Mechanisms for Force Adjustments to Unpredictable Frictional Changes at Individual Digits During Two-Fingered Manipulation

INGVARS BIRZNIKES, MAGNUS K. O. BURSTEDT, BENONI B. EDIN, AND ROLAND S. JOHANSSON
Department of Physiology, Umeå University, SE-901 87 Umeå, Sweden

Birznieks, Ingvars, Magnus K. O. Burstedt, Benoni B. Edin, and Roland S. Johansson. Mechanisms for force adjustments to unpredictable frictional changes at individual digits during two-fingered manipulation. J. Neurophysiol. 80: 1989 ± 2002, 1998. Previous studies on adaptation of fingertip forces to local friction at individual digit-object interfaces largely focused on static phases of manipulative tasks in which humans could rely on anticipatory control based on the friction in previous trials. Here we instead analyze mechanisms underlying this adaptation after unpredictable changes in local friction between consecutive trials. With the tips of the right index and middle fingers or the right and left index fingers, subjects restrained a manipulandum whose horizontal contact surfaces were located side by side. At unpredictable moments a tangential force was applied to the contact surfaces in the distal direction at 16 N/s to a plate at 4 N. The subjects were free to use any combination of normal and tangential forces at the two fingers, but the sum of the tangential forces had to counterbalance the imposed load. The contact surface of the right index finger was fine-grained sandpaper, whereas that of the cooperating finger was changed between sandpaper and the more slippery rayon. The load increase automatically triggered normal force responses at both fingers. When a finger contacted rayon, subjects allowed slips to occur at this finger during the load force increase instead of elevating the normal force. These slips accounted for a partitioning of the normal-tangential force ratios to the local friction at each digit. This mechanism required a fine control of the normal forces. Although the normal force at the more slippery surface had to be comparatively low to allow slippage, the normal forces applied by the nonslipping digit at the same time had to be high enough to prevent loss of the manipulandum. The frictional changes influenced the normal forces applied before the load ramp as well as the size of the triggered normal force responses similarly at both fingers, that is, with rayon at one contact surface the normal forces increased at both fingers. Thus to independently adapt fingertip forces to the local friction the normal forces were controlled at an interdigital level by using sensory information from both engaged digits. Furthermore, subjects used both short- and long-term anticipatory mechanisms in a manner consistent with the notion that the central nervous system (CNS) entertains internal models of relevant object and task properties during manipulation.

INTRODUCTION

When humans manipulate small objects in various self-paced tasks, they adjust the fingertip forces to the frictional condition of the grasp (Cadoret and Smith 1996; Flanagan and Wing 1995; Flanagan et al. 1995; Forssberg et al. 1995; Johansson and Westling 1984a; Westling and Johansson 1984). This also applies to reactive tasks in which people restrain objects subjected to unpredictable load perturbations oriented tangential to the grasp surfaces (Cole and Johansson 1993; Häger-Ross et al. 1996). Specifically, people adjust the balance of the forces applied normal (‘‘grip force’’) and tangential (‘‘load force’’) to the object’s surfaces to obtain normal:tangential force ratios that are high enough to prevent slippage, while at the same time avoiding excessive normal forces. Grasp stability is thus maintained by using a controlled grip force safety margin against slips.

During both the self-paced lifting tasks and the reactive restraining tasks, the adjustments of the fingertip forces to friction primarily depended on tactile sensory information obtained from the initial contact with the contact surfaces and on the memory traces from previous trials (Cole and Johansson 1993; Johansson and Westling 1984b, 1987). Moreover, the normal:tangential force ratio is adapted to the local frictional condition at the individual digit-object interfaces in both types of tasks (Burstedt et al. 1997a,b; Edin et al. 1992). This adaptation means that subjects lifting objects with vertical parallel grip surfaces take up more of the load at the digit exposed to the less slippery surface than at the cooperating digit; the normal forces are bound to be nearly equal at the two opposing digits (Burstedt et al. 1997b; Edin et al. 1992). Interestingly, during a restrain task, which also allowed the use of different normal forces (in addition to different tangential forces), subjects still apply similar normal forces by the two engaged digits (Burstedt et al. 1997a). In both types of tasks the normal forces are scaled to the average friction at the digit-object interfaces.

On the basis of studies of lifting tasks we hypothesized that the ratio at each digit is controlled by digit-specific tactile sensory information and sensorimotor memories related to the local frictional condition (Edin et al. 1992). Furthermore, we recently concluded that adjustments of the fingertip forces can emerge from the action of anatomically independent neural networks controlling each engaged digit. This conclusion was made in light of the fact that the lifting task was accomplished in a similar manner whether it was carried out by one subject or cooperatively by two subjects, each contributing with one digit (Burstedt et al. 1997b). However, in the restrain task we noted that sensory information related to the local frictional condition at the respective digit-object interfaces controlled the normal force at both digits (Burstedt et al. 1997a). Thus at some level of control frictional information must be compiled from both engaged digits. In the case of the lifting task carried out cooperatively by two subjects, the necessary interdigital coordination could well have developed by learning about which forces to apply during the sequence of practice trials always performed before data collection. Likewise, subjects could have exploited
digit-specific anticipatory mechanisms by using frictional experiences accumulated across a series of consecutive trials also in the restrain task by Burstedt et al. (1997a). Indeed, it is well documented that manipulative tasks can be controlled in a predictive feed-forward fashion, based on internal models of environmental objects (Flanagan and Wing 1997; Ghez et al. 1991; Johansson 1996a; Johansson and Cole 1992; Lacquaniti 1992). It was also demonstrated in monkeys that grip force gradually increases from trial to trial if perturbations are repeatedly applied to test object (Dugas and Smith 1992).

We instead analyze mechanisms by which human subjects adapt the fingertip forces to unpredictable changes in the local frictional condition between consecutive trials. We adopted a restrain task in which the subjects were free to use different normal forces and tangential forces at the two engaged digits. Tangential loads were delivered to a manipulandum that had two parallel horizontally oriented contact surfaces, one for each digit (Burstedt et al. 1997a). By letting the subjects perform the task both unimanually and bimanually we could determine if the interdigital coordination operated in a similar fashion despite obvious differences in the anatomic substrates implementing the control. We conclude that subjects actively can exploit controlled slips during the initial dynamic phase of trials to adopt normal/tangential force ratios suitable to the local frictional condition.

**METHODS**

**Subjects and general procedure**

Experiments were performed on six healthy, right-handed subjects (3 female and 3 male), ranging in age from 18 to 26 yr. The local ethics committee approved the experimental protocol. All participants gave their informed consent to the experimental procedures, although the specific purpose of the experiment was not made known. The subjects were seated in a chair with their upper arms approximately parallel to the trunk and their forearms extended anteriorly. The hands were pronated with palms facing downward and the wrist slightly dorsiflexed (~30°). Vacuum casts supported the forearms up to the palms. A curtain prevented the subjects from seeing their hands and the manipulandum during the experimental trials. The subjects washed their hands with soap and water ~5 min before the experiment. Before data collection, subjects were shown the manipulandum and given ~10 practice trials to familiarize themselves with the apparatus and the task.

**Manipulandum**

The manipulandum was described in detail in a previous report (Burstedt et al. 1997a). In short, it had two horizontal exchangeable flat contact surfaces (30-mm diam, spaced 32 mm center to center; cf. Fig. 2, top panels). It could be loaded in the distal direction by a force servomechanism (0–10 N load force amplitude, bandwidth 0–15 Hz) but when not touched was servo regulated to a constant position (stiffness 1.2 N/mm). A strain gauge transducer system measured the forces applied perpendicular (normal force) and tangential to each contact surface (DC-120 Hz) with a maximum cross talk between the forces of <5%. The displacement of the manipulandum was gauged at 50-μ resolution.

**Test series and subjects’ task**

The subjects were instructed to prevent the manipulandum from moving during the trials. To achieve this, the subjects used the tips of two fingers positioned side by side (cf. Fig. 2, top panels). They received no instructions about what forces to apply and were free to adopt any strategy required to restrain the manipulandum. However, if during the practice trials a subject applied prerespone normal forces of such high magnitudes that their force responses to the load ramp were severely attenuated (Cole and Johansson 1993), the experimenter asked the subject to apply less force. No penalty was imposed if subjects accidentally lost the manipulandum because of slippage; if a slip occurred the manipulandum was simply returned to its starting position, the trial was repeated, and the test series resumed. The fingers were slightly flexed, and the plane of the contact surfaces approximately intersected the centers of the metacarpophalangeal joints. With such a passive, normal force changes caused by movements of the manipulandum were reduced to a minimum.

Before each load trial a brief sound cue prompted the subject to contact the manipulandum with the tips of the two fingers. A trial commenced when the computer detected a background normal force of ±0.7 N at both contact surfaces. Each trial could conveniently be divided in four phases (Fig. 1). The preload phase was of a duration randomly distributed between 1.0 and 3.0 s and began when the subject touched the contact surfaces; the load force was 0 in this phase. During the load phase the load force increased at 16 N/s for a period of 0.25 s. During the subsequent hold phase the total load was maintained at 4 N. The duration of the hold phase was randomized between 3 and 6 s. A second sound cue instructed the subject to initiate the release phase, i.e., to slowly decrease the grip forces until the manipulandum was lost because of slips. The manipulandum was then returned to its starting position, and a sound cue was given to the subject to start a new trial. Five to 10 s elapsed between successive trials.

Each subject was run in two test series with different grasp configurations. 1) In the unimanual series, subjects restrained the manipulandum with the right index and middle fingers, and 2) in the bimanual series subjects used the left and right index fingers. Each test series consisted of 60 trials of pulling loads applied in the distal direction. In all trials the right index finger was exposed to fine-grained sandpaper (no. 320), which showed a high and rather stable friction in relation to the digit. The cooperating right middle or left index finger was exposed to sandpaper in 30 trials and in 30 trials to rayon that was more slippery. These two surface conditions appeared in an unpredictable order (the grip surfaces could be changed quickly). Three subjects were run first with the unimanual series followed by the bimanual series, and another three subjects were run in the reverse order.

**Data collection and analysis**

Data were collected, stored, and analyzed with a custom-built data acquisition and analysis system (SC/ZOOM; Department of Physiology, Umeå University). The force and position signals were sampled at 12-bit resolution with 400 samples/s. Event markers related to onsets and offsets of the various phases of each load trial were sampled with ±0.1-ms time resolution. Force rates and movement velocity of the manipulandum were obtained by ±6-point symmetrical numerical time differentiation (~3 dB at 26 Hz). The instantaneous ratio between the normal and tangential forces was also computed off-line for each digit.

The following measurements were made in each single trial for each digit. 1) The preload normal force was the mean normal force during the 0.3-s period before the onset of the load force increase (load phase). This measure represented forces used by subjects to hold the manipulandum in the absence of a load force. 2) The onset of the normal force response was the point in time when the normal force rate exceeded 1 N/s, i.e., the minimum force rate that empirically could be reliably distinguished in single trials (Fig. 1). 3) The prerespone normal and tangential force were forces
FIG. 1. Sample trial and points of measurements. Single trials performed bimanually. Both fingers contacted sandpaper in A, and the right index finger contacted sandpaper and left index finger rayon in B. Thick and thin lines refer to data for the right index finger and the cooperating finger, respectively. The load increased with 16 N/s during the load phase that lasted 250 ms. The normal force response onset was detected at each digit separately when the normal force rate reached 1 N/s. The black arrows indicate the points at which the moment of normal force response onset and the moment of peak normal force were defined. Load force represented by dashed lines. Dashed vertical line in B indicates a sudden redistribution of tangential force during the load phase because of slippage. During the release phase, the subjects gradually decreased the normal force until the digits slipped and the object escaped from grasp. Horizontal dashed lines in A and B represent the static slip ratio obtained for each digit at the end of the trial; see arrowheads at the end of the trials.

measured at this onset. 4) The peak normal force was the maximum normal force measured ≤0.5 s after the start of the load phase (Fig. 1). At this point we also measured the tangential force. 5) The magnitude of the triggered increase in normal force was assessed as the difference between the peak normal force and the prerespone normal force. 6) The static normal and tangential forces were measured as the mean forces during a 0.3-s time window starting 0.5 s after the onset of the hold phase. 7) Normal:tangential force ratios were collected at normal force response onset, peak normal force, and at static force.
The normal:tangential force ratio at the onset of the slip generated at the end of each trial was assessed for each digit as previously described (Burstedt et al. 1997a). This ratio represented the inverse of the coefficient of static friction at the end of the trial. The occurrence of slips was established by examining the force ratios and their changes, movements of the manipulandum, and, most importantly, sudden changes in distribution of the load force between the digits (see Fig. 3). The average of ratios obtained for the current trial and the four nearest trials with the same surface structure was used as an estimate of the static slip ratio for that trial. It was $0.70 \pm 0.10$ (mean $\pm SD$ for data from all subjects) for the right index finger while it was always in contact with sandpaper and $0.69 \pm 0.09$ for the cooperating right middle or left index finger in contact with sandpaper or $1.53 \pm 0.32$ with the more slippery rayon (see also horizontal lines in top panels of Fig. 2). Additional measurements of static and dynamic slip ratios were made during the load phase of many trials and will be more fully described in RESULTS.

**Statistical analysis**

Numerical values of normal:tangential force ratios, normal forces, and tangential forces were transferred to a statistical program (STATISTICA, Statsoft, Tulsa, OK). Unless otherwise stated, repeated measures analysis of variance (ANOVA) was performed to analyze main effects of four repeated measures (within subjects) factors: prevailing surface condition (2 levels: sandpaper—sandpaper and sandpaper—rayon), surface condition in the immediate previous trial (2 levels), phase of trial (4 levels: preload phase, onset of normal force response, peak of normal force response, and hold phase), and digit (4 levels: right index and middle finger in the unimanual task and right and left index finger in the bimanual task). Phase was not used as a factor in the analyses of the triggered increase in normal force because this increase was computed as the difference between two succeeding points of measurements. Data referring to each subject and each of the experimental conditions were averaged and used in the ANOVA analyses. All possible effects were not examined. Rather, the analyses focused on planned comparisons and specific effects as described in RESULTS. The Pearson coefficient of correlation ($r$) was used as a measure of correlation. The paired $t$-test was used for pairwise comparison of two variables. The Pearson $x^2$ test was used to evaluate the significance of the relationship among categorized variables. The level of probability selected as statistically significant was $P < 0.05$, and, unless otherwise indicated, population estimates are presented in the form of means $\pm SD$ values based on data pooled across all trials by all subjects.

**RESULTS**

Whether subjects used their right index and middle fingers (‘‘unimanual grasp condition’’) or the right and left index fingers (‘‘bimanual grasp condition’’), the loading of the manipulandum triggered normal force responses at both fingers in a similar fashion. Figure 1 shows examples of behaviors in two single trials, with both fingers contacting sandpaper (Fig. 1A) or the right index finger contacting sandpaper and the accompanying finger rayon (Fig. 1B). After a delay after the onset of the load ramp ($0.12 \pm 0.02$ s), the digits responded to the loading with a rapid increase in normal force corresponding to the ‘‘catch-up response’’ described in previous studies (Johansson et al. 1992b,c; see also Cole and Abbs 1988). Because the period of this unitary response ($\sim 0.25$ s) extended into the hold phase there was neither time nor need for a subsequent ‘‘tracking response’’ (cf. Johansson et al. 1992b). The normal force peaked $0.09 \pm 0.05$ s after the end of the load force ramp. Then the normal force decayed to its static value and was maintained during the hold phase (Fig. 1).

To restrain the manipulandum during the load trials subjects were triggered normal force responses at both fingers that always contacted the same surface material, i.e., sandpaper that showed a high friction in relation to the skin. The material in contact with the cooperating finger was varied unpredictably between sandpaper and the more slippery rayon surface. Thus, even when both fingers contacted the same surface structure (sandpaper), subjects tended to apply on average larger normal and tangential forces by the right index finger than by the cooperating finger (Fig. 2). This bias was statistically reliable in the bimanual grasp condition ($P < 0.05$ for normal and tangential forces, respectively) but not in the unimanual grasp condition where it was not observed in all subjects. Despite the occurrence of this bias, the normal:tangential force ratios were purposefully adapted to the local frictional condition at each digit, that is, the response to friction was superimposed on the digital bias.

**Normal:tangential force ratios in various phases of load trials**

To successfully restrain the object, two principal constraints have to be fulfilled: 1) the sum of the tangential forces applied by the two engaged digits must equal the load force imposed on the hand by the manipulandum, and 2) at least one of the engaged digits the subject had to apply a normal force that was large enough in relation to the tangential force to prevent initiation of slips or the manipulandum would escape, that is, the normal:tangential force ratio had to exceed the prevailing static slip ratio, which corresponds to the inverse of the coefficient of static friction.

Between the onset of the load force increase and the start of the subjects’ normal force response, the normal:tangential force ratios fell precipitously at both fingers because the tangential forces increased, whereas the normal forces remained at the preload values (Fig. 1). The normal force responses triggered by the load increase served to dampen this steep fall in force ratios and thus helped to prevent slips when the tangential forces continued to increase during the load phase. Because of the decline in normal force after its peak, the force ratio further decreased during the hold phase toward the hold phase values (Fig. 2, top and bottom panels), although this was not associated with any systematic change in tangential forces (Fig. 2, middle panels). The horizontal lines in the top panels of Fig. 2 show slip ratios that were determined at the end of each trial. The difference between the force ratios used and the corresponding slip ratios represents a measure of the safety margin against slips. However, as will be detailed below, these slip ratios may not be representative for the ratios prevailing during the early period of the trials.

The force ratio at the digit subjected to frictional changes between trials was influenced by the surface in contact with that digit ($P < 0.005$). The force ratio was higher at each point of measurement when the digit contacted rayon compared with the less slippery sandpaper surface (Fig. 2, cf. open and closed corresponding symbols for the right middle
Fig. 2. Force coordination during various phases of the restrain task in unimanual and bimanual grasp configurations. Force ratios and tangential and normal forces during preload phase, at normal force response onset, at peak normal force, and during static hold phase. Filled symbols refer to sandpaper at both fingers, and open symbols refer to condition when finger cooperating with right index finger was exposed to rayon. Thick and thin solid horizontal lines refer to data for finger exposed to sandpaper when cooperating finger was exposed to rayon and sandpaper, respectively, and dashed lines refer to rayon. Horizontal lines in the top panels show static slip ratios measured during the release phase at the end of the trials. Note that these slip ratios underestimate the true static slip ratios during the load phase (see text). The height of the bars in the bottom panel corresponds to the amplitude of the triggered increase in normal force; trials in which both fingers were exposed to sandpaper are represented with filled bars, and trials with rayon at the cooperating finger are represented with open bars. All data points represent means of values from single trials (data from all subjects pooled). This explains why the normal/tangential force ratios in the top panel may be slightly different from the values that would be obtained if calculating the quotient of the corresponding mean normal and tangential forces shown in the bottom and middle panels.
and left index finger in top panels; cf. Fig. 1, A and B). The subjects implemented these ratio adjustments to the frictional condition at the individual contact surfaces by changing both the normal and tangential forces. The higher force ratio observed when a digit was in contact with rayon was caused by a combination of higher normal force and lower tangential force (Fig. 2, middle and bottom panels; cf. open and filled symbols). As a result of the lower tangential force at the cooperating finger, the right index finger was subjected to higher tangential forces in this surface condition (Fig. 2, middle panels). The force ratio was, however, kept at the same level as in the sandpaper–sandpaper surface combination because the normal force was also higher on the right index finger when the cooperating finger contacted rayon (Fig. 2, bottom panels).

Slips contributed to the distribution of tangential force between the two cooperating fingers

Slips and sliding appeared to be a principal mechanism accounting for the redistribution of load between the fingers after a change from sandpaper to rayon. This slippage took place during the load phase and at the finger contacting the more slippery (rayon) surface when the normal:tangential force ratio fell below a critical level at that digit (Figs. 1B and 3). Its onset was characterized by a sudden redistribution of load force between the digits, i.e., the tangential force fell on the slipping digit and increased on the nonslipping right index finger in contact with sandpaper. Consequently, the normal:tangential force ratio transiently increased at the slipping digit while it simultaneously decreased at the right index finger. After this event the tangential force increased at a higher rate at the nonslipping digit and at a considerably slower rate at the slipping digit. As will be further described, this modest increase in tangential force could be explained by frictional sliding or creep between the digit and the rayon surface occurring in parallel with an increase in normal force, that is, the increase in normal force and the coefficient of dynamic friction can be seen to define the increase in tangential force.

Interestingly, the transient slips that occurred during the load phase neither appeared to robustly trigger additional increases in normal force at the slipping digit nor upgrade the normal:tangential force ratios at the nonslipping digit (Fig. 3) (cf. Edin et al. 1992; Johansson and Westling 1984a). Normal force responses were, however, regularly observed in response to slips that occurred in the hold phase later during the trials (e.g., Fig. 4). Thus it appeared that the subjects’ sensitivity to slips was markedly reduced during the load phase, when they allowed slips to partition the load force between the digits to restrain the manipulandum.

Slips during the load phase were observed in all test series for trials with rayon on one digit, but they appeared most distinctly in the bimanual grasp configuration. Indeed, in the latter condition an abrupt and marked redistribution of the load force between the digits was observed in nearly all trials (Fig. 3). The development of the tangential forces at specific points in time (Fig. 2, middle panels) revealed that the frictional condition influenced the partitioning of the load between the digits largely during the period from the onset of the triggered normal force response to the moment of peak normal force. In 65% of all trials with the sandpaper–rayon surface combination an obvious load force redistribution resembling slippage was detected during the period of the triggered increase in normal force, and in another 16% of the trials such redistribution occurred earlier, during the preresponse period. The sudden load redistribution in the preresponse period occurred mainly with the bimanual grasp and accounted for the frictional effect observed on the partitioning of tangential forces at the onset of the normal force response in Fig. 2 (middle panels, bimanual grasp).

Loss of the manipulandum caused by slips

During the slip-mediated redistribution of load force between the digits the tangential force increased on the nonslipping right index finger. This finger was in contact with sandpaper, and the applied normal force was usually high enough to prevent a slip at this digit. However, in 12% of trials with the sandpaper–rayon surface combination, slips occurred at
force ratio after the tangential force at a slipping digit ceased to decrease. This measurement of the dynamic slip ratio was also applied to those successful trials in which slippage occurred during the load phase. For the finger in contact with rayon the dynamic slip ratio was on average $37 \pm 16\%$ higher than the matching static slip ratio ($n = 121$; $P < 0.001$; paired t-test). In contrast, for the finger in contact with sandpaper there was no obvious difference between the static and dynamic slip ratio (Fig. 5C).

Interestingly, the static slip force ratios when unequivocal slippage occurred during the load phase could be substantially higher than the corresponding static slip ratios recorded at the end of the trials (see right index finger data in Figs. 1B and 4). For the finger in contact with rayon the static slip ratio during the load phase was on average $138\%$ ($\pm 27\%$, $n = 179$; $P < 0.001$, paired t-test) of the corresponding static slip ratio measured at the end of the trials. The consecutive slip events at the digit in contact with the rayon surface in the exceptional trial shown in Fig. 4 illustrates the decrease in the static slip ratio during the course of a trial. This observation implies that the slip ratio measurements given in Figs. 1 and 2 (and in Fig. 9) underestimate the true static slip ratios during the load phase.

Control of normal forces

A successful digit-specific adjustment of the normal:tangential force ratio that exploits slip-mediated load force par-

Dynamic friction and sliding of the manipulandum

The trials in which the manipulandum was lost because of slippage revealed some important frictional characteristics of the digit–object interface. These characteristics allowed us to interpret the sliding events that occurred also during the dynamic phase of successful trials as well as during the frictional measurements at the end of each trial. Measurements of the force ratios at the onset of these slips and during the fast movement of the manipulandum before it was lost allowed reliable comparisons between static and dynamic slip ratios at each digit–object interface. With rayon, the dynamic slip ratio was often fairly constant during the movement of the manipulandum and in most cases substantially higher than the static slip ratio measured during the initiation of the slip (Fig. 5, A and B). Furthermore, inspection of the time course of the force ratio revealed that a good early measure of the dynamic slip ratio was the normal:tangential
titioning between the digits clearly relies on an appropriate control of the normal forces in relation to the frictional condition at each digit–object interface. The normal force applied at the more slippery contact surface had to be weak enough to permit slippage, whereas that at the less slippery surface had to be high enough to prevent accidental slippage as a consequence of the increased load. Both the size of the triggered force response and the size of the preload normal force on which the triggered response was superimposed were important. 1) Most slips that contributed to a purposeful load redistribution actually took place during the triggered normal force increase, and, 2) because of the delayed onset of the normal force responses, subjects had to maintain normal forces that were sufficiently high before the commencement of the triggered normal force response to prevent the loss of the manipulandum during the initial load force increase.

**Triggered normal force response**

Although the friction was changed at just one of the digits, the amplitude of the triggered increase in normal force was influenced at both engaged digits (Fig. 2, filled vs. open inset histograms in bottom panels), that is, statistically, the prevailing surface condition had a primary effect on response amplitude ($P < 0.005$), but no reliable interaction was found between the finger and the prevailing surface factors. When shifting from sandpaper to rayon, the size of the normal force responses increased at both fingers in a manner that suggested that they were scaled in parallel. In the bimanual grasp condition all subjects showed a parallel change in the normal force responses (Fig. 6A, right panel). In the unimanual grasp four of six subjects scaled the responses in parallel (Fig. 6A, left panel). However, the other two subjects still scaled the normal force response of the right index finger by the frictional change at the cooperating middle finger. The robust effect on the right index finger was highly functional because this digit took up the load increase when slippage occurs on the accompanying finger when in contact with rayon. In agreement with previous findings, the frictional input scaled the amplitude of the triggered increase in normal force, whereas its duration and shape were less influenced (Fig. 6B) (see “catch-up” response in Cole and Johansson 1993). There were no reliable influences by the frictional condition in the previous trial on the magnitude of the triggered response nor were there significant interactions between finger and surface condition in the previous trial, or between the present and previous surface condition.

**Normal forces applied before onset of triggered normal force responses**

Frictional changes at the digit accompanying the right index finger not only influenced the triggered normal force responses but also the normal forces applied by both fingers before the onset of these responses ($P < 0.05$; planned comparison). Again, the two engaged digits were influenced in a similar manner (Fig. 2, bottom panels; cf. corresponding filled and open symbols). In addition, the magnitude of the preload normal forces was influenced by the frictional condition in the preceding trial ($P < 0.005$; Fig. 2, bottom panels; cf. corresponding squares and circles). Overall, subjects used somewhat higher preresponse normal forces with more slippery frictional conditions in the current and in the previous trial. These effects were consistent throughout the different conditions, i.e., there were no interactions among prevailing surface, previous surface, and finger ($P > 0.5$).

Because the triggered normal force responses were superimposed on the preload normal forces, the frictional condition in the previous trial influenced the amplitude of the employed normal forces more or less throughout the trials (Fig. 2, bottom panels; cf. squares and circles). Although it was modest, this effect turned out to dramatically influence the probability of losing the manipulandum because of slippage in trials with rayon ($P < 0.001$; $\chi^2$ test; Fig. 7). In the unimanual grasp condition, for instance, the risk of losing the manipulandum during the load phase was 6% if the middle finger had been in contact with rayon in the previous trial but 26% if it had been in contact with sandpaper. The influence of friction in the previous trial was similar but less pronounced during the bimanual condition (Fig. 7). These results indicate that the control of preresponse normal forces was highly critical for a successful performance of the present restrain task.

**Theoretical model of tangential force development**

To verify that we understood the key mechanism involved in the digit specific adaptation of the fingertip forces to the frictional condition, we constructed a theoretical model that simulated tangential force redistribution caused by slippage. We used the model to predict the onset of force redistribution and the final tangential force distribution in single trials with sandpaper at the right index finger and rayon at the cooperating finger. The friction at the contact surface of the right index finger was assumed to be high enough to prevent sliding in all trials. The model was evaluated by comparing its outcome with experimental results obtained in single trials. The following parameters, referring to the finger in contact with rayon, were derived from our experiments and used to compute the development of the tangential force in the model: 1) static and dynamic friction assessed during the load phase, 2) tangential and normal forces at onset of the load phase (preload forces), and 3) fractional contribution by the target finger to the total stiffness in the loading direction. The fractional stiffness ($S$) was estimated from the increase in tangential force of the target finger ($\Delta F_t$) in relation to the total load increase ($\Delta L$) during the first 100 ms after onset of the load phase ($S = \Delta F_t / \Delta L$). The tangential force at each digit before any slippage was modeled based on this fractional stiffness measure, i.e., it was used to determine the fraction of the servo-controlled load force that was taken up by each digit. Furthermore, the contribution by the triggered normal force response was characterized by 4) its response onset latency and 5) its amplitude and time course (waveform). Measurements were obtained from single trials except for estimates of the dynamic and static friction and the waveform of the triggered normal force response. These estimates were derived from data averaged across all available measurements from trials in a single test series (for waveform cf. Fig. 6B).
CONTROL OF FINGERTIP FORCES 1997

FIG. 6. Triggered normal force response. A: mean amplitude of the triggered increase in normal force shown for the each subject and grasp separately. Response amplitude of right index finger (x-axis) plotted against that of the cooperating finger (y-axis). Open circles represent mean values obtained when both fingers contacted sandpaper, and black circles represent when the cooperating finger contacted rayon. Data obtained for one subject are connected with lines, and the shaded ellipses correspond to the 95% confidence intervals in x and y. B: mean rate of the normal force response shown as a function of time for each digit, grasp, and surface condition separately. Each record was constructed from amplitude measurements at 10-ms intervals obtained from single trials that were synchronized at the moment of normal force response onset at the particular finger; vertical bars correspond to SE. Solid and dashed lines represent the normal force rate at the right index finger and the cooperating finger, respectively. Thick lines represent data obtained when both fingers contacted sandpaper, and thin lines represent data when the cooperating finger contacted rayon. The insets show the same data after normalization for amplitude.

We confined the modeling to trials with sandpaper at the contact surface, that is, the tangential force was suddenly reduced to increase the normal: tangential force ratio to make the finger ‘stick.’ The model thus can be represented by the following pseudocode

\[
\text{IF } F_t < F_n / R_{\text{stat}} \\
\quad \quad \text{THEN } F_{t_{i+1}} = F_t + S \cdot \Delta L_{i+1} \\
\quad \quad \text{ELSE } F_{t_{i+1}} = F_{n_{i+1}} / R_{\text{dyn}}
\]

The model simulations were in good qualitative agreement
with the empirically observed data (Fig. 8). For instance, as a consequence of the dynamic friction, during periods of sliding the tangential force that was generated at the slipping digit slightly increased with the increasing normal force as observed with experimental data (Fig. 1B and Figs. 3 and 5). Moreover, once the frictional sliding started the sliding typically continued until the end of the load phase (shaded area in Fig. 8). Because of the continual increase of normal force for some time after the end of the load ramp, a safety margin against further slips was restored also at the previously sliding digit. The simulations were also in rather good quantitative agreement with the empiric data. In particular, the model was reliable in predicting how the final load force would be partitioned between the digits during the static hold phase with either grasp configuration. In the experimental data, load force redistributions because of distinct slips were discerned in 141 of the 170 trials (83%) with the bimanual grasp configuration. Of those 141 trials, the model predicted slips in 131 (94%). Moreover, the point of onset of load force redistribution between the digits was predicted to occur 146 ± 34 ms after the onset of the ramp load increase, and this correlated well with the experimental data, i.e., 146 ± 42 ms ($R^2 = 0.50; P < 0.001, 131$ trial). The model likewise identified $24$ of the $29$ trials in which no marked load redistribution occurred. The subjects behavior was thus predicted correctly in $155$ of $170$ trials (91%). Moreover, the predicted tangential force during the hold phase at the left index finger correlated well with the observed values ($R^2 = 0.42; P < 0.001; 170$ trials): $1.00 ± 0.35$ versus $1.05 ± 0.48$ N. (Notably, the total load force, $4$ N, was under servo control.) We observed fewer trials with load force redistribution having likely been caused by slips in the experimental unimanual grasp condition than with the bimanual grasp configuration (94/128; 73%). The model predicted an even lower frequency of frictional related redistribution in this grasp condition (59% of all trials). This agrees with the generally weaker effect of the frictional condition on load redistribution and adaptation of normal/tangential force ratio for the right middle finger compared with the left index finger (Fig. 2, top panels). Furthermore, on average, the predicted onsets of slip-induced force redistribution and final static load forces reasonably matched the experimental data ($142 ± 52$ vs. $152 ± 40$ ms and $1.33 ± 0.51$ vs. $1.44 ± 0.50$ N). However, on the single trial level the correlation between the predicted and observed data was rather poor ($R^2 = 0.08, P < 0.02$ and $R^2 = 0.28, P < 0.0001$ for onset latency and static force, respectively; $128$ trials).

In summary, the model seemed to efficiently capture two essential peripheral mechanisms involved in the adaptation to differential frictional conditions, load partitioning mediated by slip and sliding at the digit contacting the most slippery contact surface. The subjects did indeed take advantage of this mechanism, but additional factors may have contributed, especially during the unimanual grasp condition.

**Differences between the unimanual and bimanual grasp configurations**

In ~30% of the trials during the unimanual grasp condition we observed a change in partitioning of the load between the engaged fingers that appeared close to the onset of the triggered normal force response; only a few such trials were observed with the bimanual grasp configuration. The stiffness in the loaded direction suddenly decreased, and the force ratio markedly increased at the middle finger (Fig. 9A). Frictional sliding was considered an unlikely explanation of these redistributions of tangential force because they occurred at normal/tangential force ratios more than twice the estimated static slip ratio. Furthermore, such redistributions were observed when the middle finger was in contact with rayon as well as with sandpaper. Figure 9A actually shows a trial with sandpaper at both contact surfaces. In this

![Fig. 7. Percentage of “lost” trials with the sandpaper-rayon surface combination when the cooperating finger in the immediate previous trial was in contact with sandpaper or rayon. Note the stronger influence of the previous trial in the unimanual than in the bimanual grasp condition.](image-url)
Slip based mechanism for adjustment of local normal:tangential force ratios

It could be difficult to identify precisely how subjects partitioned the load force in individual trials. Slips and anticipatory differential changes of digital stiffness in the loading direction could ride on top a significant bias to rely more on the right index finger. Nevertheless, subjects seemed to depend almost entirely on the “slip strategy” in the bimanual grasp configuration for an adequate load force partitioning, but such a slip strategy was also observed in a majority of the trials in the unimanual grasp condition. We conclude that these slips were planned because they did not induce the overall upgrading of the normal force level to avoid the further slippage as it was repeatedly demonstrated in lifting tasks (Edin et al. 1992; Johansson and Westling 1984a; see also Edin et al. 1993). There are reasons to believe that the slip-based mechanism for load partitioning is common to different type of tasks, that is, slips probably account for load partitioning during the phase of parallel force increase also when people lift objects immediately after a change to a more slippery surface condition on one digit (Edin et al. 1992). Notably, both in the restraint of active objects and in the lifting of passive objects the tangential forces applied by the two engaged digits are constrained in a similar manner: the sum of the tangential forces has to be equal to the load force imposed by the manipulandum or
by the lifting force to overcome object weight, respectively. In the study by Edin et al. (1992) we did not explicitly consider this slip-based strategy of load partitioning mainly because the normal:tangential force ratios recorded in the load phase generally were higher than the static slip ratios measured at the end of trials. These results however indicate that a true slip ratio can be substantially higher during the early phase of a trial, i.e., shortly after that the object was gripped, than a couple of seconds later. That friction increased during a trial may be due to an increased adhesion while the finger gradually molds to the details of the contact surface (cf. deforming friction in Moore 1972). It is also possible that sweat accumulated at the skin–object interface; sweat increases the friction particularly for materials with smoother surfaces, e.g., the rayon surface in this study (Johansson and Westling 1984a; Smith et al. 1997).

**Parametric adjustments of normal forces**

The slip-based mechanism for adjusting the local normal:tangential force ratios requires a fine-tuned coordination of normal forces, that is, although the normal force at the more slippery surface has to be comparatively low to allow for slippage to occur, the normal force applied by the non-slipping digit at the same time has to be high enough to prevent loss of the manipulandum when this digit receives the higher tangential load because of the slippage at the accompanying finger. In line with this we observed that the adjustments in normal force induced by frictional changes was similar, or even stronger, on the right index finger at which the friction remained constant compared with the cooperating finger subject to frictional change (also see Burstedt et al. 1997a). This also applies when people lift passive objects with vertical parallel grip surfaces with two-fingered opposition grasps (Burstedt et al. 1997b; Edin et al. 1992); in this task the normal forces are mechanically constrained to be similar. In either type of task the employed normal forces are scaled at both engaged digits by the “average” friction at the various digit–object contact areas. As previously shown in restrain experiments in which the subject took up the load only at one digit (Cole and Johansson 1993), the frictional condition “globally” scaled the amplitude of the normal force while the waveform of the triggered normal force responses was little influenced. This adjustment of the normal force “gain” is primarily controlled in a feedforward manner. Subjects extract friction-related information from signals in cutaneous sensors during the initial skin–object contact (Cole and Johansson 1993; Johansson and Westling 1987) and use frictional information gained in previous interactions with the object as demonstrated in the current results. Interestingly, some subjects reported that they were not aware of a surface change when initially touching the manipulandum or even after a particular trial had been completed. Still, forces were adequately adapted to the prevailing surface condition.

Successful digit specific adjustment of the normal:tangential force ratio that exploits controlled slips not only results from scaling the normal forces in relation to frictional condition but also to the load force rate. It was previously demonstrated that response requirements imposed by the rate of the load force change during the load phases (and unload phases) in manual restrain tasks are met automatically and parametrically (Johansson et al. 1992b). The rate of normal force change varies linearly with the load force rate, and the initial catch-up responses are controlled by sensory information according to a “pulse height control policy” (cf. Freund et al. 1978; Ghez and Vicario 1978; Gordon and Ghez 1987). Signals from digital (tactile) afferents reflecting the initial load force rate during the response latent period specifies the rate of the triggered normal force changes in a forward manner (Häger-Ross and Johansson 1996; Johansson et al. 1992a). FA I afferents (Meissner endings) with receptive fields in the glabrous skin areas in contact with the manipulandum seem to be in a unique position to both initiate and scale the reactive normal force responses (Macefield et al. 1996). Moreover, the FA I afferents are the primary candidates to convey frictional information (Johansson and Westling 1987). Interestingly, afferents from muscles do not respond until the normal force response is initiated by commands to the muscles and therefore seem to reflect ongoing muscular activity rather than any object property (Macefield and Johansson 1996; see also Häger-Ross and Johansson 1996).

Occasionally we observed normal force responses to distinct slips late during the trials, i.e., during the hold phase (Fig. 4). These slip-triggered responses tended to increase the normal:tangential force ratios at both fingers, i.e., a motor response most likely mediated by cutaneous afferent signals as previously demonstrated in lift experiments (Edin et al. 1992; Johansson and Westling 1984b, 1987). However, the quite dramatic slips during the load phase accounting for the principal adaptation of the force ratios to the local frictional conditions did not elicit obvious normal force responses. Such a variation in the sensitivity to slips seems purposeful because the slips that occurred during the load phase appeared to specifically serve to partition the load and should therefore not necessarily induce an overall upgrading of the normal:tangential force ratios. Phase-dependent responses to slips are also observed in lifting tasks. Slip events during the load phase before object lift-off trigger changes in both the lift force (decrease) and the normal force (increase) drive, but, when the object is held in air, however, just the grip force is influenced (increase) (Johansson and Westling 1984a). This phase dependence is functional because, in this task, gravity restrains the response alternatives preventing efficient load force adjustments during the hold phase. A similar dependence on the phase of movement or postural situation was described with other multiarticulate actions triggered by somatosensory input (e.g., Rossignol et al. 1988).

**Anticipatory mechanisms**

Subjects’ behaviors in these experiments indicated that the control of fingertip forces was influenced by the operation of various anticipatory mechanisms. Influences by the surface condition in previous trials were expressed differently in the unimanual and bimanual grasp conditions. As such, the expression of various anticipatory mechanisms supporting adaptation of limb mechanics according to task demands are consistent with the notion that the CNS uses internal models...
of relevant object and task properties during manipulation (Flanagan and Wing 1997; Johansson 1996b; Johansson and Cole 1992; Lacquaniti 1992), including related postural actions (Hugon et al. 1982; Massion 1994; Miall and Wolpert 1996; Paulignan et al. 1989).

Anticipatory effects related to surface condition in the previous trials

Not only did the prevailing surface condition influence the employed grip forces but so did the frictional condition in the previous trial. Influences of the frictional condition in previous trials were attributed to a frictional memory, which, as a part an anticipatory parameter control policy, is employed in the control of fingertip forces (Johansson 1996b). Such effects were observed in lifting tasks at the level of the hand (Forssberg et al. 1995; Johansson and Westling 1984a) but also at the level of separate digits or grasp surfaces (Burstedt et al. 1997b; Edin et al. 1992).

When subjects were exposed to a low-friction surface in one trial, they used larger normal forces throughout the subsequent trial. However, the magnitude of the triggered increase in normal force was not significantly influenced by the frictional condition in previous trials. Thus, in contrast to the prereponse normal force, the triggered response appeared to be influenced only by sensory input obtained in the current trial, before its onset. Likewise, in studies by Johansson et al. (1992b,c) the size of the triggered response in restraint tasks was not influenced by load rate and amplitude in immediate previous trials.

Paradoxically, the impact on the preload normal forces of the anticipatory effects related to surface condition in the previous trial was negative. A strong reliance on the frictional condition in the previous trial increased the probability of losing the manipulandum because of slips if the manipulandum was equipped with a less slippery surface in the previous trial. Either the subjects could not fully suppress the influences of memory traces of the last performed trial or they were not always able to adequately assess the prevailing frictional condition before any tangential forces were applied. It is, however, likely that with instructions that strongly forbid the subjects to lose the object they would have used stronger preload normal forces, and consequently the frequency of lost trials would have been lower.

Besides anticipatory effects related to memory mechanisms operating on a relatively short timescale pertaining to the surface conditions in the immediate previous trials, we interpreted the digital “bias” to reflect an anticipatory strategy developed as a consequence of the long-term properties of the manipulandum. To restrain the manipulandum, especially in the bimanual condition, subjects relied more on the finger at which the friction was high and predictable (sandpaper surface) than the accompanying digit subject to unpredictable frictional variation (sandpaper or the slippery rayon surface). In contrast no such bias developed in similar bimanual and unimanual experiments when the two fingers encountered the same overall variations in frictional conditions (Burstedt et al. 1997a). This kind of behavior might emerge from a control process that uses previous experiences to differentially regulate the fractional stiffness in the loading direction and to distribute the normal forces among the digits on the basis of the long-term asymmetric properties of the manipulandum. Importantly, despite the presence of a digital bias in favor of the right index finger, the normal:tangential force ratios were adjusted to the local friction at both digits.

We considered similar anticipatory mechanisms to have a major input on the control of the local force ratios in our previous studies in which the surface materials were kept constant in blocks of trials (Burstedt et al. 1997a,b). These memory mechanisms are expressed after learning from previous trials about which forces and force ratios to apply by using the individual digits. Such a strategy may also explain the coordinated behavior when two subjects repetitively lifted a test object whose surface materials were kept constant with each subject contributing by one finger in an opposition grip (Burstedt et al. 1997b). Indeed, subjects evidently attempted to use such anticipatory control also in the current study, primarily in the unimanual grasp condition. However, the unpredictable frictional variation at one digit eliminated its effective use.

Unimanual versus bimanual tasks

The unimanual grasp condition involved fingers that were controlled by partially overlapping muscle groups rather than by separate muscles, whereas in the bimanual grasp configuration there was no such overlap. On the basis of these results and our previous observations (Burstedt et al. 1997a), we nevertheless propose that similar interdigital control mechanisms may operate at the fingers of one and two hands. Such “motor equivalence” allows humans and animals to flexibly employ various effectors or combination thereof to carry out defined tasks under conditions that may require novel joint configurations (e.g., Abbs and Cole 1987). It is today well documented that the basic coordination of digits for grasp stability shows effector invariance for a variety of grips, including one- and two-handed grips, “inverted” grips (Burstedt et al. 1997a,b; Flanagan and Tresilian 1994), and multidiigit grips (Flanagan et al. 1997; Kinoshita et al. 1995). However, one interesting difference that we observed between the two grasp configurations concerned the effects by the frictional condition of the previous trial; the risk of losing the object after a change from sandpaper to rayon at one contact surface was clearly higher in the unimanual grasp condition (Fig. 7). This suggests that the adaptation of the local normal:tangential force ratios was more influenced by the previous frictional condition in the unimanual than in the bimanual grasp configuration. Rather than anatomic constraints this difference would reflect differences in the control of the two grasps. It is evident from our previous study in which the surface materials were kept constant in blocks of trials that the digits have a similar capacity to work independently in the unimanual and bimanual condition in the current type of restraint task (Burstedt et al. 1997a).

We thank A. Backström and L. Backström for technical support. This study was supported by the Swedish Medical Research Council (Project 8667), Department of Naval Research, Arlington, VA (Grant N00014-92-J-1919) and the Goran Gustafsson Foundation for Research in Natural Sciences and Medicine. I. Birznieks was supported by the bilateral cooperation grant between University of Umeå and University of Latvia. Address reprint requests to I. Birznieks.

Received 20 October 1997; accepted in final form 15 June 1998.
REFERENCES


JOHANSSON, R. S. AND WESTLING, G. 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, 1984a.


