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Coordinated isometric muscle commands adequately and erroneously programmed for the weight during lifting task with precision grip

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Summary. Small objects were lifted from a table, held in the air, and replaced using the precision grip between the index finger and thumb. The adaptation of motor commands to variations in the object's weight and sensori-motor mechanisms responsible for optimum performance of the transition between the various phases of the task were examined. The lifting movement involved mainly a flexion of the elbow joint. The *grip force,* the *load force* (vertical lifting force) and the *vertical position* were measured. *Electromyographic activity* (e.m.g.) was recorded from four antagonist pairs of hand/arm muscles primarily influencing the grip force or the load force. In the *lifting series with constant weight,* the force development was adequately programmed for the current weight during the *loading phase* (i.e. the phase of parallel increase in the load and grip forces during isometric conditions before the lift-off). The grip and load force rate trajectories were mainly single-peaked, bell-shaped and roughly proportional to the final force. In the *lifting series with unexpected weight changes* between lifts, it was established that these force rate profiles were programmed on the basis of the previous weight. Consequently, with lifts programmed for a lighter weight the object did not move at the end of the continuous force increase. Then the forces increased in a discontinous fashion until the force of gravity was overcome. With lifts programmed for a heavier weight, the high load and grip force rates at the moment the load force overcame the force of gravity caused a pronounced positional overshoot and a high grip force peak, respectively. In these conditions the erroneous programmed commands were automatically terminated by somatosensory signals elicited by the start of the movement. A similar triggering by somatosensory information applied to the release of programmed motor commands accounting for the *unloading phase* (i.e. the parallel decrease in the grip and load forces after the object contacted the table following its replacement). These commands were always adequately programmed for the weight.

Key words: Precision grip – Motor control – Human hand – Somatosensory input – Long latency reflexes – Motor programs – Sensorimotor memory – Mechanoreceptors

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Introduction

The motor act in which an object is lifted from a table and then replaced using the precision grip may be divided into a series of separate phases of coordinated movements (Johansson and Westling 1984b). During the various phases the balance between the grip force and the vertical lifting force is programmed to match the frictional conditions between the object manipulated and the fingers, i.e. these forces automatically change in *parallel* so maintaining an approximately constant ratio and provide a relatively small safety margin to prevent slips. This ratio is initially set to fit the anticipated frictional condition and seems to be defined by a sensorimotor memory which is intermittently updated by tactile information whenever the frictional conditions are changed (Johansson and Westling 1987). Thus, the control processes apparently utilize an internal representation of frictional conditions to allow anticipatory control of the force balance. From our experiences of lifting objects in every-day situations it seems reasonable to assume that the weight of handled objects also maybe internally represented. This would allow anticipatory control of the force development during manipulation. An often quoted example is the vigor with which we pick up a heavy-looking suitcase. If it turns out to be empty, the excessive force that we have applied because of the erroneous programming will topple us backwards. The aim of the present study was to investigate how past weight experiences may be utilized to program the load and grip forces during lifts involving a precision grip, and to elucidate the sensorimotor mechanisms underlying the matching between different phases of the lifting task.

Methods

Fifteen healthy subjects (6 women and 9 men, 16–49 years old), who were completely naive with regard to the specific purpose of the experiments, participated in the present study. The subject sat in a chair with the right upper arm parallel to the trunk, and with the unsupported forearm extending anteriorly. In this position, he/she was asked to lift a small object from a table. The object was grasped between the tips of the index finger and thumb of the right hand and the lifting movement mainly involved a flexion of the elbow joint. For timing purposes, a large illuminated clock with a second hand was placed in front of the subject. Five to ten minutes prior to the experiments the subjects had washed their hands with soap and water.

Apparatus

The test object used has been described earlier (Johansson and Westling 1984b). The surfaces touched by the subjects were two discs (diameter: 30 mm) mounted in two parallel vertical planes (distance: 30 mm). The *grip force* and the vertical lifting force (denoted as the *load force*), were measured continuously (d.c.–120 Hz) using strain gauge transducers attached to the object. The *vertical position* of the object was measured with an ultrasonic device (d.c. – 560 Hz), including a transmitter mounted at the top of the object and a receiver mounted in the ceiling of the laboratory. Two 21 cm long thin metal rods, attached to the base of the manipulandum, passed through holes in the table. At the lower ends of the rods a weight carrier was mounted and loaded with various weights, shielded from the subject's view by the table top. Thus, the center of gravity was below the table top. The moment the object started to move vertically and its terminal contact with the table during the replacement were electrically detected by galvanic contact between the object and a metal plate on the table. To distinctly define these moments, the object's contact with the table was limited to one point, i.e. while standing on the table the object balanced on a peg with a hemispherical tip (see Fig. 1 in Johansson and Westling 1984b).

Experiments

During the *lifting trials* the object was lifted about 2 cm above the table, held in this position for 10 s, and then replaced and released. The interval between successive lifts was ca. 10 s. Before the experiments the subjects received verbal instructions from the experimenter, who also carried out a demonstration trial. Thus, the subjects were only instructed to pay attention to the timing and to the positioning of the object in space.

The general structure of the lifts was the same as previously described (Johansson and Westling 1984b). Thus, each lift could be divided into different phases. During the first phase, the *preload phase,* the grip was established and the grip force increased for about 0.1 s. There were only small changes in the load force. During the *loading phase* the load force and the grip force increased in parallel during isometric conditions. The loading phase was terminated when the load force overcame the force of gravity and the lifting movement began. During the following *transitional phase* the object was lifted mainly by a nearly isotonic elbow flexion until the intended vertical position was reached. Early during this phase, the two forces reached peak values and the object accelerated. A small load force overshoot accounted for the reaction force due to acceleration (see for instance Fig. 1). Later, during the deceleration of the lifting movement, a small dip in the load force accounted for the reaction force due to deceleration (e.g. Fig. 1). The transitional phase was followed by a *static phase,* during which the two forces and the position of the object were nearly constant. During the ensuing *replacement phase* the object was lowered, and when it contacted the table, there was a short *delay,* after which the *unloading phase* commenced. During this phase the two forces fell in parallel until the object was released.

Ten subjects each performed a series of 16 lifts in which the *weight* (200 g, 400 g or 800 g) was the experimental variable and it was varied in an pseudorandom manner. This was done by altering the object's mass by attaching weights to the weight carrier below the table-top between successive lifts. A similar series involving 49 lifts was run with e.m.g. recording on five more subjects (see below). Another series in which the weight was constant at 200 g, 400 g or 800 g (9–25 trials) was also carried out during e.m.g. recording.

In another experiment, also with e.m.g. recording, the *height of the support* was pseudorandomly varied between three levels (1 cm between the levels, 49 lifts by each of five subjects, weight constant). Then the object rested on a vertically-movable metal frame mounted underneath the table-top so its support was shielded from the subject's view. In contrast to the "weight" series in which the subject could see the point of contact between the object and the table, in these series the subject could neither see nor adequately anticipate the height of the support.

The above described experiments were also repeated on three subjects who wore sound-proof earphones. They were instructed to close their eyes during the approach toward the object and keep them closed until the trial was over. This procedure was carried out to eliminate auditory and visual cues related to the moment of lift-off and the moment of table contact following the replacement.

The surface of the object touched was suede (soft leather).

Electromyography (e.m.g.)

Electrical activity was recorded from eight hand/arm muscles. A pair of flexible silver-coated PVC-electrodes (4 mm diameter, Medicotest a/s A-5-VS) filled with conducting jelly was applied to the skin over the belly of each muscle (15 mm inter-electrode distance along the muscles). The electrodes were connected through short flexible cables (ca. 2 cm) to small differential amplifiers taped onto the skin. This minimized movement artifacts. The e.m.g. signals were amplified (6 Hz – 2.5 kHz) and rectified using a root-mean-square (r.m.s.) processing with rise and decay time constants of 1 ms and 3 ms, respectively.

Two intrinsic hand muscles which quite selectively influence the grip force during the lifting task were selected: the *1st dorsal interosseous* muscle which supports the grip, and one of its antagonists, the *abductor pollicis brevis.* Recordings were also made from two extrinsic hand muscles: the *flexor pollicis longus* and the *abductor pollicis longus.* These act as antagonists with regard to the grip force, but, due to their action across the wrist, as synergists in supporting the weight. We also recorded from muscles primarily acting over the wrist: the *flexor carpi ulnaris* and the *extensor carpi radiales*. Due to their ability to cause ulnar and radial flexion of the wrist, respectively, they work as antagonists during the lifting motion in the present task. Finally, activity in the *brachioradialis* and the *triceps brachii* muscles were recorded. These act as antagonists over the elbow joint and influence the load force and the vertical position of the object after it has been lifted.

These particular recording sites were chosen because they provided good functional selectivity and small cross contamination between the various e.m.g. channels. During positioning of the electrodes, the subjects were asked to make various voluntary contractions with the intent to activate only one e.m.g. channel at a time. After some practice they became successful (cross contamination less than –20 dB). To evaluate the functional selectivity and action of the muscles, the experimenter monitored the various reaction forces.

Data collection and analysis

The signals describing the grip force (average of the forces produced by the index finger and the thumb), the load force, the vertical position and the e.m.g. signals were stored and analyzed using a flexible laboratory computer system. These variables were each sampled at 500 Hz by a 12-bit A/D converter (e.m.g. signals were r.m.s. processed before A/D conversion). The points in time when the object lost and regained contact with the table were also stored. For each trial, the data acquisition started ca. 1 s prior to the moment the object was touched and lasted until ca. 0.5 s after the lift was over and the subject no longer touched the object. The force and position signals were digitally low-pass filtered (forward and backward, d.c. – 50 Hz). The rates of change of the load and grip forces were calculated from the difference in force between consecutive samples. To analyze the coordination between the two forces these were graphically displayed against each other and their time derivatives were displayed against the load force. During averaging of trials, depending on the type of analysis (see results), each trial was synchronized in time to the moment the load force reached a prescribed level (0.5 Newton or 1.0 N), at the start of the vertical movement, or at the moment of terminal table contact. The e.m.g. analysis was always based on averaged data obtained from individual subjects. The latency measurements given in the text refer to the ranges observed for all subjects.

Results

Programmed force development during the loading phase

Lifting series with constant weight. The weight of the object clearly influenced the rate of force increase during the loading phase and the duration of the loading phase (Fig. 1A), i.e. the heavier the object, the faster the increase of the grip and load forces and the longer the time of the parallel force increase before the object started to move. The approximately bell shaped and single peaked force rate profiles were scaled from the force onset to the final force. The force rates at the point when the object started to move were low (see below). This indicated that the force development was programmed for the current weight. Trials showing such force rate profiles were denoted *adequately-programmed* trials. The programmed nature of the force development appears even more clearly from Fig. 1B, which shows the load force rate (middle graph) and the grip force rate (bottom graph) as a function of the load force for the same data as in Fig. 1A. Since absolute information about the current weight was available only after the lifting motion had begun, it seems reasonable that the programming was made on the basis of the experiences from the weight in the preceding (equal-weight) lift. In contrast to the force rates, the balance between the grip force and the load force was only little influenced by the weight. This is seen in the top graph in Fig. 1B in which the two forces are plotted against each other.

The e.m.g. profiles shown in Fig. 1, which are averaged data referring to the 800 g lifts represented by the solid curves, were typical for adequately-programmed trials. A striking finding with all subjects and all such lifts was the parallelism in signals from the antagonist muscles operating on the elbow joint, i.e. the triceps brachii and the brachioradialis muscles were always co-activated. A similar pattern was observed with the pair of antagonists principally acting on the wrist, the extensor carpi radiales and the flexor carpi ulnaris muscles. With the more distal muscles, a reciprocal activation pattern was observed during the grasping movement prior to contact and often initially during the loading phase. The abductor pollicis longus and the abductor pollicis brevis decreased their activity (though they never became silent), whereas the flexor pollicis longus and particularly the 1st dorsal interosseous muscle markedly increased their activity. The fairly high activity of the abductors before the object was gripped was probably related to an active spacing of the thumb and index finger.

Lifting series with variation in weight. The experiments with pseudorandom weight changes between consecutive lifts provided further evidence that the muscle commands accounting for the loading phase were programmed on the basis of the weight during the previous lift. The experiments also showed the effects of *erroneous programming* if a weight other than expected was presented. Depending on whether the weight of the object in the previous trial was heavier or lighter than the current weight, two different patterns of influences from the previous weight were distinguished.

Regarding the pattern when the current lift was *preceded by a heavier weight* the force development during the preload and loading phases was similar to that observed initially during the loading phase with

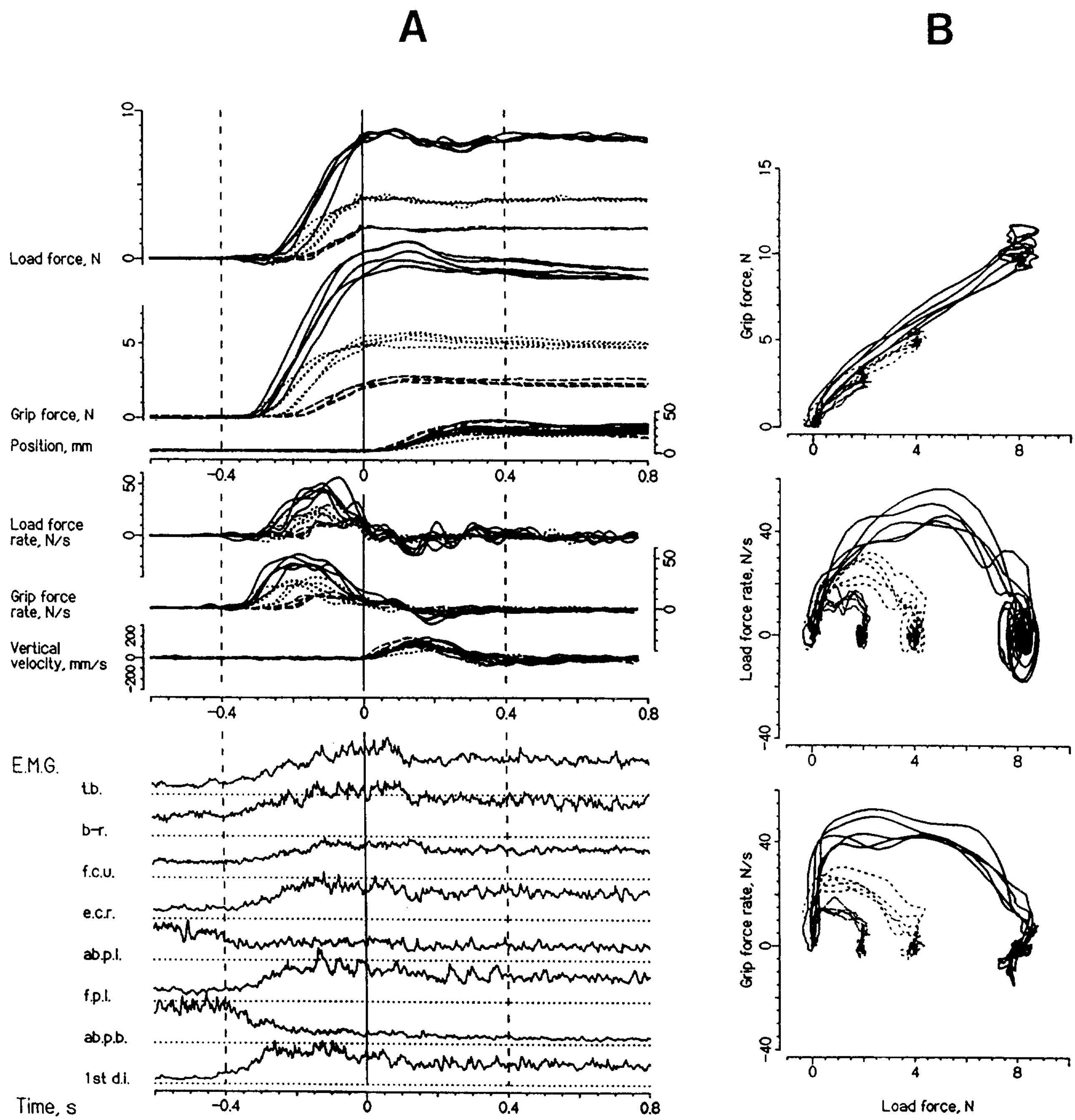

Fig. 1A, B. Initial parts of adequately-programmed lifts with 200 g (- - - - - -), 400 g (. . . . . .) and 800 g (—). **A** Load force, grip force, vertical position and their time derivatives as a function of time for 15 lifts (superimposed) by a single subject. E.m.g. signals refer to 800 g lifts (averaged data). Abbreviations: t.b. – triceps brachii, b-r. – brachioradialis, f.c.u. – flexor carpi ulnaris, e.c.r. – extensor carpi radiales, ab.p.l. – abductor pollicis longus, f.p.l. – flexor pollicis longus, ab.p.b. – abductor pollicis brevis, 1st d.i. – 1st dorsal interosseous. Trials synchronized in time at the moment the object started to move (time = 0). **B** Grip force, load force rate and grip force rate displayed in relation to the load force for the same trials as in **A**

the preceding heavier weight. However, soon after the object unexpectedly started to move, the erroneously-programmed lift showed a pronounced overshoot in the grip force and the position signals, but neither the grip force nor the load force increased to levels comparable to the previous heavier-weight trial. This kind of erroneous programming is shown in the mechanograms of Fig. 2A, B which represent individual lifts (synchronized at the moment of lift-off). The solid curves refer to lifts with 200 g which

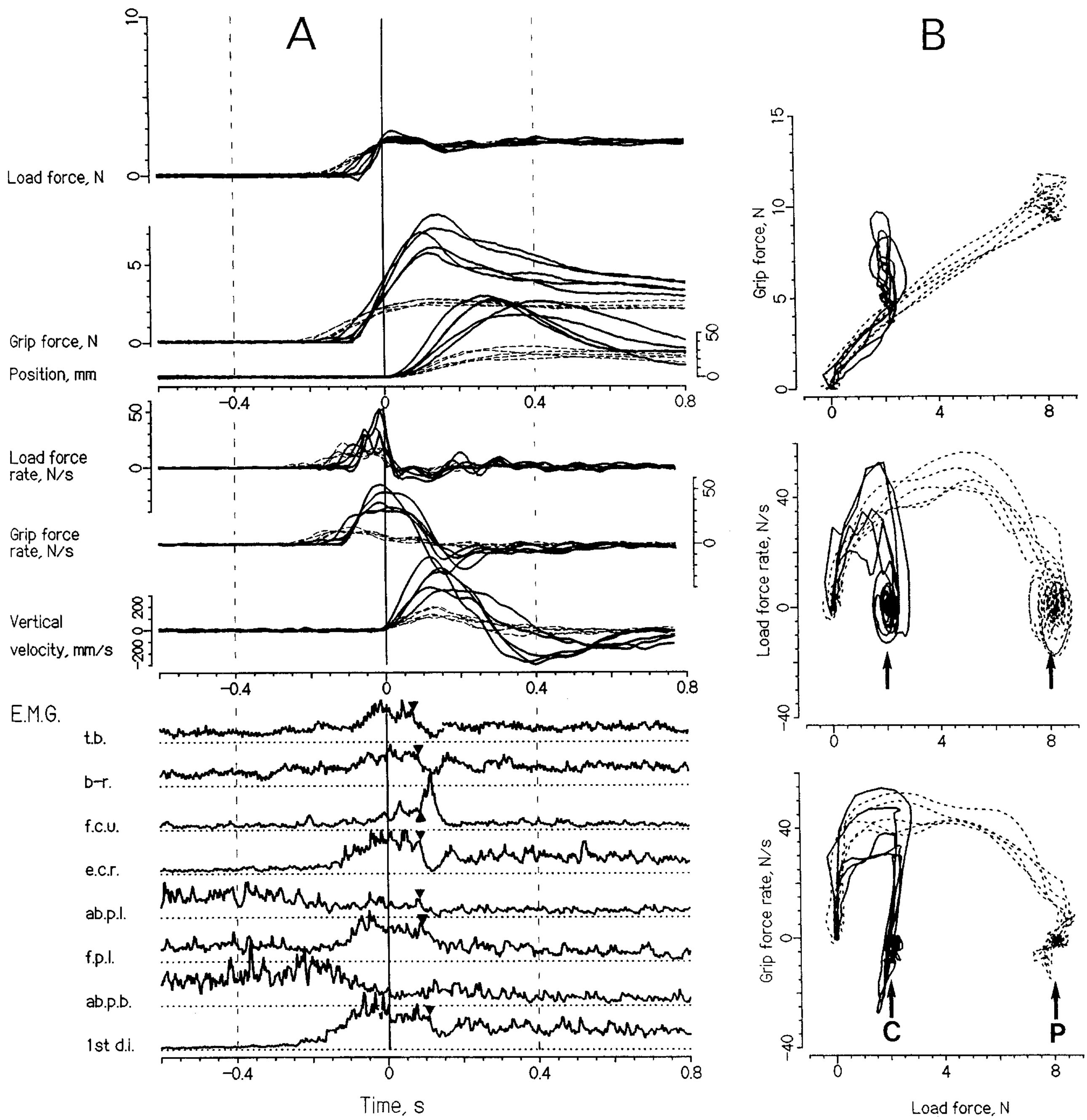

Fig. 2A, B. Initial parts of lifts erroneously programmed for a heavier weight. **A** Load force, grip force, vertical position and their time derivatives as a function of time for 5 lifts with 200 g programmed for 800 g (—) and for 5 adequately-programmed 200 g trials (- - - - - -). E.m.g. signals refer to the erroneously-programmed 200 g lifts (average data). Arrowheads indicate points with fairly abrupt changes in the e.m.g. signals. Trials synchronized in time at the moment the object started to move (time = 0). **B** Grip force, load force rate and grip force rate displayed in relation to the load force for the erroneously-programmed trials in **A** (—) and for 5 adequately-programmed 800 g trials (- - - - -). Arrows labelled C and P indicate the load force at which the object started to move in the current and previous trial, respectively. Single subject. For further details see legend to Fig. 1 and text

were preceded by adequately-programmed 800 g lifts. For comparison, the dashed curves in A and B represent adequately-programmed 200 g and 800 g lifts, respectively. As can be seen in A, the erroneously-programmed lifts showed considerably higher grip and load force rates during the loading phase than the adequately-programmed 200 g trials. As shown in Fig. 2B, the rates would have been adequate for a 800 g weight (arrows labelled by C and P indicate the load forces at which the object started to

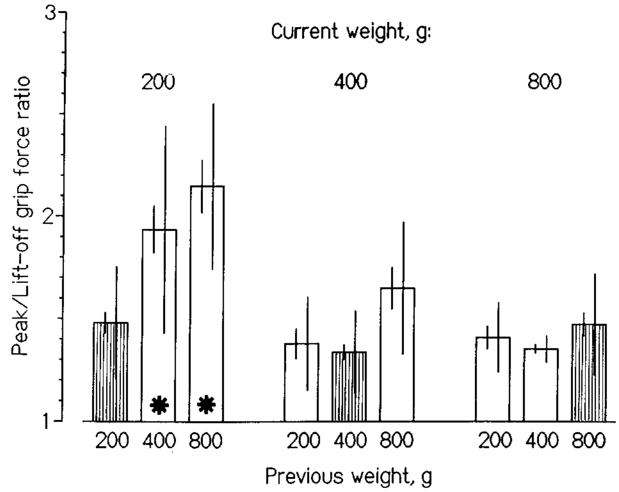

Fig. 3. Influence of the weight of the object in the previous trial on the size of the grip force overshoot defined as the ratio between the peak grip force and the grip force at the moment the object started to move ("lift-off" grip force). The three groups of columns refer to lifts with 200 g, 400 g and 800 g. The columns in each group labelled 200 g, 400 g and 800 g refer to the weight in the previous lift. Column height gives mean and bars S.E.M. and S.D. Stars indicate statistically significant differences between the trials represented by the starred columns and adequately-programmed trials represented by the shaded column ($p < 0.002$, Wilcoxons paired test). Data based on lifting series with pseudorandom changes in weight between consecutive trials (160 trials, 10 subjects)

move in the current 200 g and previous 800 g lifts, respectively). Hence, the aforementioned overshoots in the grip force and position signals were probably related to the high force rates at the point when the load force counterbalanced the force of gravity and the object started to move. In agreement with the influences of the weight on the force rates as shown in Fig. 1, the size of these overshoots was related to the difference in weight between consecutive trials. As illustrated in Fig. 3, the greater the difference, the stronger the grip force overshoots. The abrupt cessation of the load force increase at the moment the lifting movement began was probably related to the change from isometric to shortening contractions of the lifting muscles (cf. the "force-velocity" relationship of muscles during shortening contractions). Moreover, ongoing contractions of antagonists to the lifting muscles (see below) would further accentuate the load force loss, since these muscles would not be subjected to the same force loss as those that were shortened. In addition, muscular force must have been utilized to accelerate the hand and forearm.

By analyzing the e.m.g. signals from the hand/arm muscles in the erroneously-programmed lifts, it was found that the muscle commands which brought about the loading phase were quite abruptly disrupted after various latencies following the moment of unexpected lift-off. This is illustrated in Fig. 2A in which the e.m.g. traces came from the erroneously-programmed 200 g lifts represented by the solid curves in the upper half of the figure. There was a distinct fall in the e.m.g. activity of the first dorsal interosseous muscle (a muscle primarily contributing to the grip force) 100–110 ms after the moment of lift-off. In addition, the muscles primarily contributing to the load force during these lifts (extensor carpi radiales and brachioradialis) showed distinct decreases in activation appearing 80–90 ms after the unexpected lift-off. Again, the activity in the triceps brachii and the brachioradialis muscles varied in parallel, whereas there was a reciprocal relationship between the flexor carpi ulnaris and the extensor carpi radiales.

These distinct changes in the muscle commands indicate that they were triggered by sensory signals related to the lift-off. In addition to triggering a termination of the loading phase commands, such signals might have played a role in the release of the following "new" set of muscle commands accounting for the vertical positioning of the object. During the adequately-programmed lifts there were no clear indications of a similar triggering (cf. e.m.g. traces in Fig. 1). Regarding the type of sensory information utilized, it was established that somatosensory signals can provide the relevant information. Compared to the normal hearing and seeing condition, no obvious differences were found in the motor behavior when auditory and visual cues related to the moment of lift-off were eliminated.

Regarding the effect of a *lighter weight in the previous lift,* the force development followed a course similar to that of the foregoing weight until the point when the object would have started to move with the previous weight. In the absence of movement, the grip and load forces continued to increase, but at lower rates, until the force of gravity was overcome. This pattern is illustrated in Fig. 4A, B representing individual trials with 800 g (solid curves) preceded by adequately-programmed 400 g trials (dotted curves). The initial bell shaped force rate profiles aiming at a load force target corresponding to ca. 4 N force (P in Fig. 4B) reflect the programmed nature of the muscle commands. With the erroneously-programmed trials (solid curves), the movement failed to start at the anticipated point and during the following part of the loading phase, the isometric force increase took place more slowly and in a discontinuous fashion until the moment of take-off. Consequently, the loading phase was pro-

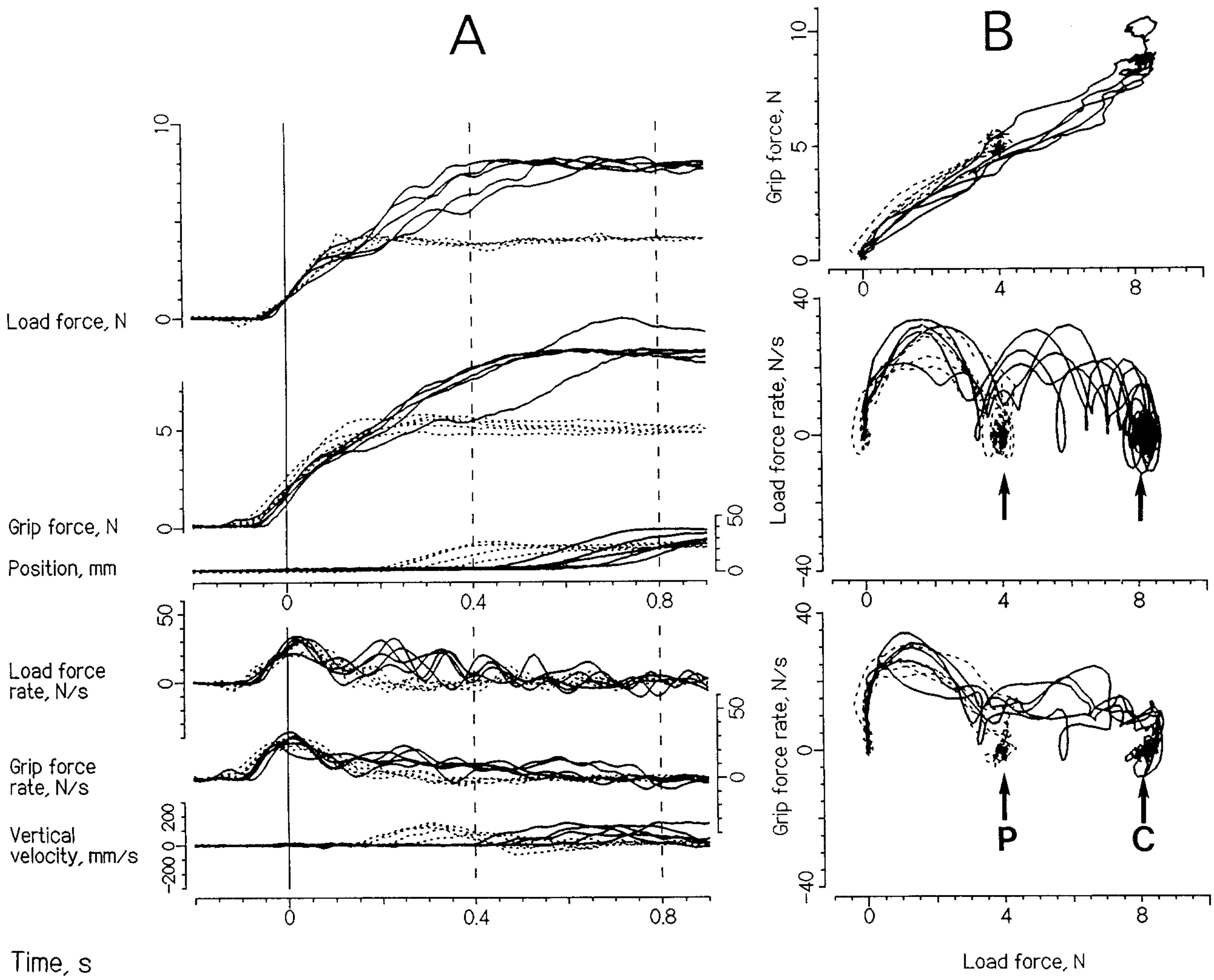

Fig. 4A, B. Initial parts of lifts with 800 g erroneously programmed for a lighter weight (400 g). **A** Load force, grip force, vertical position and their time derivatives as a function of time for 5 sample trials with 800 g (—) preceded by adequately-programmed 400 g lifts (- - - - - -). Trials synchronized in time at the moment the load force reached 1 N (time = 0). **B** Grip force, load force rate and grip force rate displayed in relation to the load force for the same data as in **A.** Arrows labelled C and P indicate the load force at which the object started to move in the current and previous trial, respectively. Single subject. For further details see legend to Fig. 1

longed compared to the corresponding adequately-programmed trials. In general, these discontinuities showed a repetition rate which was similar to the frequency range of the physiological muscle tremor, i.e. ca. 5–12 c/s. As with adequately-programmed trials, there were fairly small position and grip force overshoots, i.e. the load and grip force rates were generally low when the load force just overcame gravity (C in Fig. 4B). As shown in Fig. 3, for lifts preceded by a lighter weight the grip force overshoots were similar to those observed with adequately-programmed lifts. Indications of triggered responses appearing in the e.m.g. records similar to those illustrated in Fig. 2 were occasionally observed during lifts programmed for a lighter weight, although the triggered responses were much weaker.

Programmed force changes during the unloading phase

After the replacement movement the object contacted its support and motor commands were released causing a parallel decrease in the grip and load forces, i.e. the lift entered into the *unloading phase* as illustrated in Figs. 5A and 6. When the object contacted the table, there was a small but distinct dip in the load force related to the sudden deceleration. Then the two forces decreased showing force rate profiles which, apart for the polarity, resembled those of the loading phase of adequately-programmed trials (compare force rate curves in Figs. 1A and 5A). Thus, these profiles exhibited a decrease in the absolute force rates when the grip and load forces approached zero, indicating that the

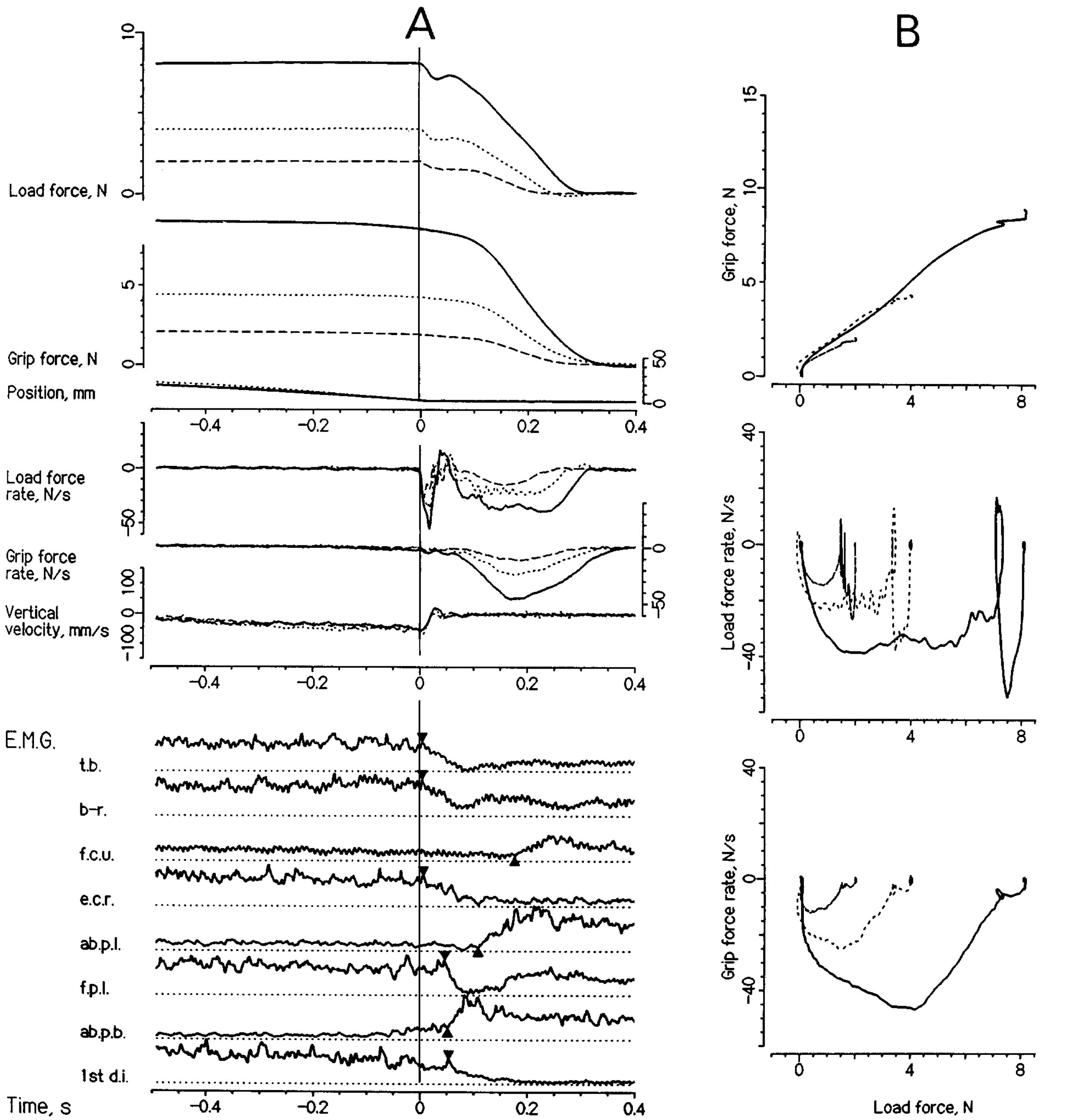

Fig. 5A, B. Unloading phases of lifts with 200 g (- - - - - -), 400 g (. . . . . .) and 800 g (—). **A** Load force, grip force, vertical position and their time derivatives as a function of time. Averaged data from lifting series in which the table support point was constant at the table top and the weight was pseudorandomly varied between trials (16 trials for each separate weight). Averaging synchronized in time at the moment the object contacted the table-top (time = 0). E.m.g. signals refer to the 800 g trials. **B** Grip force, load force rate and grip force rate displayed in relation to the load force for the same data as in **A**. Single subject. For further details see legend to Fig. 1 and text

unloading phase was adequately programmed for the current weight. Moreover, there were no obvious influences of the weight in the previous trial. This indicates that the programming of the unloading phase took place on the basis of weight related information gained during the current lift.

Regarding the *commencement of the unloading phase* it seems reasonable that the release of the appropriate muscle commands might have been programmed on the basis of visual or memory information from the spatial relation between the support point and the table-top. This would apply to

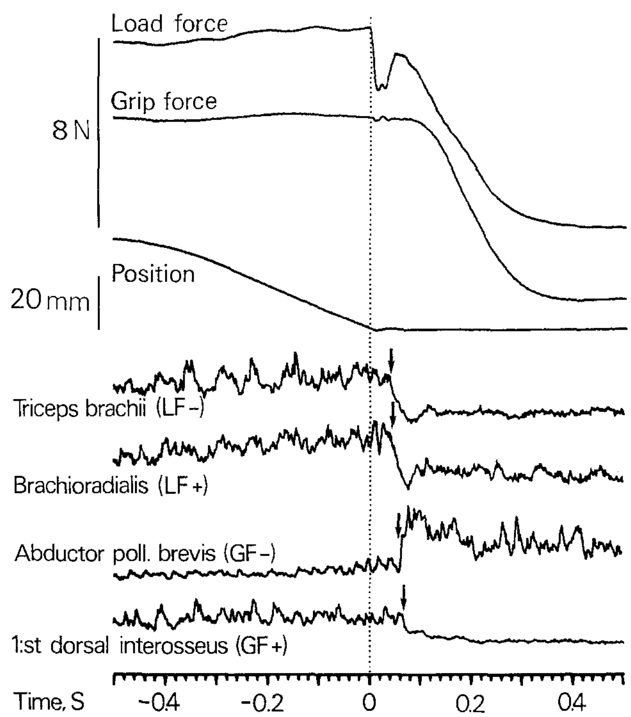

Fig. 6. Abrupt changes in muscle commands (arrows) following sudden cessation of movement due to unexpected table contact. E.m.g. signals from two arm and two intrinsic hand muscles. Averaged data from 9 lifts by a single subject gathered during a lifting series with changes in the height of the table support. (Lifts with a constant support height selected.) Averaging synchronized at the moment of table contact. Weight 800 g. For further details see text

the experiments in which the support point of the object was at the table top (constant position and within the subject's view). On the basis of the e.m.g. data it was apparent that an anticipation of the moment of contact occurred during these conditions. As illustrated in Fig. 5A, the e.m.g. activity in the proximal arm muscles and the extensor carpi ulnaris started to decline close to, or just before, the moment that the object contacted the table. Thus, the moment of table contact must have been fairly accurately anticipated. Instead of showing a reciprocal pattern of activation, the activity in the proximal pair of antagonists changed in parallel maintaining a stable co-contraction superimposed on the force changes. A similar co-contraction pattern was sometimes observed during the early part of the unloading phase with the extensor carpi radiales and the flexor carpi ulnaris operating over the wrist. Generally, however, the activity in the wrist flexor was weak during this part of the unloading phase and this parallelism was not always that obvious (Fig. 5A). As to the more distal muscles influencing the grip force, the activity in the intrinsic hand muscles also seemed to be influenced close to, or even before, the moment of table contact as in Fig. 5A. Accordingly, there was often a slight decay in the grip force before the moment of contact. However, 60–70 ms after the moment, these antagonists often showed fairly abrupt reciprocally organized activity shifts: the activity decreased in the 1st dorsal interosseous and increased in the abductor pollicis brevis (arrowhead in Fig. 5A). Similar activity shifts were observed in the flexor pollicis longus whose activity began to decrease 60–70 ms after table contact and in the abductor pollicis longus whose activity increased but slightly later (latency 100–115 ms). Thus, in contrast to the more proximal muscles, the two pairs of antagonist operating on the fingers showed a reciprocal activity pattern during the unloading phase. Moreover, the distinct activity shifts often occurring after fairly constant delays in these muscles suggest that the underlying motor commands were triggered by the sudden cessation of the replacement movement, i.e. at the moment of table contact. A triggered release of motor commands accounting for a decrease in the grip force is also in keeping with the finding that the principal decline in the grip force started 0.07 ± 0.01 s (mean, SD, n = 245, five subjects analyzed) after table contact (Johansson and Westling 1984b, see also Fig. 5A).

The reliance on a triggered onset of the unloading phase was more explicit in the lifting series with *changes in the support height* between lifts. Since the subject in these experiments could not see the point of support, the moment of table contact could not be anticipated. Not surprisingly, there were no anticipatory changes in the muscle activation, but all muscles showed sharp activity shifts after various latencies following the moment of table contact. Figure 6 shows e.m.g. recordings from the triceps brachii, the brachioradialis, the 1st dorsal interosseous and the abductor pollicis brevis in such lifts. There was a distinct decrease in the drive to the proximal pair of muscles operating over the elbow and to the 1st dorsal interosseous whereas the activity in the abductors, the flexor pollicis longus and the extensor carpi radiales abruptly increased. The latencies were 60–70 ms in the intrinsic hand muscles, 100–110 ms in the abductor pollicis longus, 45–50 ms with the flexor pollicis longus and the extensor carpi radiales and ca. 40–50 ms in the muscles operating over the elbow. As to the flexor carpi ulnaris, its response was fairly variable both with regard to intensity and latency. Often, however, there was an increase in its activity ca. 60–70 ms after table contact.

Thus, during these conditions without sight, the muscle commands accounting for the unloading phase appeared to fully rely on somatosensory feedback. Moreover, there were no obvious influences from the support height in the previous trial indicating that there were no anticipatory mechanisms in operation. This suggests that visual information accounted for the programming of the motor commands giving rise to the early e.m.g. changes as illustrated in Fig. 5A. This idea was supported in the lifting series using a constant support height but during which the subject could not see the point of support (underneath the table top). Again there were no changes in the muscle activation close to the moment of table contact, but all muscles showed triggered activity shifts. This was also the case if the subjects were asked to close their eyes during the lifts and/or if wore soundproof earphones.

Additional considerations

The patterns of motor output described above were observed with all fifteen subjects, although the force rates varied between subjects. Some subjects lifted more abruptly than others even though they were all instructed in the same manner. On the other hand, for the individual subject and a given weight condition, the time course of load force changes were fairly constant (see Figs. 1, 2, 4 and 5).

The data illustrated above were all gathered in lifting series with suede as the surface structure. Throughout these experiments it was striking to find that for any given subject the ratio between the load force and the grip force was approximately constant during the loading and the unloading phases (see top panels in Figs. 1B, 2B, 4B and 5B). Experimental series with sandpaper and silk were also carried out, i.e. materials which were less and more slippery than suede, respectively. It was found that the principles described in the present results applied throughout, but the force ratio was adjusted to the frictional conditions between the object and the skin according to principles previously described (Johansson and Westling 1984b). Thus, there were no obvious differences in the load forces. Only the grip forces differed: the more slippery the material the higher the grip force rates. This was true for the loading phase and for the unloading phase (cf. Fig. 5 in Johansson and Westling 1984a).

Discussion

The present results emphasize the programmed nature of the muscle commands used during precision grip and the capacity to adapt program parameters to the properties of the manipulated objects. As with the frictional adaptation (Johansson and Westling 1984b; Johansson and Westling 1987), the weight adaptation primarily relied on stored information gained during the previous lift. Likewise, if the programmed output was inadequate, weight-related program parameters may be efficiently updated on the basis of somatosensory signals entering during the actual lift. Hence, following unexpected weight changes, erroneous weight programming only occurred during the loading phase before unequivocal information about the new weight had been gained, i.e. before the start of the vertical lifting movement. Consequently, the unloading phase was always adequately programmed.

The principal evidence that the force development during the loading and unloading phases represented the expression of central programs was the fact that the rate profile of the grip and load forces was mainly single-peaked, bell-shaped and scaled from its onset to the target force. These rate profiles resemble the "continuous" (Brook's term) or the "bell shaped" (Bizzi's term) velocity profiles frequently reported for programmed intended arm/hand movements toward a target position (see Bizzi and Abend 1983; Brooks 1984). Similar rate profiles have been described during programmed isometric actions (Gordon and Ghez 1984). It is clear that the establishment of such predictive behavior must be based on memory information: in the present experiments the course of the parallel increase in the load and grip forces was adapted appropriately for a weight similar to that in the previous trial. This kind of predictive control may be critical for smooth accurate movements in an "evolving situation" because of the long time which usually elapses between the release of the muscle commands and the feedback from the command (see Welford 1976). That is, the parallel isometric force increase may occur for a long time in the present task before lifting movement occurs. Hence, during adequately-programmed lifts the motor drive appeared optimal in the sense that the object fairly rapidly reached the intended vertical position in a smooth, critical damped fashion, and no pronounced grip force overshoots occurred. In contrast, during the loading phase erroneously programmed for a heavier weight, the high force rates at the moment the gravity was counterbalanced caused a jerky lift with a pronounced positional overshoot together with a high grip force peak. This occurred even though the programmed commands were prematurely terminated, i.e. the changes in the motor output triggered by the too early lifting occurred too late to forestall these disadvantageous effects. There are illusions in daily life situations which may be related to this kind of erroneous weight programming (e.g. Ross 1969; McCloskey 1974). During lifts programmed for a lighter weight, on the other hand, the object did not move at the end of the continuous force increase. However, the parallel force increase persisted, but with multiple force rate peaks, until feedback about the lifting motion was obtained and the transitional phase commenced. Consequently, the moment of lift-off was delayed compared to adequately-programmed trials. Interestingly, the force rate profiles during this probing behavior resembled the multi-phase, "discontinuous", velocity profiles observed during "minimally programmed" movements during target reaching tasks (e.g. Brooks 1979, 1984; Abend et al. 1982) which require external feedback for a successful target acquisition.

Triggering of muscle commands

To accomplish the present multiphasic lifting task there must have been information available about when to switch from one phase to the next. For the commencement of the loading phase, it has previously been suggested that the release of the motor commands accounting for this phase may be triggered by tactile signals verifying that an appropriate contact is established between the fingers and the manipulated object (Johansson and Westling 1984b; Westling and Johansson 1987).

Considering the termination of the loading phase with erroneously-programmed lifts, it appeared to be triggered by sensory signals related to the moment of lift-off. The muscle activation patterns of the loading phase were disrupted and new sets of muscle commands accounting for the vertical positioning of the object must have been released. The present experiments do not reveal whether this kind of triggering might have occurred also during adequately-programmed lifts or whether this transition between the loading phase and the transitional phase was programmed completely.

A similar kind of triggering by sensory information seemed to account for the release of the motor commands giving rise to the unloading phase. In the lifting series in which the subject could not see the site of contact between the object and the table, the commencement of the unloading phase appeared to completely rely on somatosensory signals arising from the sudden cessation of the vertical movement at table contact. In contrast, during lifts in which the support point of the object was within the subject's view, the commands to muscles primarily operating over the wrist and the elbow were released on the basis of an anticipation of the moment of table contact originating from visual information. Moreover, this appeared to be true to a certain extent with the commands to the more distal muscles influencing the grip force, although clear triggered responses were also observed in these muscles.

The triggered changes in the muscle commands following the moments of lift-off and terminal table contact clearly involved task-specific sensorimotor actions. There is plenty of evidence that the current "sensorimotor set", which depends on the goal, the context, the phase of the specific movement, and previous experience, determine both how sensory input will be processed in sensorimotor pathways (e.g. Phillips and Porter 1977; Abbruzzese et al. 1981; Nelson 1985), and the nature of the elicited motor responses (cf. Evarts and Tanji 1974; Houk and Rymer 1981; Rack 1981; Ghez et al. 1983; Gracco and Abbs 1985; Horak and Nashner 1986). This has also been previously shown for nonautogenic motor responses to disturbances of finger movements (Marsden et al. 1981; Cole et al. 1984; Cole and Abbs 1987), and the response latencies reported are in the same order of magnitude as those observed in the present study. The rather long response latencies, 100–110 ms (lift-off) and 60–70 ms (terminal table contact) observed for the intrinsic hand muscles, suggest that the appropriate commands may be organized at a rather complex level. But nevertheless, the motor responses appeared to be automatically initiated (cf. Cole and Abbs 1987; Johansson and Westling 1987). The latencies after the moment of terminal table contact were similar to those typically observed during nonautogenic compensations described in hand/finger movements (Marsden et al. 1981; Cole et al. 1984; Cole and Abbs 1987), and were similar to the latencies generally reported for automatic digital motor responses elicited by exteroceptive input (Garnett and Stephens 1980; Darton et al. 1985; Marsden et al. 1985; Johansson and Westling 1987).

As to the somatosensory input that accounted for the triggered changes in the motor output following lift-off and the terminal table contact, the central nervous system probably relied on the afferent system that most reliably, quickly and accurately signalled these mechanical events. In a previous study on the responses of tactile afferent units in the glabrous skin area of the hand during similar lifting trials (Westling and Johansson 1987), we showed that the fast adapting type II units (FA II, also denoted Pacinian corpuscle units) reliably responded with distinct impulse bursts particularly at lift-off and terminal table contact. Hence, these burst responses might provide trigger signals for the subsequent changes in the muscle commands. The fact that the termination of the loading phase and the start of the unloading phase appears normal during anesthesia of the fingers contacting the object (Johansson and Westling 1984b) does not dispute this idea. A number of FA II's with endings adjacent to the anesthetized regions still would respond (Westling and Johansson 1987). Indeed, evidence is rapidly accumulating that signals in cutaneous mechanoreceptors in the human hand may play important roles in triggering manual motor responses of various complexities (Denny-Brown 1966; Garnett and Stephens 1980, 1981; Marsden et al. 1985; Darton et al. 1985; Johansson and Westling 1987). The high innervation density of the mechanoreceptors and their location close to the points of contact with the manipulated object should make them the most efficient to provide feedback signals about various mechanical events as the object/hand interface during manipulation.

Whatever the underlying afferent mechanisms, it seems unlikely that the sensitivity of musculotendinous afferents to mechanical transients originating from the manipulated object would match that of the FA II units. Available data on responses of muscle spindles in human finger muscles to external disturbances indirectly support this view (Vallbo 1985; Å. B. Vallbo, personal communication). According to Vallbo, the impulse modulation is generally stronger in dynamically sensitive spindle afferents during slow precision movements than it is in response to small external disturbances which give rise to substantial motor responses. Thus, the muscle spindles (as well as the Golgi tendon organs) seem to be much more concerned with proprioceptive function during actively generated movements than with small external disturbances.

Co-activation of antagonist muscles

During lifting, all hand and arm muscles recorded from were co-activated to differing extents although not all of them acted as prime movers. This agrees with other studies on muscle activation during precision grip in man (Long et al. 1970; Rasch and Burke 1974; Basmajian 1978; Muir 1985; Johansson and Westling 1988) as well as in monkey (Smith 1981), and with elbow movements, particularly with displacement loads (Patton and Mortensen 1981). The co-contraction has been considered necessary to provide postural stabilization of the multiarticulate hand/arm system and to increase the mechanical advantage of the long flexors of the fingers. However, initially during the loading phase and during the unloading phase the activity changes in the two antagonistic pairs of intrinsic and extrinsic hand muscles, superimposed on a basic co-activation, were reciprocally organized. This makes sense when considering that the two muscles contributing to the grip force operated against a resistance offered by the rigid object (also partly supported by the table) which prevented them from shortening. Thus, the impedance of the hand/object system increased and the appropriate stiffness may have been provided without additional co-contraction. Consequently, these muscles would be free to operate reciprocally. Accordingly, the pairs of antagonists acting over the elbow joint which operate more remote from the object being held maintained a high degree of co-activation stabilizing the arm by increasing its stiffness.

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References

Abbruzzese G, Ratto S, Favale E, Abbruzzese M (1981) Proprioceptive modulation of somatosensory evoked potentials during active or passive finger movements in man. J Neurol Neurosurg Psychiat 44: 942–949

Abend W, Bizzi E, Morasso P (1982) Human arm trajectory formation. Brain 105: 331–348

Basmajian JV (1978) Muscles alive. Their function revealed by electromyography. The William & Wilkins Company, Baltimore

Bizzi E, Abend W (1983) Posture control of trajectory formation in single- and multi-joint arm movements. In: Desmedt RE (ed) Motor control mechanisms in health and disease. Advances in neurology, Vol 39. Raven Press, New York, pp 31–45

Brooks VB (1979) Motor programs revisited. In: Talbott RE, Humphrey DR (eds) Posture and movement. Raven Press, New York, pp 13–49

Brooks VB (1984) How are "move" and "hold" programs matched? In: Bloedel et al. (eds) Cerebellar functions. Springer, Berlin, pp 1–23

Cole KJ, Abbs JH (1987) Kinematic and electromyographic responses to perturbation of a rapid grasp. J Neurophysiol 57 (in press)

Cole KJ, Gracco VL, Abbs JH (1984) Autogenic and nonautogenic sensorimotor actions in the control of multiarticulate hand movements. Exp Brain Res 56: 582–585

Darton K, Lippold OCJ, Shahani M, Shahani U (1985) Long-latency spinal reflexes in humans. J Neurophysiol 53: 1604–1618

Denny-Brown D (1966) The cerebral control of movement. The Liverpool Univ Press, Liverpool

Evarts EV, Tanji J (1974) Gating of motor cortex reflexes by prior instruction. Brain Res 71: 479–494

Garnett R, Stephens JA (1980) The reflex responses of single motor units in human first dorsal interosseous muscle following cutaneous afferent stimulation. J Physiol (Lond) 303: 351–364

Garnett R, Stephens JA (1981) Changes in the recruitment threshold of motor units produced by cutaneous stimulation in man. J Physiol (Lond) 311: 463–473

Ghez C, Vicario D, Martin JH, Yumiya H (1983) Sensory motor processing of target movements in motor cortex. In: Desmedt JE (ed) Motor control mechanisms in health and disease. Raven Press, New York, pp 61–92

Gordon J, Ghez C (1984) EMG patterns in antagonist muscles during isometric contraction in man. Exp Brain Res 55: 167–171

Gracco VL, Abbs JH (1985) Dynamic control of the perioral system during speech: kinematic analyses of autogenic and nonautogenic sensorimotor processes. J Neurophysiol 54: 418–432

Horak FB, Nashner LM (1986) Central programming of postural movements: adaptation to altered support surface configurations. J Neurophysiol 55: 1369–1381

Houk JC, Rymer WZ (1981) Neural control of muscle length and tension. In: Brooks VB (ed) Handbook of physiology. The nervous system, Vol 2. Am Physiol Soc, Bethesda, MD, pp 257–323

Johansson RS, Westling G (1984a) Influences of cutaneous sensory input on the motor coordination during precision manipulation. In: von Euler C, Franzen O, Lindblom U, Ottoson D (eds) Somatosensory mechanisms. Macmillan Press, London, pp 249–260

Johansson RS, Westling G (1984b) Roles of glabrous skin receptors and sensorimotor memory in automatic control of precision grip when lifting rougher or more slippery objects. Exp Brain Res 56: 550–564

Johansson RS, Westling G (1987) Signals in tactile afferents from the fingers eliciting adaptive motor responses during precision grip. Exp Brain Res 66: 141–154

Johansson RS, Westling G (1988) Programmed and triggered actions to rapid load changes during precision grip. Exp Brain Res 71: 72–86

Long CH, Conrad PW, Hall EA, Furler SL (1970) Intrinsic and extrinsic muscle control of the hand in power grip and precision handling. J Bone Joint Surg 52A: 853–867

Marsden CD, Merton PA, Morton HB (1981) Human postural responses. Brain 104: 513–534

Marsden CD, Merton PA, Morton HB (1985) New observations on the human stretch reflex. J Physiol (Lond) 360: 51P

McCloskey DI (1974) Muscular and cutaneous mechanisms in the estimation of the weights of grasped objects. Neuropsychologia 12: 513–520

Muir RB (1985) Small hand muscles in precision grip: a corticospinal prerogative. In: Goodwin AW, Darian-Smith I (eds) Hand function and the neocortex. Springer, Berlin, pp 155–174

Nelson RJ (1985) Sensorimotor cortex responses to vibrotactile stimuli during initiation and execution of hand movement. In: Goodwin AW, Darian-Smith I (eds) Hand function and the neocortex. Springer, Berlin, pp 59–76

Patton NJ, Mortensen OA (1971) An electromyographic study of reciprocal activity of muscles. Anat Rec 170: 255–268

Phillips CG, Porter R (1977) Corticospinal neurones. Academic Press, London

Rack PMH (1981) Limitations of somatosensory feedback in control of posture and movements. In: Brooks VB (ed) Handbook of physiology. The nervous system, Vol 2. Am Physiol Soc, Bethesda, MD, pp 229–256

Rasch PJ, Burke PK (1974) Kinesiology and applied anatomy. Lea & Febiger, Philadelphia

Ross H (1969) When is a weight illusory? Q J Exp Psychol 21: 346–355

Smith AM (1981) The coactivation of antagonist muscles. Can J Physiol Pharmacol 59: 733–747

Vallbo ÅB (1985) Proprioceptive activity from human finger muscles. In: Barnes WJP, Gladden MH (eds) Feedback and motor control in invertebrates and vertebrates. Croom Helm Ltd, London, pp 411–430

Welford AT (1976) Skilled performance: perceptual and motor skills. Scott Foresman and Company, Glenview, Ill

Westling G, Johansson RS (1987) Responses in glabrous skin mechanoreceptors during precision grip in humans. Exp Brain Res 66: 128–140

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