm wide were placed around the subject's forearms just proximal to the wrists. A pulley was rigged 25 cm above the edge of the table opposite the subject at the same height as the cuff on the wrist. The inextensible line passed from the cuff, over the pulley, to a bucket supporting the weights.

The fourth task allowed the subjects to choose their own strategy for lifting, using muscles acting across the metacarpophalangeal, wrist, elbow and even shoulder joints (Fig. 1). The subjects grasped a light piece of plastic shaped to fit the volar aspect of the proximal phalanges of all digits (except the thumb) while seated. A line was attached to the plastic piece. The same pulley system and reference weights were used as for elbow flexion. Electromyography was used to monitor muscle activity during the tasks in two subjects. The muscles monitored included: (i) FDI, (ii) flexor carpi ulnaris, (iii) biceps brachii, and (iv) latissimus dorsi. Surface electrodes were closely spaced (20 mm apart) over prepared skin. These electromyographic recordings confirmed that the subjects were required to use muscles acting over the finger, wrist and elbow joint (Fig. 2) for the composite task. In addition, for the other three lifting tasks, remote, non-lifting muscles were not phasically active to a significant extent. For example, recordings from FDI and EF, during thumb flexion showed that they generated less than 2% of the integrated activity associated with a maximal voluntary contraction.

Two additional studies were performed in which weights were lifted by FDI with the same position of the index as in Fig. 1. In the first, reference weights of 3, 12 and 20% of the predicted maximum voluntary force were used. In a second group of naive subjects, we examined whether the width of the band on the digit to support the weight altered the perceived heaviness. Two sizes of bands were used, 50 and 18 mm wide. The mid positions of the bands were aligned with the middle of the index digit. The lifting conditions studied were: (i) wide bands on both index fingers, (ii) narrow bands on both fingers and (iii) a wide band on the right index finger and a narrow band on the left. In each study, the three series of lifts were randomized.

Data analysis

The accuracy of weight matching for repeated trials was defined as the coefficient of variation for the sets of fifteen trials in the first study and ten trials in the subsequent studies. The coefficient of variation is the standard deviation of the subject's estimates divided by the mean estimate and expressed as a percentage: it is dimensionless. This measurement focuses on the reliability or reproducibility of judgements about perceived heaviness and it allows comparisons across and within tasks. The mean estimates and standard deviations from one subject for the four lifting tasks are shown in Fig. 3; the coefficient of variation, calculated for each task, is also shown. Use of the coefficient of variation is considered further in the Discussion. Data were also analysed in terms of precision or absolute error, i.e. the relative proximity of the mean estimate to the reference weight. The absolute difference between the mean estimate and the reference weight was expressed as a percentage of the reference weight. This measurement focused on the ability to judge the absolute weight of an object. The weight of the lifting apparatus was included in all calculations. Two-way analyses of variance were completed to look for effects due to the different lifting tasks, the heaviness of the reference weight, and intersubject variation. *Post hoc*, protected t tests were performed if significant effects ($P < 0{\cdot}05$) were detected (Welkowitz, 1982).

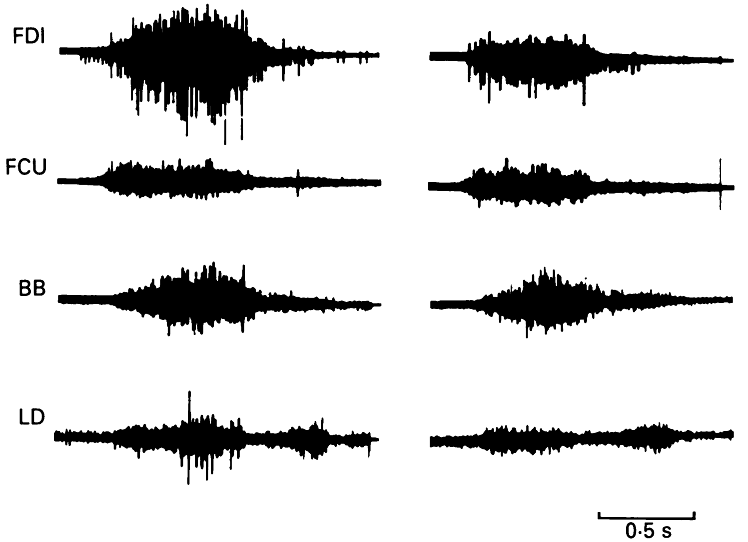

Fig. 2. Raw EMG traces recorded while the subject performed the composite lifting task on two trials. From above downward, the muscles are first dorsal interosseous (FDI), flexor carpi ulnaris (FCU), biceps brachii (BB), and latissimus dorsi (LD). The subject lifted the weight by pulling the bar that supported the weight across the metacarpophalangeal joints, while extending the shoulder. The elbow was not resting on the table (see Fig. 1). Phasic activity during each lift was present in both the proximal (e.g. latissimus dorsi) and distal (e.g. first dorsal interosseous) muscles.

RESULTS

The present study focused upon the accuracy and precision in estimation of weight when using different muscles of the upper limb. Tasks were designed to use specifically an intrinsic muscle of the hand, the long flexor of the thumb (a muscle located in the forearm), the flexors of the elbow, or a combination of proximal and distal muscles (acting over shoulder, elbow, wrist and fingers; see Fig. 1).

The coefficient of variation for repeated estimates of perceived heaviness by a subject was used as the estimate of accuracy or reproducibility: it is the standard deviation of the estimates, expressed as a percentage of the mean estimate. Accuracy differed between muscles (analysis of variance, $P < 0{\cdot}001$) and it was not greatest for the most distal muscle. As a group, subjects were more accurate in lifting with the EF than with FDI ($P < 0{\cdot}05$). Furthermore, the group of subjects were equally accurate when forced to use multiple proximal and distal muscles in the composite task, as when using single muscles. Data are shown for an individual subject and the group in Figs 3 and 4 respectively.

There was a significant effect on matching accuracy due to the size of the reference weight ($P < 0{\cdot}01$). Subjects were more accurate when lifting a heavy weight (15% of maximal force, see Methods) than when lifting a light weight (3% of maximal force). Protected t tests revealed that subjects were more accurate when lifting the heavier weights with EF ($P < 0.01$), and when the composite task ($P < 0.05$) was used. This trend was evident for FPL and FDI but did not reach statistical significance (FPL: $P = 0.07$; FDI: $P = 0.30$). One factor that could confound the data would be learning during the four experimental sessions in which a different lifting task was tested. However, there was no progressive improvement or decrement in accuracy when the data were reanalysed according to the sequence of the experimental sessions.

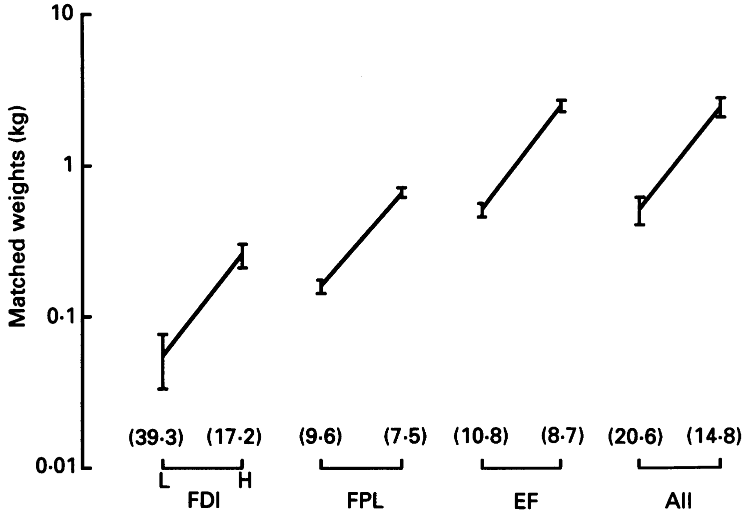

Fig. 3. Results (mean ± one standard deviation) are shown from a single subject for each of the lifting tasks, i.e. using first dorsal interosseous (FDI), flexor pollicis longus (FPL), elbow flexors (EF), and the composite task (All). For each task, on the left is data obtained when a light reference weight (3% of maximal voluntary force, L) was used and on the right, when the heavy reference weight (15% of maximal voluntary force, H) was used. The coefficient of variation for each task is shown (in parentheses) along the horizontal axis. The subject was least accurate when lifting the low weights with FDI. The coefficient of variation was consistently lower when the subject matched the heavy rather than the light reference weight.

The FDI showed the lowest accuracy for both reference weights and it was the muscle that did not demonstrate a clear difference in accuracy when forces of 3% and 15% of maximum were exerted. To assess these trends for a wider range of reference weights, a second series of trials was completed by seven subjects who had not participated in the first study. The reference weights were 3, 12 and 20% of maximal voluntary force. The mean coefficient of variation when lifting the 3% reference weight was 22%, similar to that in the first study (23%) (Fig. 5). There were significant effects due to both the size of the reference weight (analysis of variance, $P < 0.05$) and individual variation between subjects ($P < 0.05$).

As the analysis above relied only on the *scatter* of individual estimates of perceived heaviness and not *absolute* force, the ability of subjects to match the absolute weight was also examined, i.e. 'precision'. Precision was calculated as the difference between the subject's mean estimate and the reference weight, expressed as a percentage of the reference weight. There was no significant difference in precision between muscles used to lift weights, nor was it greater when the composite lifting task was used. Unlike the estimate of accuracy, precision was not affected by the heaviness of the reference weight. Two-way analyses showed that there were significant differences between subjects in nearly all assessments of accuracy, but not of precision.

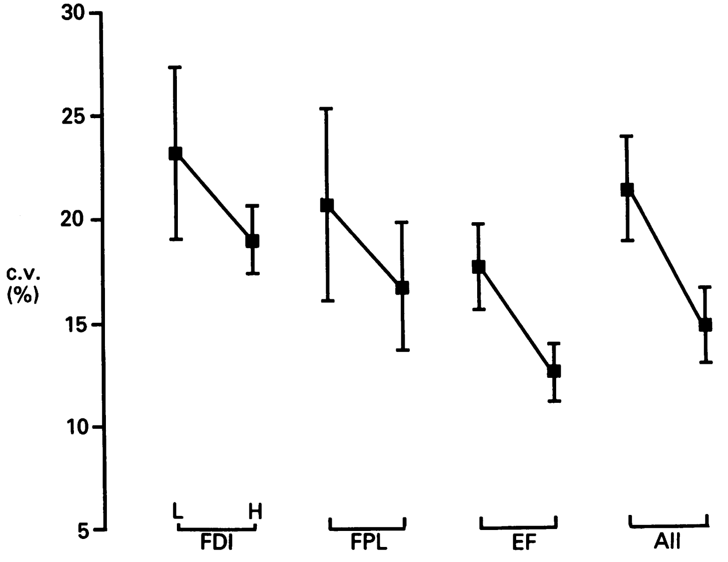

Fig. 4. Accuracy when matching the light (3% of maximal voluntary force, L) and heavy (15% of maximal voluntary force, H) reference weight for each of the lifting tasks. The lifting tasks using FDI, FPL, EF and the composite task (All) are shown. The left of each data pair is when a light reference weight was used and the right is when a heavy reference weight was used. The mean of the subjects' coefficients of variation (c.v.; ± S.E.M.) is plotted. There is a significant trend for the proximal EF to be more accurate (see text). Accuracy was greater when heavier reference weights were used.

Finally, given that the assessment of neither accuracy nor precision revealed that the performance of the distal muscle was enhanced, the cutaneous facilitation provided by the band supporting the weight was considered. Cutaneous afferents from the digits exert short- and long-latency reflex effects on FDI (e.g. Garnett & Stephens, 1980; Jenner & Stephens, 1982; Johannson & Westling, 1984) and they bias perceived heaviness depending upon whether there is net excitation or inhibition (Aniss *et al.* 1988; see also Gandevia & McCloskey, 1977*a*, *b*). Thus, the final study examined the effect on accuracy and precision in six subjects when the reference weight was constant (12% maximal force) but the width of the bands supporting the weight for FDI was changed. There was no significant difference in accuracy when lifting with the narrow bands (18 mm) over the middle phalanx on both index fingers, with wide bands (50 mm) covering most of the index finger or with one narrow and one wide band. The estimate of precision was also not affected by the size of the band. In particular, perceived heaviness was not altered when there was a narrow band on one index and a wide band on the other.

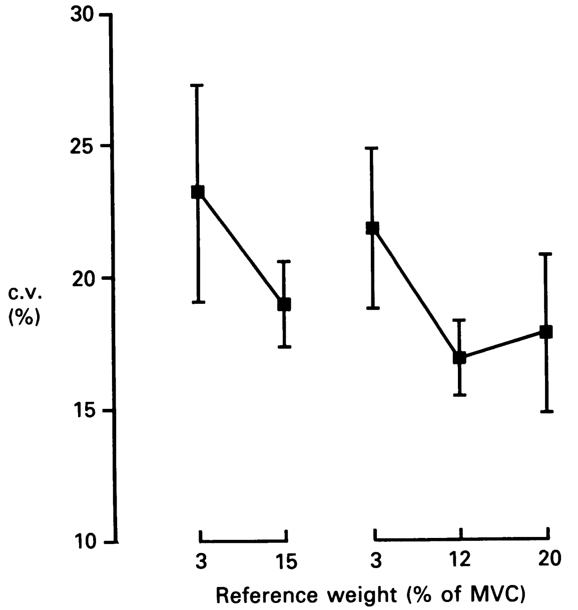

Fig. 5. Comparison of accuracy using FDI to lift in two naive groups of subjects. Results from Fig. 3 are shown on the left (nine subjects; represents weights of 3% and 15% of maximal voluntary contraction, MVC); results from another group (seven subjects; 3%, 12% and 20% of MVC) on the right. The mean of the subjects' coefficients of variation ($\pm$S.E.M.) is plotted. In both groups, accuracy was low with the lower reference weight.

DISCUSSION

The present study has failed to find evidence that the ability to match forces is greater for single, intrinsic hand muscles than for muscles located in the forearm and upper arm, or for a natural combination of proximal and distal muscles. The forces to be matched by the different muscles were approximately the same fractions of the maximal voluntary forces. Secondly, operation of muscles at low force levels relative to their maximum is associated with lower rather than greater accuracy in judgements about force.

Accuracy of force estimation has been calculated here as the coefficient of variation from a group of trials (standard deviation/mean, expressed as a percentage). It normalizes 'accuracy' for the level of force exerted, thereby allowing comparison between lifting conditions. Thus, when measured this way, there is a statistically greater accuracy shown by the EF compared to FDI. The *absolute* standard deviation of the estimates clearly increases as muscle size and force increase. However, the relative increase in the standard deviation is smaller than the increase in mean matching force. Expression of accuracy in absolute terms (i.e. standard deviation) and relative terms (i.e. coefficient of variation) is shown in Fig. 6.

It is not surprising that accuracy of a proprioceptive sensation, namely weight estimation, should differ for proximal and distal muscles depending upon the way it is expressed. Hall & McCloskey (1983) showed that the acuity of another proprioceptive sensation, the detection of limb movement, depends upon how it is measured: acuity is greater for distal muscles when expressed in terms of absolute movement, i.e. millimetres of the extremity, but greater for proximal muscles when expressed in terms of angular movement of the moved segment (see also De

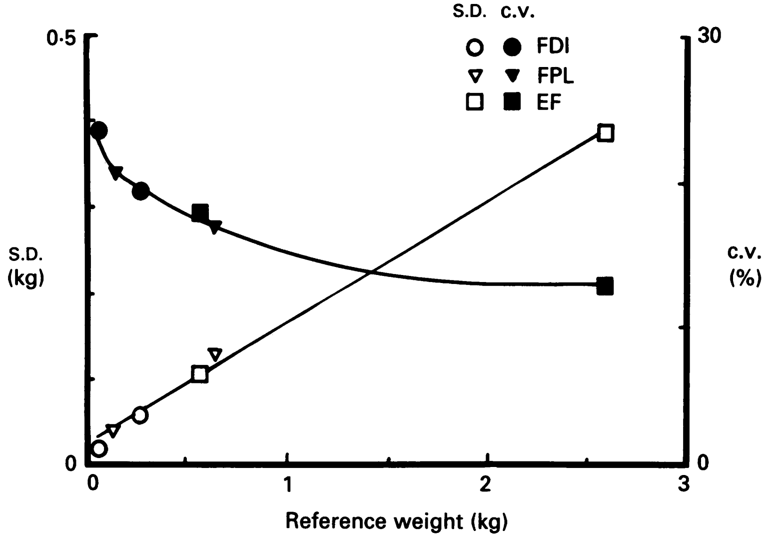

Fig. 6. Comparison of data for accuracy when analysed in 'relative' terms (coefficient of variation, C.V.) and 'absolute' terms (standard deviation, S.D.) for three muscle groups. The mean coefficients of variation are shown as filled symbols and the standard deviations as open symbols. Lifting with FDI is represented by circles, with FPL by triangles, and with EF by squares. Lines of best fit are plotted based on a linear regression for the standard deviations ($P < 0.01$), and a logarithmic regression for the coefficients of variation ($P < 0.01$).

Domenico & McCloskey, 1987). Interestingly, acuity for movement detection was similar for proximal and distal muscles when expressed in terms of relative changes in muscle length. Their study did not include an intrinsic hand muscle. The present difference in accuracy of force estimation occurred even when the forces exerted were a constant fraction of the maximal voluntary force. While it is possible that learning may influence the accuracy of weight estimation, we found no evidence that this occurred sequentially during the study. Also, it is difficult to see why one particular muscle group in the upper limb (e.g. EF) should be influenced preferentially by any learning effect due to the usual daily activities. It is possible that the accuracy shown by the EF reflects the use of several individual muscles, although we have no direct data to confirm this.

Given that sensation of heaviness of lifted objects and of force are biased by signals related to the size of centrally generated signal of motor command (e.g. McCloskey, Ebeling & Goodwin, 1974; Gandevia & McCloskey, 1977*a*, *b*; Jones & Hunter, 1983; reviews: McCloskey, 1981; Gandevia, 1987; Cafarelli, 1988; Jones, 1988) we have no evidence that these signals can be graded more finely for the distal compared to the proximal muscles. Afferent signals are important in the estimation of weights and tensions in that they provide a critical signal that the weight has actually been lifted

(Gandevia & McCloskey, 1978). Furthermore, the reflex inputs from muscle, joint and cutaneous receptors can excite or inhibit the motoneuron pool and thus reduce or increase (respectively) perceived heaviness by changing the required signal of central motor command (McCloskey *et al.* 1974; Aniss *et al.* 1988). These latter mechanisms cannot explain the present results, given that the distal extremity, with the highest tactile acuity, was not the most accurate for judgements of force. The difference remained even when the force exerted by the index finger was dispersed over a large area of the digit and not confined to a narrow region over the distal phalanx (see Results). In addition, the differences in force accuracy remain when the gravitational torques exerted by the finger, thumb tip and forearm/hand are considered.

A second finding was that the accuracy was low when weights corresponding to 2–5% of maximal voluntary force were estimated and significantly higher for weights corresponding to 15–20% of maximal voluntary force. This difference is unexpected, given that the experimental evidence in animals (e.g. Henneman & Olson, 1965) and human subjects (e.g. for FDI see Milner-Brown *et al.* 1973; Stephens & Usherwood, 1977; Dengler *et al.* 1988) that the twitch force of newly recruited motor units increases progressively as the background force level increases. These data would suggest that with progressive motor unit recruitment the ability to grade muscular force may remain relatively constant. This is not so, at least across the comfortable 'working' range of forces estimated here (2–20% of maximal voluntary force). At below 2% of maximal voluntary force there is occasional failure to detect the presence of the weight and at above 20% of maximal voluntary force muscular fatigue develops (see Aniss *et al.* 1988). Our results are less paradoxical given the known propensity for the Weber fraction to increase at the extremes of a sensory continuum (Stevens, 1983). Accordingly, the just noticeable change in weight is probably relatively larger at the lower extreme used here. The critical finding is that the recruitment of many small motor units is not necessarily associated with accuracy of force estimation.

The present findings may seem contradictory to those when motor cortical stimuli were used to evaluate the recruitment of the first voluntarily recruited motor units in pairs of human intrinsic hand muscles or muscles in the forearm (Gandevia & Rothwell, 1987). In the absence of specific peripheral feedback, subjects could learn to recruit these motor units following motor cortical stimulation only for intrinsic muscles of the hand and not more proximal muscles. However, this may reflect the inability of motor cortical output to access a single muscle in isolation, due to collaterals of corticospinal axons (e.g. Shinoda, Zarzecki & Asanuma, 1979). The ability to grade the suprathreshold output to various proximal and distal muscles may not differ, merely the ability to fractionate the final output to a single motoneuron pool.

One implication from the present study is that for optimal performance, weights or forces should be matched to the muscle group which lifts or supports them: the lifted weight should be within the range of 2–20% of maximal voluntary force for the muscle or muscle group. If relative accuracy of performance is desired then the weight should be towards the upper end of this range. This fits with everyday experience in which it is common for objects of unknown weight to be moved first by distal muscles (e.g. across metacarpophalangeal and interphalangeal joints) and then by more proximal muscles (e.g. wrist and elbow) if the weight is heavier than expected.

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REFERENCES

ANISS, A. M., GANDEVIA, S. C. & MILNE, R. J. (1988). Changes in perceived heaviness and motor commands produced by cutaneous reflexes in man. *Journal of Physiology* **397**, 113–126.

CAFARELLI, E. (1988). Force sensation in fresh and fatigued human skeletal muscle. *Exercise and Sports Science Review* **16**, 139–168.

COLEBATCH, J. G. & GANDEVIA, S. C. (1989). The distribution of muscular weakness in upper motor neuron lesions affecting the arm. *Brain* **112**, 749–763.

DE DOMENICO, G. & MCCLOSKEY, D. I. (1987). Accuracy of voluntary movements at the thumb and elbow joints. *Experimental Brain Research* **65**, 471–478.

DE LUCA, C. J., LEFEVER, R. S., MCCUE, M. P. & XENAKIS, A. P. (1982). Behaviour of human motor units in different muscles during linearly varying contractions. *Journal of Physiology* **329**, 113–128.

DENGLER, R., STEIN, R. B. & THOMAS, C. (1988). Axonal conduction velocity of single human motor units. *Muscle and Nerve* **11**, 136–145.

GANDEVIA, S. C. (1987). Roles for perceived voluntary motor commands in motor control. *Trends in Neurosciences* **10**, 81–85.

GANDEVIA, S. C. & MCCLOSKEY, D. I. (1977*a*). Sensations of heaviness. *Brain* **100**, 345–354.

GANDEVIA, S. C. & MCCLOSKEY, D. I. (1977*b*). Changes in motor commands, as shown by changes in perceived heaviness during partial curarization and peripheral anaesthesia in man. *Journal of Physiology* **272**, 673–689.

GANDEVIA, S. C. & MCCLOSKEY, D. I. (1978). Interpretation of perceived motor commands by reference to afferent signals. *Journal of Physiology* **283**, 493–499.

GANDEVIA, S. C. & ROTHWELL, J. C. (1987). Knowledge of motor commands and the recruitment of human motoneurons. *Brain* **110**, 1117–1130.

GARNETT, R. & STEPHENS, J. A. (1980). The reflex responses of single motor units in human first dorsal interosseous muscle following cutaneous afferent stimulation. *Journal of Physiology* **303**, 351–364.

HALL, L. A. & MCCLOSKEY, D. I. (1983). Detection of movements imposed on finger, elbow and shoulder joints. *Journal of Physiology* **335**, 519–533.

HENNEMAN, E. (1957). Relations between size of neurons and their susceptibility to discharge. *Science* **126**, 1345–1346.

HENNEMAN, E. & MENDELL, L. M. (1981). Functional organization of motoneuron pool and its inputs. In *The Nervous System, Handbook of Physiology,* section 1, vol. 2, part 2, ed. BROOKHART, J. M. & MOUNTCASTLE, V. B., pp. 423–508. American Physiological Society, Bethesda, MD, USA.

HENNEMAN, E. & OLSON, C. B. (1965). Relations between structure and function in the design of skeletal muscles. *Journal of Neurophysiology* **28**, 581–598.

JENNER, J. R. & STEPHENS, J. A. (1982). Cutaneous reflex responses and their central nervous pathways studied in man. *Journal of Physiology* **33**, 405–419.

JOHANSSON, R. S. & WESTLING, G. (1984). Roles of glabrous skin receptors and sensorimotor memory in automatic control of precision grip when lifting rougher or slippery objects. *Experimental Brain Research* **56**, 550–564.

JONES, L. A. (1988). Motor illusions: what do they reveal about proprioception? *Psychological Bulletin* **103**, 72–86.

JONES, L. A. & HUNTER, I. W. (1983). Effect of fatigue on force sensation. *Experimental Neurology* **81**, 640–650.

KILBREATH, S. L. & GANDEVIA, S. C. (1989). Accuracy of weight estimation for proximal and distal muscles of the upper limb. *Neuroscience Letters* **34**, suppl., S104.

LIDDELL, E. G. T. & PHILLIPS, C. G. (1950). Threshold of cortical representation. *Brain* **73**, 125–140.

McCLOSKEY, D. I. (1981). Corollary discharges: motor commands and perception. In *The Nervous System, Handbook of Physiology,* section 1, vol. 2, part 2, ed. BROOKHART, J. M. & MOUNTCASTLE, V. B., pp. 1415–1447. American Physiological Society, Bethesda, MD, USA.

McCLOSKEY, D. I., EBELING, P. & GOODWIN, G. M. (1974). Estimation of weights and tensions and apparent involvement of a 'sense of effort'. *Experimental Neurology* **42**, 220–232.

MILNER-BROWN, H. S., STEIN, R. B. & YEMM, R. (1973). The orderly recruitment of human motor units during voluntary isometric contractions. *Journal of Physiology* **230**, 359–370.

PHILLIPS, C. G. & PORTER, R. (1964). The pyramidal projection to motoneurones of some muscle groups of the baboon's forelimb. In *Progress in Brain Research,* vol. 12, ed. ECCLES, J. C. & SCHADE, J. P., pp. 222–242.

SHINODA, Y., ZARZECKI, P. & ASANUMA, H. (1979). Spinal branching of pyramidal tract neurons in the monkey. *Experimental Brain Research* **34**, 59–72.

STEPHENS, J. A. & USHERWOOD, T. P. (1977). The mechanical properties of human motor units with special reference to their fatiguability and recruitment threshold. *Brain Research* **125**, 91–97.

STEVENS, S. S. (1983). *Psychophysics: Introduction to its Perceptual, Neural, and Social Prospects.* John Wiley & Sons, New York.

WELKOWITZ, J. (1982). *Introductory Statistics for the Behavioral Sciences*, 3rd edn. Academic Press, New York.