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Roles of glabrous skin receptors and sensorimotor memory in automatic control of precision grip when lifting rougher or more slippery objects

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Summary. To be successful, precision manipulation of small objects requires a refined coordination of forces excerted on the object by the tips of the fingers and thumb. The present paper deals quantitatively with the regulation of the coordination between the *grip force* and the vertical lifting force, denoted as the *load force*, while small objects were lifted, positioned in space and replaced by human subjects using the pinch grip. It was shown that the grip force changed in *parallel* with the load force generated by the subject to overcome various forces counteracting the intended manipulation. The balance between the two forces was adapted to the *friction* between the skin and the object providing a relatively small safety margin to prevent slips, i.e. the more slippery the object the higher the grip force at any given load force. Experiments with local anaesthesia indicated that this adaptation was dependent on *cutaneous afferent input.* Afferent information related to the frictional condition could influence the force coordination already about 0.1 s after the object was initially gripped, i.e. approximately at the time the grip and load forces began to increase in parallel. Further, "secondary", adjustments of the force balance could occur later in response to small short-lasting slips, revealed as vibrations in the object. The new force balance following slips was maintained, indicating that the relationship between the two forces was set on the basis of a *memory trace.* Its updating was most likely accounted for by *tactile afferent information* entering *intermittently* at inappropriate force coordination, e.g. as during slips. The latencies between the onset of such slips and the appearance of the adjustments (0.06–0.08 s) clearly indicated that the underlying neural mechanisms operated highly automatically.

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Introduction

Sensations from the glabrous skin are essential for the explorative functions of the hand but also for refined manual manipulation, particularly if involving the precision grip between the tips of the fingers and the thumb. Indeed, patients with impairments of the sensory capacity of the median nerve typically describe the effect of the injury by saying: "I can't grip with may hand", "I can't hold anything" etc., i.e. they make complaints about the motor deficiences rather than emphasizing the loss of sensibility (Moberg 1962). Except for the realization of its importance for a normal hand function, little is known about the functional connection between the sense organs of the glabrous skin and the muscles accounting for the motor functions of the hand. Input from receptors in the fingers has been considered to provide a general tonic facilitatory effect on motor commands accounting for certain finger movements (e.g. Gandevia and McCloskey 1977a, b; Garnett and Stephens 1981; Marsden et al. 1977; Torebjörk et al. 1978) or to influence the balance between agonist and antagonist action during thumb movements (Marsden et al. 1979).

Recently, however, one specific functional role immediately related to the gripping function of the hand has been suggested for cutaneous afferent input (Westling and Johansson 1984). While holding stationary small objects using the pinch grip, the magnitude of the static grip force is adapted to the friction between skin and object as well as to the weight of the object so that the employed grip force is greater by a relatively small safety margin than the minimal force required to prevent slip. The adaptation to the frictional condition appears to be dependent on signals in afferent terminating in the fingers, most likely tactile afferents, since it was impaired during blockage of the afferent signals in the digital nerves.

This observation as well as the aforementioned difficulties in gripping and holding objects observed in patients with lesions of sensory nerve branches supplying the fingers, suggest that cutaneous input somehow would influence the force balance, i.e. the coordination, between the grip forces, on the one hand, and the load forces within the grip which tend to cause slips, on the other hand. In the present study, this idea was tested during dynamic as well as static phases of manipulation of small object using the precision grip between the index finger and thumb.

Preliminary reports of some of the present results have been given (Westling and Johansson 1980; Johansson and Westling 1981).

Material and methods

Nine healthy, right-handed subjects (4 women and 5 men, 20–39 years old), who were completely naive with regard to the purpose of the experiments, participated in the present study. The subjects sat in a chair with their right upper arm parallel to the trunk, and with their unsupported forearm extending anteriorly. In this position, they were 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 took place mainly as a flexion of the elbow joint. For timing purposes, a large illuminated clock with a second-hand was placed in front of the subject. Prior to the experiments (5–10 min) the subjects had washed their hands with soap and water.

Apparatus

The object used, diagramatically shown in Fig. 1, was a modified version of one described earlier (Westling and Johansson 1984). The surfaces touched by the subjects were two easily exchangeable discs (diameter: 30 mm) mounted in two parallel planes (distance: 30 mm). Likewise, the weight of the object could be changed between trials. The *grip force* and the vertical lifting force, denoted as the *load force*, could be measured continuously (d.c. –120 Hz) using strain gauge transducers attached to the object. As to the grip force, two separate transducer systems could be used to obtain separate force measurements from the index finger and the thumb, respectively. However, it turned out that the two grip force signals were virtually identical, except for during the initial contact between the object and the two fingers, i.e. the index finger and thumb touched the object slightly asynchronously (see below). 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. *Vibrations* in the object were recorded with an accelerometer (noise level corresponding to less than ± 0.1 m/s^2, 20–600 Hz).

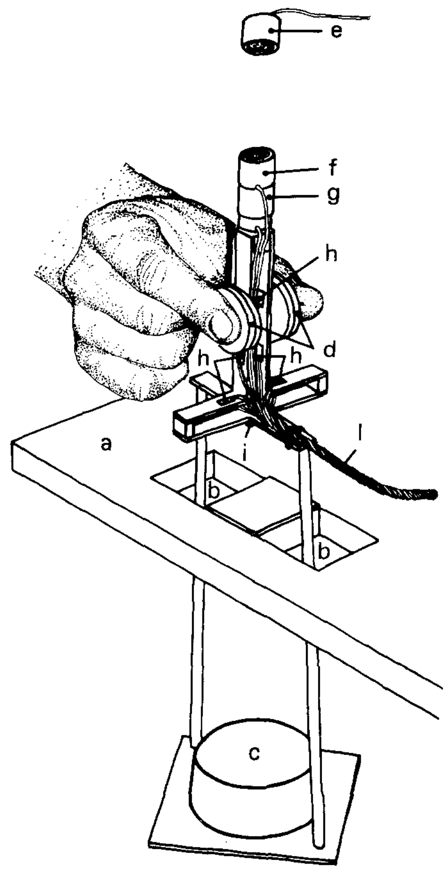

Fig. 1. Schematic drawing of the apparatus. a – table; b – holes in table; c – exchangeable weight shielded from the subject's view by the table; d – exchangeable discs; e and f – vertical position transducer with an ultrasonic receiver (e) and an ultrasonic transmitter (f); g – accelerometer; h – strain-gauge force transducers for measurement of grip force and load force (vertical lifting force); i – peg with an hemispherical tip on which the object rests while standing on the table

Experiments

During the *lifting trials* the object was lifted to about two cm above the table, held in this position for 10 s, and then replaced and released (cf. Fig. 2). Each subject carried out a series of 32–48 such trials with intertrial intervals of 10–15 s. To reveal possible influences on the motor behaviour from the surface structure of the object in the current trials as well as from the structure in the previous trials (cf. Westling and Johansson 1984), the surface structure was pseudorandomly varied between consecutive trials. Three structures were used, sandpaper (No. 320), suede and a finely textured silk. These materials were chosen on the basis of their different frictional properties in relation to the skin (cf. Johansson and Westling 1984; Westling and Johansson 1984). The light in the room was adequate to find the object but not to visually discriminate the structures of the touched surface. As a rule, the weight of the object was 400 g. When other weights (200 g and 800 g) are used, they are specified. Before the experiments the subjects received verbal instructions from the experimenter, who also carried out a demonstration trial. Thus, the subjects were *not* instructed to pay attention to the grip force but to the timing and to the positioning of the object in space.

All series of trials were followed by trials in which the subjects were asked to *slowly* separate the thumb and index finger until the object was dropped (cf. Fig. 2B). For each subject, four such trials were run with each of the three surface structures, respectively. This procedure was carried out to obtain an estimate of the minimal ratio between the grip and load force required to prevent slipping, denoted as the *slip ratio* (see Fig. 2B). It can easily be shown that this ratio is determined by the static coefficient of friction between the skin and the touched surface, i.e. it coincides with half the inverse of this coefficient. (The explanation for the factor half is that the load force was distributed on two fingers.) The slip ratios quoted below were mean values of the obtained single trial ratios.

In two different experiments, additional tasks implying load force changes were superimposed while the object was held in air. In one of these, upon verbal instruction, a ball was lifted from the table with the free hand (left) and gently placed onto the weight carrier of the object. About 8 s later, the subject was asked to pick up the ball and replace it on the table. After consecutive loading the object (200 g) with balls of three different weights (100 g, 300 g, and 500 g) in this manner, the object was replaced at the table. In the other experiment, in addition to the mass-load (400 g), the object was spring-loaded by using a rubber band attached between the object and its support. This rubber band was stretched when the object had been lifted ca. 4 cm above the table, i.e. further lifting added a spring-load who varied proportionally to the vertical position of the object. The task of the subject was to track the vertical position on the basis of a visually displayed error signal, i.e. compensatory tracking (cf. Poulton 1981). The position command signal, which was composed of ramp (ca. 4 mm/s) and hold phases, included positions with and without the spring contributing to the load.

Anaesthesia

The same kind of experiments as described above were repeated on 3 of the subjects during local anaesthesia of the index finger and thumb. The digital nerves were blocked by Marcain® at the mid level of the proximal phalanges (5 mg/digit). This produced a complete clinical anaesthesia of the fingers to light touch, heavy touch, pin-prick and squeezing; thus, also the afferents fibres to the interphalangeal joints and other deep tissues may be presumed to have been paralysed. To investigate whether cutaneous anaesthesia alone could affect the motor behaviour, in separate experiments we anaesthetized the skin of the pads of the distal phalanx of the index finger and the thumb by local intradermal infiltration of ca. 2.5 mg Marcain®.

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 and the vertical position were stored and analysed using a flexible laboratory computer system. These variables were each sampled at 100 Hz by a 12 bit A/D converter. For each trial, the data acquisition started 0.5 s prior to the moment at which the load force reached 0.5 N (Newton), and lasted until the trial was over and the subject no longer touched the object. The *ratio* between the grip force and the load force, as a function of time, was calculated by the computer. This ratio described the balance, or coordination, between the two forces. During analyses involving *averaging of trials*, each trial was synchronized in time at the moment the load force reached 0.5 N.

In analyses involving measurements of *latencies* and *acceleration events*, stored data recorded on tape (d.c. –2.5 kHz) during the experiments were used. These were played back and displayed on a storage oscilloscope or on an electrostatic chart recorder (d.c. –1 kHz). To facilitate the detection of the force changes used during latency measurements (192 trials, 5 subjects), the grip and load force signals were analogously differentiated. The moments the index finger and thumb, respectively, first touched the object were assessed from the differentiated grip force records. The reliability of this method was confirmed in a separate series of trials during which the moments of contact between the fingers and the surface structures were electrically detected. In this experiment, the ordinary surface structures were substituted with an electrically conductive material (carbon coated discs), and an electrical circuit (max 80 nA) was closed, generating a contact pulse when the resistance between the object and the skin was below 8 G-ohm.

Results

General structure of lifting trials

The general structure of the lifting trials in which the subjects gripped and lifted the object from the support, held it in air, replaced and released it is illustrated in Fig. 2A. The grip and load forces and their ratio as well as the vertical position are shown as a function of time for a sample trial. To facilitate the analysis, these trials were divided into six distinct elements or phases. During the first phase, denoted as the *preload phase* (a in Fig. 2A), the grip force increased while there were only small changes in the load force. The preload phase lasted for 0.08 ± 0.04 s (mean ± S.D.) if defined from the moment when index finger *and* thumb first touched the object. (The leading finger contacted the object on an average of 0.05 s before this moment.) During the subsequent *loading phase* (b in Fig. 2A), the grip and load forces increased in parallel. However, soon the load force overcame the force of gravity and the object started to move, indicating the beginning of the *transitional phase* (c in Fig. 2A). Early during this phase, which lasted while the object was moved from the table to the intended vertical position, the two forces reached peak values. After its peak, the grip force decayed at a rate that gradually declined with time. For the vast majority of trials, the two forces as well as the vertical position reached fairly stable values within about 1 s after the start of the movement and the trial went over into a *static phase* (d in Fig. 2A). The *replacement* of the object (e in Fig. 2A), which took place without marked force changes, was terminated when the object contacts the table, giving rise to a small but sudden fall in the load force. Then there was a short, but fairly stable, delay of 0.08 ± 0.01 s (f in Fig. 2A) after which the grip forces and the load force declined in parallel. This parallel force decrease, denoted as the *unloading phase* (g in

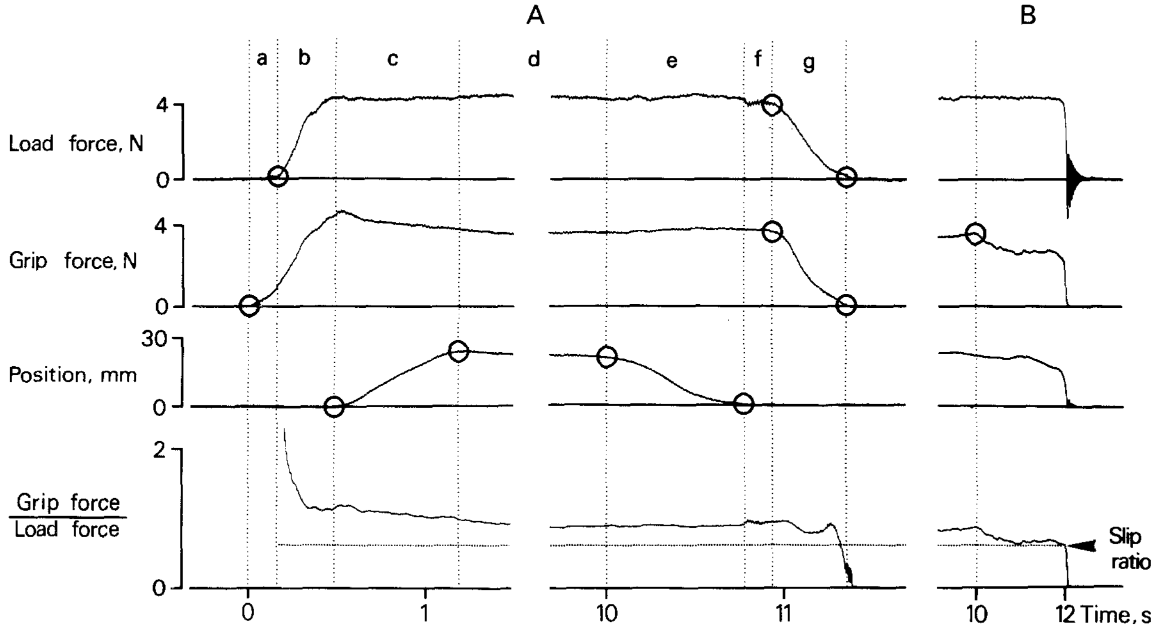

Fig. 2. **A** Load force, grip force, vertical position and ratio between grip and load force as a function of time for a sample trial (weight of object = 400 g, surface structure = sandpaper). The phases indicated were common for all lifting trials: a – preload phase; b – loading phase; c – transitional phase; d – static phase; e – replacement phase; f – delay; g – unloading phase. Force ratio not shown for the preload phase. Note the interrupted time scale. **B** Slip ratio measurement carried out at the end of a separate trial subsequent to the trial shown in **A**. Surface structure and weight of object, and subject same as in **A**. Vertical dashed line indicates the start of the slow voluntary spacing of the fingers. Horizontal dashed line in **A** and **B** indicate the obtained estimate of the slip ratio. For further details see text

Fig. 2A), continued until the object was completely supported by the table and the subject released the object. The two forces reached zero at virtually the same time.

The *coordination* of the two forces as a function of time was analysed in terms of the ratio between the grip and load force (bottom trace in Fig. 2A). To prevent slips, this ratio must exceed a minimal ratio determined by the coefficient of friction between the object and the skin, i.e. the *slip ratio* (cf. Methods). An estimate of the slip ratio for the trial shown in Fig. 2A is indicated by the horizontal segmented line, whereas Fig. 2B illustrates how this estimate was obtained. Thus, the difference between the employed ratio and the slip ratio represents the *safety margin* to prevent slips. For the individual trial the employed force ratio was remarkably constant, except for the preload phase (a in Fig. 2A) and early during the loading phase (b in Fig. 2A). During the preload phase it was difficult to define since the load force was irregular and close to zero. The rapid fall of the ratio early in the loading phase was accounted for by the increasing load force while the relative change of the grip force was still small due to the "offset" acquired during the preload phase. Hence, the safety margin, from being very high late in the preload phase and early during the loading phase, rapidly decreased with time and reached, already at the end of the loading phase, a value close to that maintained during the remaining part of the trial.

To be accepted, this inference regarding the magnitude of the safety margin requires, however, that the slip ratio was constant at any load force level, i.e. the size of the coefficient of friction between the object and the skin must not be influenced by the magnitude of the load or grip forces. This problem was studied in separate experiments during which the slip ratio was measured at different load forces ranging between 80 g and 780 g weight (50 g steps) and for each of the three surface structures, sandpaper, suede and silk, respectively. It turned out that this coefficient was fairly constant within this force range (Johansson and Westling 1984). However, at even lower forces one would expect that the coefficient would increase due to an increased relative contribution of adhesive forces to the friction (cf. Bowden and Tabor 1973; Comaish and Bottoms 1971).

Force coordination adapted to different frictional demands

By analysing trials carried out with each of the three surface structures, sandpaper, suede and silk, it was found that the material in contact with the skin principally influenced the rate of grip force change: the more slippery the material the higher the rate. This was true during the preload and loading phases, as can be seen in Fig. 3, as well as during the

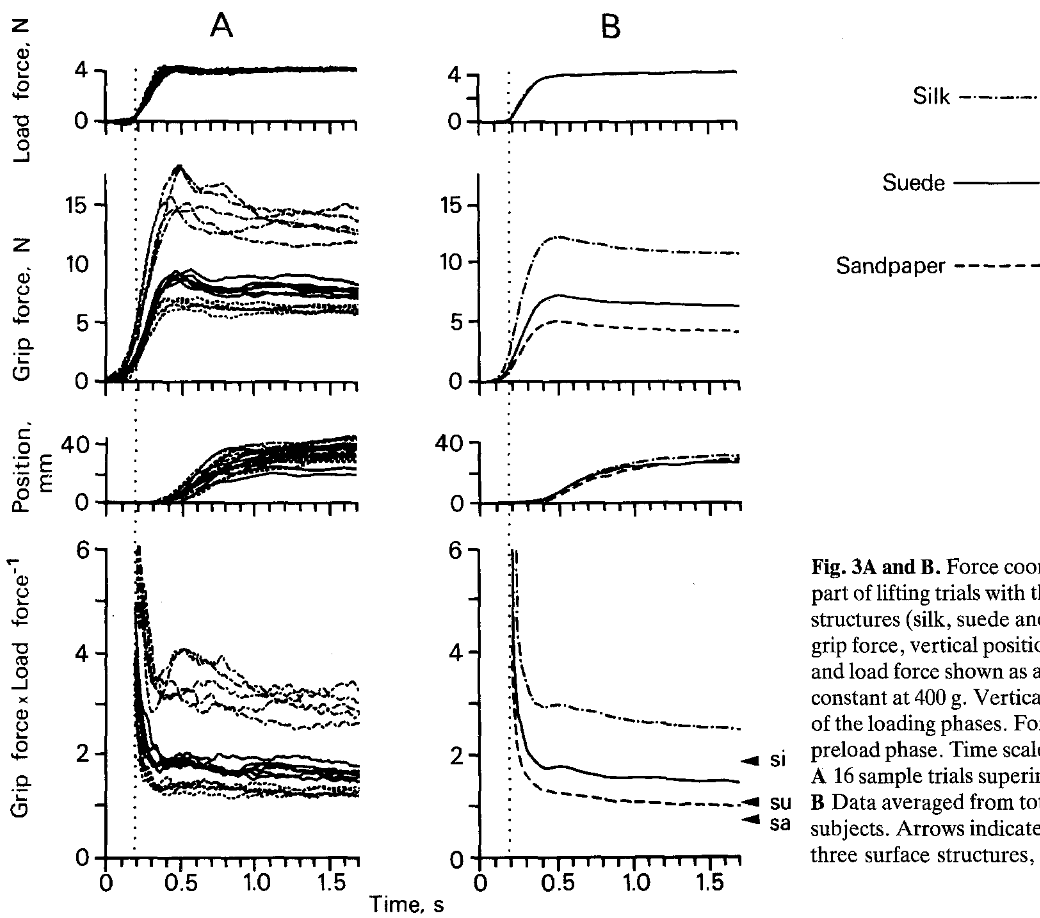

Fig. 3A and B. Force coordination during the initial part of lifting trials with three different surface structures (silk, suede and sandpaper). Load force, grip force, vertical position and ratio between grip and load force shown as a function of time. Weight constant at 400 g. Vertical lines indicate the beginning of the loading phases. Force ratio not shown for the preload phase. Time scale with an arbitrary origin. **A** 16 sample trials superimposed (single subject). **B** Data averaged from totally 120 trials by 9 different subjects. Arrows indicate mean slip ratios for the three surface structures, respectively

corresponding unloading phases. In contrast to the grip force, the time courses of the load force and vertical position were similar for all three structures. Consequently, the force coordination was different for the three structures. A comparison between the employed force ratios and the corresponding slip ratios (arrows in Fig. 3B) indicates that this difference was compatible with an adaptation to the frictional demands, i.e. the higher the slip ratio the higher the employed ratio. For the individual subject, the safety margin defined as a fraction of the employed grip force was fairly similar for the different surface structures. The size and variability between subjects of the safety margin during the static phases of similar lifting trials have been considered in a previous report (Westling and Johansson 1984).

It may be argued that this adjustment of the force coordination with surface structure could have been made on the basis of the different texture properties of the touched materials rather than the friction per se. To explore this alternative, series of lifting trials were carried out immediately before and after washing (soap and water) and drying the hands of the subjects. During the washing procedure sweat was removed from the skin, i.e. the skin was made less adhesive and the friction in relation to the object was temporaly decreased. By keeping the surface structure (i.e. the texture) constant in these series, the adjustment to pure frictional changes could be studied. It was found that the force coordination clearly adapted to these changes, thus indicating that it adapted to friction rather than to texture (cf. Johansson and Westling 1984).

A further analysis of the force coordination during the phases of parallel force change indicated that the *ratio between the rates* of the two forces was approximately constant with any given surface structure, but varied between the structures. During this analysis the two forces were displayed against each other, as shown in Fig. 4A and B. A perfectly linear relationship in this kind of display would imply that the ratio between the force rates is constant and equal to the slope constant of the line. Hence, the closeness to linearity of the curves referring to the three surface structures indicated that this ratio was nearly constant during phases of parallel force change. This observation suggested that the strategy used by the nervous system to adapt the force coordination to the frictional demands included a setting of a constant ratio between the rate of change of the two forces, rather than a regulation of the force ratio.

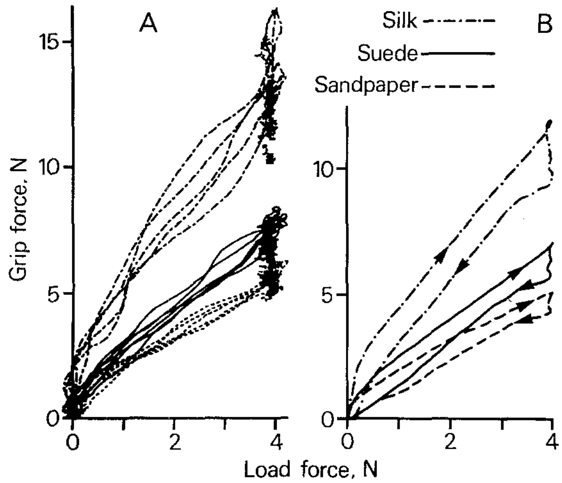

Fig. 4A and B. Coordination between grip force and load force during trials with silk, suede and sandpaper illustrated by displaying the grip force against the load force. Weight of object constant at 400 g. **A** Preload, loading and transitional phases of 16 trials superimposed (single subject). **B** Average of same trials as in Fig. 3B. Arrows indicate the course of the grip force change. **A** and **B** The preload phase appears as the small, almost vertical, part of the curves close to origin, whereas the following, approximately linear and slanted, part of the curves refer to the loading phase. The transitional phase with the force overshoots and the slow grip force decay appears as the nearly vertical part at the top of the curves. The unloading phase is represented in **B** by the approximately linear part of the curves intersecting the origin. During the averaging of the second half of the trials each trial was synchronized in time at the moment the load force had declined to 0.5 N

A constant ratio between the force rates, adequately adapted to the frictional demands, would ensure that the grip force would be adequately regulated during variations in the load force requirements such as when lifting objects of different weights. Indeed, the principal influences of the weight of the object concerned the duration of the loading and unloading phases, i.e. the heavier the object the longer the period of parallel force increase before it started to move (Fig. 5) and of parallel force decrease before it was released. That the mass-load did not appreciably influence the force balance is clearly evident from the ratio curves shown in Fig. 5.

To examine whether this principle may apply to precision manipulation in a wider context, two kinds of experiments were performed in which different tasks implying load force changes were superimposed while the object was held in air. In one, the subject was asked to slowly move the object along its vertical axis (visual tracking paradigm) as illustrated in Fig. 6A. At vertical distances between the table and the object shorter than ca. 4 cm the load was limited to the mass of the object (400 g), but at greater distances a spring-load was added, i.e. the load force increased with the vertical distance. The results showed a parallel change of the grip and load forces during changes of the spring-load, with an approximately constant force ratio adapted to the frictional demands (c in Fig. 6A). Approximately the same ratio was kept also during position changes within the pure mass-load range (b and d in Fig. 6A). However, if the position changes and thereby the load changes took place quite rapidly, the ratio tended to increase, implying an increased safety margin. A similar tendency was observed also during the loading phases if the experimenter asked the subjects to perform very rapidly, i.e. if high force rates were used.

In the second of these experiments, the subject changed the mass-load of the object by adding and removing weights using the left free hand. As for the spring-load experiments, the results indicated a fairly constant force ratio which was adapted to the actual frictional condition (Fig. 6B), i.e. the relative size of the modulations of the ratio was small compared to the corresponding modulations of the forces.

In addition to these experiments a few casual studies were made to determine whether the coordination was influenced or deranged during wrist movements which involved considerable length changes of the extrinsic hand muscles contributing to the grip force as well as to the load force. Thus, while holding the object (freed from the table arrangement, cf. Fig. 1), subjects were asked to move it horizontally by alternately flexing and extending the wrist using the full joint range. Although there was a slightly increased ripple in the grip force signal during the movements, the coordination was maintained as when holding the object still. This was true for movements carried out at low or moderate speeds (ca. < 90 deg/s). At more brisk and thereby less precise movements, the grip force could be considerably increased and thereby the ratio.

On the basis of the findings presented so far, it may be concluded that the frictional condition appeared to determine the coordination between the grip and load forces during precision manipulation of objects gripped between the tips of the forefinger and thumb. Moreover, the stability of the employed coordination at a given frictional condition implying a critically adjusted safety margin, suggests that this coordination is one output parameter regulated by the central nervous system during manual manipulation involving gripping of objects.

To restrict possible influences from a different frictional condition in the previous trial (see Westling and Johansson 1984), the hitherto analysis of the force coordination was based on trials whose previous trials were carried out using the same surface structure, respectively, i.e. these trials were *not* immediately preceded by a change in surface structure.

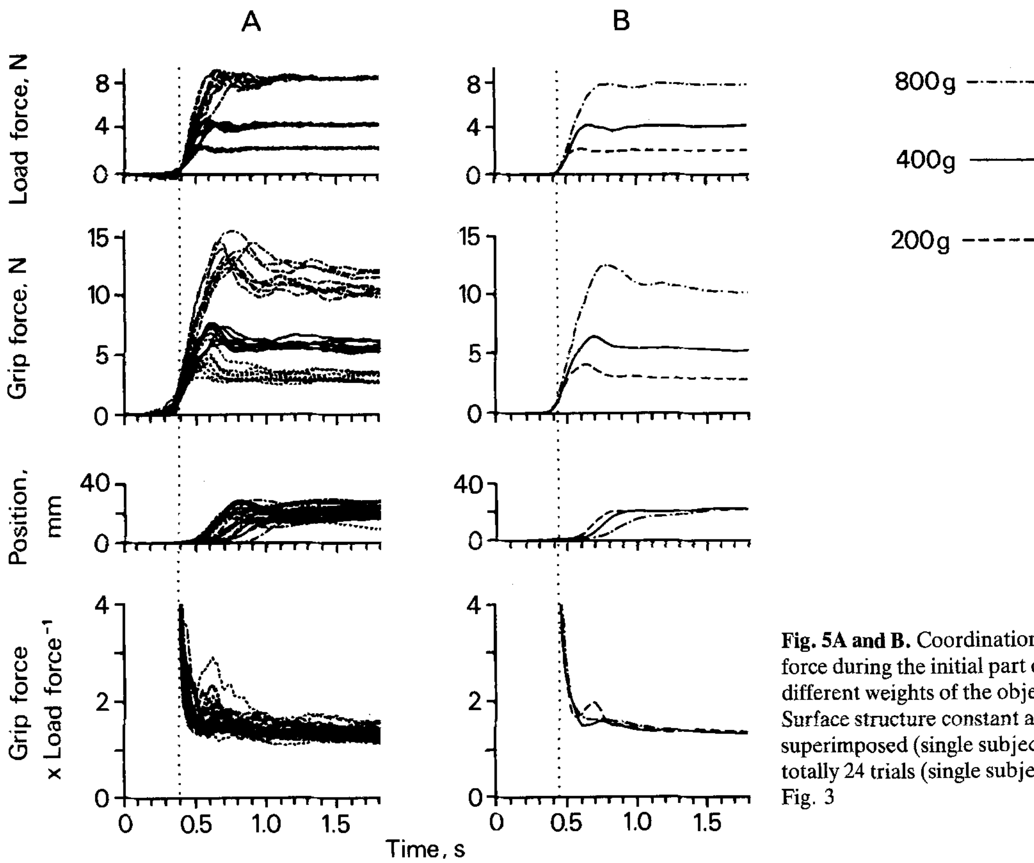

Fig. 5A and B. Coordination between grip and load force during the initial part of lifting trials with three different weights of the object (800 g, 400 g and 200 g). Surface structure constant as suede. **A** 24 sample trials superimposed (single subject). **B** Data averaged from totally 24 trials (single subject). For further details cf. Fig. 3

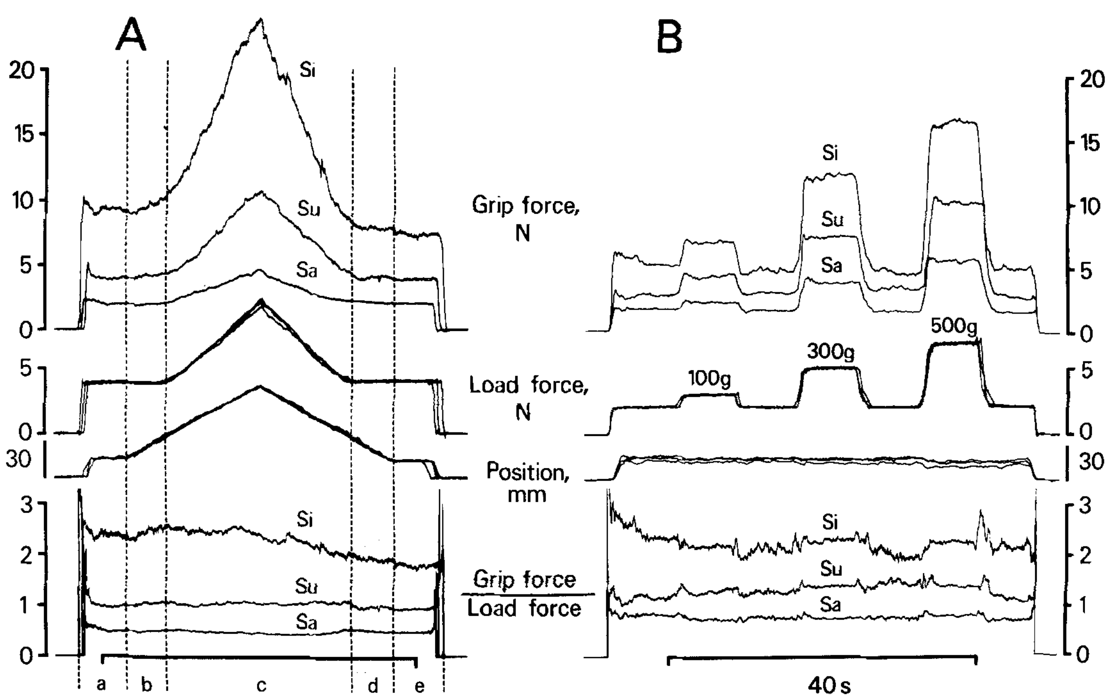

Fig. 6A and B. Coordination between grip and load force during manipulative tasks while the object was held in air. Curves show grip and load forces, their ratio and the vertical position as a function of time for three superimposed trials with different surface structure (Sa – sandpaper; Su – suede; Si – silk). **A** Vertical movement of object (visual tracking paradigm) during mass- and spring-load. a – lifting of object and holding it stationary in space during constant mass-load (400 g wt); b – upward movement during constant mass-load; c – movement during a spring-load in addition to the constant mass-load; d – downward movement during constant mass-load; e – stationary holding of object and replacing and releasing it. Horizontal time scale (solid bar) represents 40 s. **B** Changes of objects weight by successively adding and removing three different weights (100 g, 300 g, 500 g) with the contralateral free hand (start weight: 200 g)

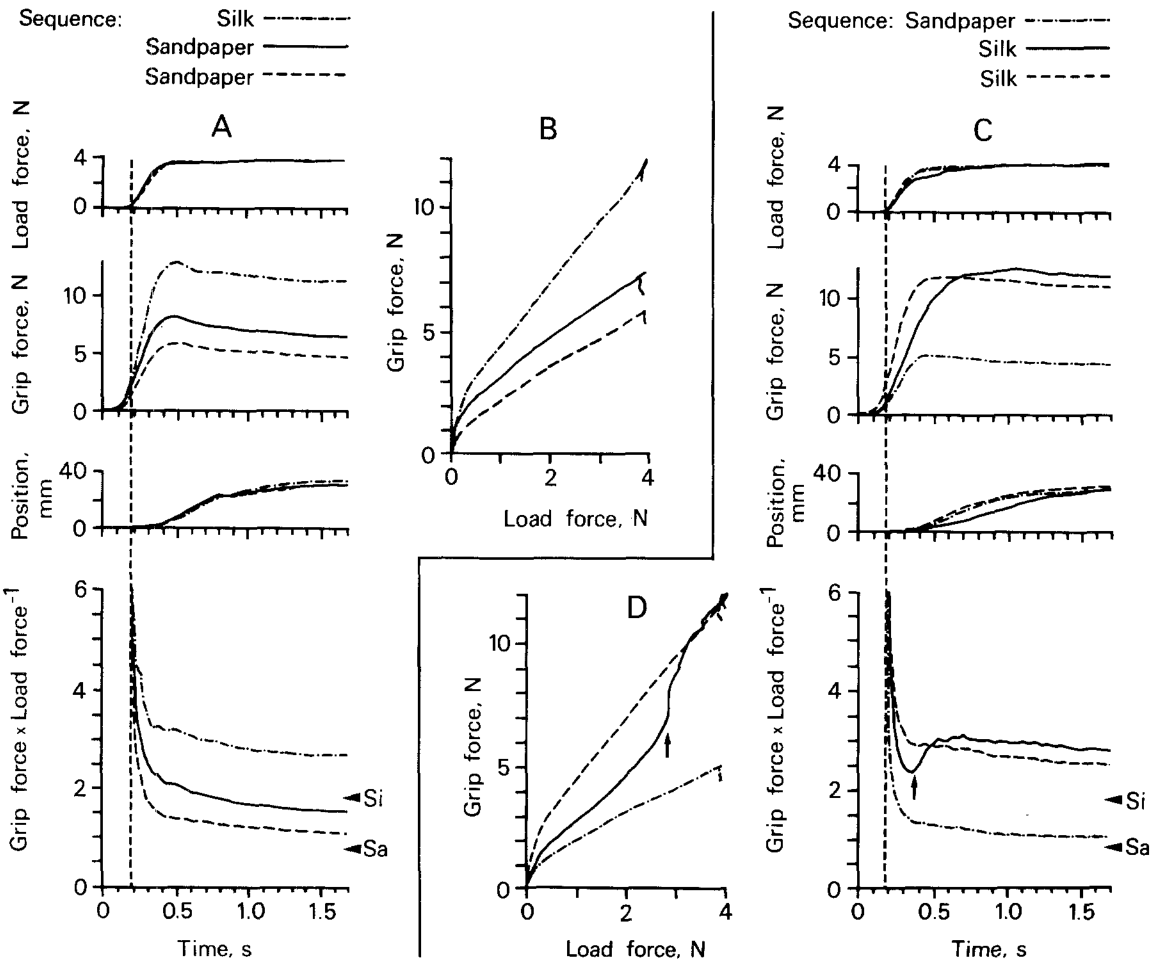

Fig. 7A–D. Adjustment to changes in friction between object and skin. Each graph represents a sequence of three consecutive trials selected from lifting series with pseudorandom changes of surface structures. Weight of object constant at 400 g. Averaged data from totally 162 trials by 9 subjects. **A** and **C** Load force, grip force, vertical position and ratio between grip and load force as a function of time. For further details cf. Fig. 3B. **B** and **D** Grip force against load force for the same data as in **A** and **C**, respectively. Vertical arrows in **C** and **D** indicate the sudden change of force balance accounted for mainly by a decrease in the load force rate

Adjustments to changes of surface structure

To elucidate when and how the adaptation of the force coordination to the surface structure took place, trials carried out subsequent to a change of the surface structure were analysed. By comparing these with corresponding trials not preceded by such a change, the course of adjustment to the new surface structure could be studied. It was generally found that the influence of the new structure commenced already about 0.1 s after the object was gripped between the index finger and the thumb.

The adjustment to a less slippery material is illustrated in Figs. 7A and B, which represent the following sequence of surface structure: silk, sandpaper and sandpaper (averaged data). It may be seen in Fig. 7A that the time course of the grip force for the sandpaper trials preceded by silk trials were similar to that of the previous silk trials during the preload phase, i.e. the grip force command appeared to be executed as if there would have been no change of the surface structure. Thus, it seemed to be prestructured to deal with the same surface structure as used in the previous trial. At about the moment when the load force started to increase, however, an adjustment to the new surface structure (sandpaper) appeared, i.e. the rate of the grip force increase was slowed down compared to the previous silk trials. Hence, afferent information related to the frictional properties of the new surface structure must have entered the central nervous system already during the preload phase. However, a comparison with the second trial with sandpaper revealed that this adjustment was not complete, i.e. a somewhat higher grip force was maintained. A substantial part of this influence from the previous trials with silk seemed to

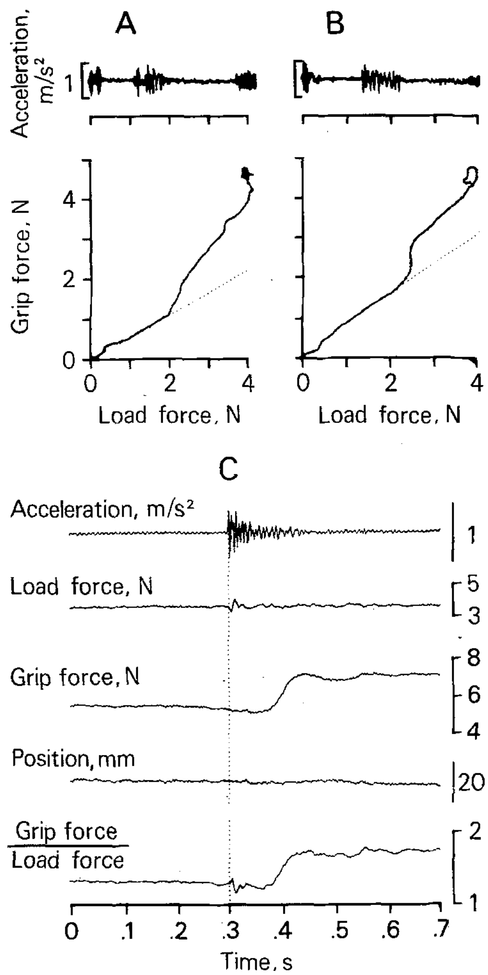

Fig. 8A–C. Late adjustments of coordination between grip and load forces of trials with silk preceded by trials with sandpaper (single trials). **A** and **B** Adjustments during the loading phase. Force coordination illustrated as in Fig. 4A. To show the load force level at which slip took place the acceleration record is displayed as a function of load force. **C** Adjustment of force balance subsequent to slip during the static phase. Vertical line indicates the onset of a slip as revealed by vibrations in the object (acceleration event)

originate from the higher grip forces arrived at the end of the preload phase rather than from an incomplete adjustment of the ratio between the force rates, i.e. the slopes of the two curves referring to the sandpaper trials in Fig. 7B were quite similar.

For trials carried out with suede and sandpaper preceded by trials with silk and suede, respectively, the adjustment followed the same principles although the influences remaining throughout the trials were smaller.

The adjustments to a more slippery surface structure are illustrated in Fig. 7C and D, representing the following sequence of trials: sandpaper, silk and silk (averaged data). In accordance with the pattern described above, the time course of the grip force of the trials with the new surface structure (first silk trials) and the preceding trials (sandpaper) were similar during the preload phase. An adjustment to the more slippery material appeared initially during the loading phase, i.e. the grip force increased more rapidly with silk than with sandpaper (Fig. 7C). For most trials, however, this early adjustment seemed not to be sufficient, since a further "secondary" adjustment of the force coordination occurred later during the loading phase. This late adjustment, which was preceded by a force ratio being close to the slip ratio, accounted for a rapid increase in the force ratio (vertical arrows in Fig. 7C and D) and thereby an increase in the safety margin. After this late correction the ratio was similar to that of silk trials preceded by silk trials.

Distinct secondary adjustments were sometimes preceded by small short-lasting slips revealed as vibrations in the object recorded by the accelerometer. This is illustrated in Fig. 8A and B which shows the grip force and the acceleration as a function of the load force for the preload and loading phases of two such trials, respectively. Just after the slip (the distinct acceleration event), the coordination changed abruptly giving rise to a higher grip force for any given load force. This change in force coordination was often due to a sudden drop in the rate of increase of the load force (Fig. 7C), but in some trials to an increase of the grip force rate or a combination of these strategies. Sometimes, late adjustments were also observed during the static phase, particularly for subjects exhibiting an extremely small safety margin. In these cases, the coordination changes appeared as a grip force increase to a new, higher stable value, as illustrated in Fig. 8C. The described coordination changes following slips all started at a latency of 60–80 ms after the onset of the vibratory event. The underlying slips were rarely noticed by the subject, and the whole process appeared to proceed in an automatic fashion without requiring directed attention of the subject. Of particular interest is that the resultant new force coordination in each instance was maintained throughout the lifting trial, suggesting that the relationship between the two forces relied on a memory trace.

The adjustments in trials with silk and suede preceded by trials with suede and sandpaper, respectively, followed a similar pattern except that secondary adjustments were less frequently observed. In their absence, the grip force and thereby the safety margin remained slightly lower throughout these trials than during suede trials preceded by suede trials (cf. Westling and Johansson 1984).

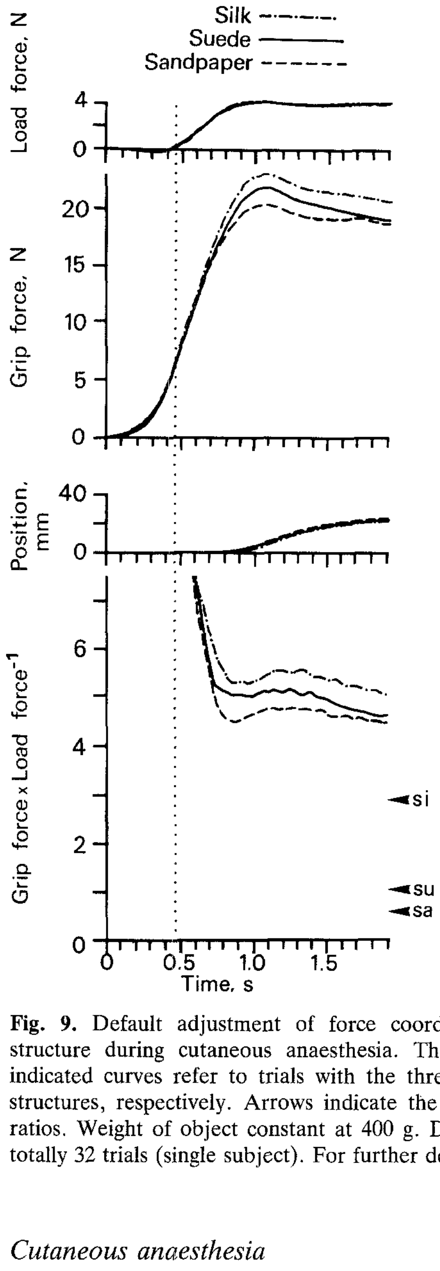

Fig. 9. Default adjustment of force coordination to surface structure during cutaneous anaesthesia. The three differently indicated curves refer to trials with the three different surface structures, respectively. Arrows indicate the corresponding slip ratios. Weight of object constant at 400 g. Data averaged from totally 32 trials (single subject). For further details cf. Fig. 3

Cutaneous anaesthesia

Complete anaesthesia of the index finger and thumb impaired the adaptation of the force coordination to the frictional condition. Since no differences could be discerned between the effects of this type of anaesthesia and cutaneous anaesthesia of the tips of the index finger and thumb, it was concluded that the adjustment to friction was dependent on signals in cutaneous afferents innervating the skin area in contact with the object.

Except for the lack of the adaptation to surface structure, as illustrated in Fig. 9, the principal structure of the lifting trials, as shown in Fig. 2A, did not change during anaesthesia, i.e. all phases could be discerned. This was true also for the motor behavior during the experiments involving weight changes and spring-loading of the object.

The grip force employed initially after the fingers were anaesthetized was high enough to successfully lift and hold objects with sandpaper and suede but usually not with silk, i.e. the most slippery material. The slipping with silk most frequently took place during the loading phase. No "secondary" adjustment, as described above occurred despite that the slips were so severe that the fingers slid over the object which remained motionless on the table. This indicated that signals in cutaneous afferents were required not only for the initial adjustments of the coordination to frictional changes but also for the "secondary" adjustments. The problem with the slip, however, was met by the subject by consciously attending to the firmness of the grip and to increase it during subsequent lifting attempts until the trial was successfully accomplished. Interestingly, this voluntary intervention in the grip force regulation evinced itself as an increased grip force rate during the loading and unloading phases, i.e. as a new force balance and not as a stepwise increase in the grip force during the preload phase. The successful coordination was approximately maintained, apparently in an automatic fashion, in the subsequent trials, including those carried out with the less slippery materials. Consequently, slips rarely occurred later in the lifting series. This behaviour explains the high grip forces in Fig. 9, which shows data of all consecutive trials (32) in a lifting series with pseudorandom changes of surface structure.

This maintained force coordination during anaesthesia and the influences during the preload phase of the surface structure in the preceding trial as well as the preservation of the new coordination arrived at following slips, suggested that the force coordination could be set via a memory trace. In an attempt to further explore this idea, the following experiment was carried out: Two of the subjects whose right hand fingers were anaesthetized were asked to lift the object alternately with the left intact hand and the right hand. The surface structure presented to the normal hand was pseudorandomly varied between sandpaper, suede and silk, whereas it was constant using sandpaper with the anaesthetized hand. Any systematic adjustment of the coordination of the anaesthetized hand with changes of the surface structure would thus be accounted for by stored information gathered during trials with the normal contralateral hand. It turned out that the more slippery the surface of the left hand trial, the higher the ratio between the grip and load force of the subsequent right hand trial. This positive correlation between force ratios of the left hand trials and the subsequent right hand trials, respectively, lasted throughout the trials, and was statistically significant even for the static ratios measured late (8 s) after the onset of the trials ($P < 0.05$, Sperman rank correlation test). Thus, stored information related to the frictional properties of the object appeared not only to influence the coordination during the entire subsequent trial, but it could be used bilaterally.

During anaesthesia, the transition between the preload and loading phases was distorted. The preload phase was prolonged and could last up to 0.5–1.0 s (Fig. 9). Consequently, compared to normal conditions the continuously increasing grip force had reached considerably higher values at the start of the loading phase (typically 5 times higher than normal). These findings suggested that afferent signals from the fingers provided information about the contact condition between the fingers and the object which were necessary for the appropriate release of the motor commands accounting for the parallel force change.

Discussion

During most goal directed manual manipulation involving gripping of objects, the intention of the subject is to move and position the objects in the extra personal space. To overcome forces counteracting the intended movements the subject must produce forces to act on the objects, i.e. load forces as defined in the present study, which, in turn, must be accompanied by appropriate grip forces. The balance, or coordination, between the magnitudes of the grip and load forces may be critical. Too weak a grip force causes slipping, whereas too strong a grip may damage the object or the hand as well as cause unnecessary muscle fatigue. Moreover, it may render difficult further manipulation superimposed on the basic grip. Consequently, there is the need to regulate the grip forces in relation to the load forces and the demands imposed by certain physical properties of the objects.

The present results elucidate some principles of how the motor output accounting for the grip and load forces was organized while small objects were lifted and positioned in space using the precision grip between the tips of the index finger and thumb. The most essential feature of this output was a parallel change of the grip force and the load force. By means of adapting the balance between the two forces, or more precisely the balance between their rates, to the friction between the skin and the object, changes in the load force were simultaneously accompanied by changes of the grip force providing a relatively small safety margin to prevent slips. It is conceivable that this motor behaviour reflects a near optimal strategy since it seems to combine economy of time and muscular force with a low probability of slipping and of cracking fragile objects. The variation in safety margin between subjects (see Westling and Johansson 1984) may be related to differences in a performance criterion, just as the decision criterion influence the costs and payoff during, for instance, a psychophysical discrimination task (e.g. Green and Sweets 1966).

The high capability to adapt the force coordination to the frictional condition is illustrated by the fact that in trials with a new surface structure the adjustment to the new frictional condition was essentially carried out already before the object left its support. A high capacity in this respect seems to be of utmost functional importance since the friction between gripped objects and the skin may vary considerably und unexpectedly between different objects and from time to time for any given object, e.g. due to variations in the rate of sweating (Johansson and Westling 1984). For instance, if comparing the number of trials required to reach a complete adaptation, the adaptation of force coordination in our experiments appear to proceed even quicker (second trial) than the adaptation of the gain of the "functional stretch reflex" following an unexpected change in its usefulness to stabilize sway during stance (Nashner 1976). Likewise, the adaptation of motor behaviour to unexpected changes in the environmental conditions observed during more artificial contexts may require many trials or lengthy of practice (e.g. Gonshor and Melvill Jones 1976a, b; Gilbert and Thach 1977).

There were different evidences in the present results indicating that the force coordination could be defined by a memory trace, which, in turn, was updated intermittently while changes occurred in the frictional condition. Its updating appeared to take place on the basis of afferent information entering early during the preload phase in trials subsequent to a change of the surface structure, but also later during the trials at inappropriate grip forces as during slips (cf. "secondary" adjustments). A reliance on a memory trace conforms to the principles of motor adaptation accomplished by anticipatory control operating on the basis of a flexible neural representation within the brain of the features of the external world (e.g. Ito 1970; Brooks 1979; Nashner 1981; Rack 1981). One advantage with an adequately updated memory defining the coordination might be that the grip and load force commands may be *simultaneously* executed in a manner appropriate for the current friction. Thus, during phases of parallel force changes (loading and unloading phases in our experiments) there would be no systematic time lag between the two forces disturbing their balance. Such a lag would occur if, for instance, the grip force was regulated exclusively, on the basis of a continuously operating feed-back loop (closed loop) involving cutaneous receptors in the fingers, e.g. a continuous tactile feed-back about incipient slip. That this was not the case is obvious since the forces changed in parallel during finger anaesthesia eliminating the cutaneous input. Furthermore, exploratory or manipulatory tasks superimposed on the basic grip temporary requiring the cutaneous sensory apparatus might interfere with such a continuous processing and *vice versa*.

The experiments with anaesthesia indicated that the adaptation of the force coordination to changes in friction was dependent on signals in afferents innervating the glabrous skin areas in contact with the object. To estimate the frictional condition between the skin and the object, it seemed as if the central nervous system, at least in certain situations, was dependent on afferent signals related to slipping events, i.e. most likely a tactile input. Usually, these slipping events appeared to be limited to only one of the two skin areas in contact with the object or perhaps to only a part of one of the areas, since the slips rarely were associated with visible slidings of the fingers relative to the object. The existance of small localized slips may be explained on the basis of the unequal distribution of pressure over the areas of contact due to the elastic properties and the curvature of the skin. With the touched surface being flat, as in the present experiments, the pressure is highest at the center of the area in contact and decreased towards its periphery. The generation of load forces (i.e. shear forces between the object and the skin) will elicit slips within the peripheral parts of the area of contact where the pressure is low, before overall slip occurs. In practice, such forces exist as soon as an object is gripped, e.g. even during the preload phase due to the physiological muscle tremor. The probability of the occurrence of this kind of slips would be related to the ratio between the two forces, but also to the coefficient of friction between the surface and the skin – the lower the friction the higher the probability. Thus, mechanoreceptive afferent units sensitive to localized slips could provide the central nervous system with signals related to the frictional conditions without the occurrence of overall slips. Indeed, mechanoreceptive units with high dynamic sensitivity to very small deformation changes of the skin are known to exist in the glabrous skin of the human hand (for refs. see Johansson and Vallbo 1983).

Signals in cutaneous afferents appeared also to be of importance for the release of the motor commands accounting for the loading phase, i.e. during anaesthesia the start of this phase was considerably delayed. Similar kinds of triggering by somatosensory input most likely contributed to the termination of the loading phase and the start of the unloading phase. The transition between the loading and transitional phase will be considered in another context (manuscript in preparation). Considering the unloading phase, there was relatively constant delay of about 0.08 s between the table contact and the onset of the parallel decrease of the grip and load forces. The sensory cues triggering the parallel force change could have been mechanical events related to the sudden cessation of the replacing movement at the moment the object contacted the table. Signals about these events would then have been transmitted in proprioceptive afferents since the onset of the unloading phase proceeded as normal during finger anaesthesia. The triggered changes of the motor output, as proposed above, as well as the updating of the grip-load force coordination following slips agrees with the notion that a particular pattern of afferent information might trigger the release of a particular set of preprogrammed motor commands or update certain parameters of the currently executed motor programmes. According to this view, the stimulus-response relations would depend on the task or the postural goal of the subject (cf. Houk 1978; Houk and Rymers 1981), i.e. during voluntary movements the brain is supposed to adjust the stimulus-response characteristics of the sensori-motor system with the intentional goals. The latencies between the onset of the slips and the elicited coordination changes and between the table contact and the start of the unloading phase were of the same order of magnitude as the minimal latencies observed during kinaesthetic triggering of "reaction-time" or "intended" arm movements (e.g. Crago et al. 1976; Evarts and Vaughn 1978). Similar latencies have also been reported for the "long loop" servo-like responses occurring when voluntary thumb flexion movements are suddenly interfered with (Marsden et al. 1977). These latencies clearly indicate that the controlling processes were too fast to involve direct voluntary intervention. To avoid interferences with the overall goal of the manipulative task, it seems reasonable that these processes should proceed without requiring much directed attention, i.e. as automatic subroutines. The overall importance of somatosensory afferent signals for automatic adjustments or "fine tuning" of preporgrammed muscle commands and for updating of motor programmes during manual motor activities has recently been emphasized in a unique study of a deafferented man (Rothwell et al. 1982).

It has recently been demonstrated that modest electrical or mechanical stimulation of fingers may elicit multiphasic reflex modulation of ongoing motor unit discharge in hand muscles (Caccia et al. 1973; Garnett and Stephens 1980). In the first human dorsal interosseus muscle, i.e. one of the muscles which significantly contributed to the grip force in the present experiments, the late and most pronounced reflex component is excitatory and appears as an increased probability of motor unit firing at 50–60 ms with a maximum probability at 70–80 ms after the stimulus onset (Garnett and Stephens 1980). These latencies are much the same as those between onset of the slipping events and the elicited grip force increases in the present experiment, if we take into account a short delay between muscle electrical activity changes and the corresponding grip force changes (8–10 ms for distal hand muscles and 10–12 ms for proximal hand muscles during isometric contractions as tested with percutaneous electrical stimulation of the muscle bellies). This reflex component is considered to be supraspinally mediated, requiring transmission of impulses through the dorsal columns and the corticospinal tract (Jenner and Stephens 1982). The participation of supraspinal mechanisms would agree with the abundant evidence that the primate motor cortex and the pyramidal tract are of fundamental importance for the performance of fine finger and hand movements, particularly those involved in the precision grip (e.g. Lawrence and Kuypers 1968; Hepp-Reymond and Wiesendanger 1972; Brinkman and Kuypers 1973; Phillips and Porter 1977; Passingham et al. 1978; Evarts 1980; Muir and Lemon 1983; see also Smith et al. 1981). Cutaneous modalities are well represented among primate motor cortex neurones with inputs from the hand or fingers (Rosen and Asanuma 1972; Lemon and Porter 1976; Wong et al. 1978; Strick and Preston 1982), some of which receive detailed information over very rapid pathways from tactile receptors in the glabrous skin (Lemon 1981). Likewise, transmission through dorsal columns appear to be a prerequisite for an adequate opposition of the thumb and forefinger, as when picking up small objects (Vierck 1978). On the basis of these considerations, it is tempting to speculate that tactile input to the sensori-motor cortex played a key role for the adaptation of the force coordination to the frictional demands. Indeed, it has been proposed that this kind of input may play a significant role during the acquisition and refinement of novel movements, i.e. during the structuring and adaptation of motor programmes (Lemon 1981). More frequently, however, the inferior olive-cerebellar system has been considered to play a role in automatic adaptation of motor behaviour, e.g. during alterations of gain of the vestibular reflex (e.g. Miles and Fuller 1974; Ito 1976; Gonshor and Melville Jones 1976a, b; Robinson 1976) and adaptation of the body and limbs to perturbations of maintained position (e.g. Nashner 1976; Gilbert and Thach 1977; Nashner and Grimm 1978). Not surprisingly, there are cerebellar neurones who modulate their firing rates with the force of precision grip. Many of these also respond to tactile stimulation of the fingers (Smith and Bourbonnais 1981). Moreover, the latencies between the slip events and the updating of the force coordination in our experiments may be compatible with the participation of such subcortical structures as the olivo-cerebellar system and thalamus in the updating of the motor commands prior to their execution over the motor cortex (cf. Evarts and Vaughn 1978; Brooks 1979). On the basis of the above considerations, it seems reasonable to assume that the neural processes underlying the coordinated motor output as considered in the present study was, at least, partly dependent on supraspinal mechanisms. Likewise, the adaptation of the force coordination via a bilaterally accessible memory as well as the variation of the safety margin between individuals suggest that complex neural processes were involved.

In as much as both neurologists and experimental neurophysiologists need a simple method for the quantitative study of coordinative aspects of the gripping function of the hand, the experiments and apparatus reported are of the kind that could easily be adapted to that end. The results can be obtained by objective measurements which make little demands on the subject. The possible clinical significance of the method hinges upon what it can be made to yield as means of analysing disturbances of the force coordination during various pathological conditions.

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