Control of Grasp Stability in Humans Under Different Frictional Conditions During Multidigit Manipulation

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Burstedt, Magnus K. O., Randall Flanagan, and Roland S. Johansson. Control of grasp stability in humans under different frictional conditions during multidigit manipulation. *J. Neurophysiol.* 82: 2393–2405, 1999. Control of grasp stability under different frictional conditions has primarily been studied in manipulatory tasks involving two digits only. Recently we found that many of the principles for control of forces originally demonstrated for two-digit grasping also apply to various three-digit grasps. Here we examine the control of grasp stability in a multidigit task in which subjects used the tips of the thumb, index, and middle finger to lift an object. The grasp resembled those used when lifting a cylindrical object from above. The digits either all contacted the same surface material or one of the digits contacted a surface material that was more, or less, slippery than that contacted by the other two digits. The three-dimensional forces and torques applied by each digit and the contact positions were measured along with the position and orientation of the object. The distribution of forces among the digits strongly reflected constraints imposed by the geometric relationship between the object's center of mass and the contact surfaces. On top of this distribution, we observed changes in force coordination related to changes in the combination of surface materials. When all digits contacted the same surface material, the ratio between the normal force and tangential load (F_n:L ratio) was similar across digits and scaled to provide an adequate safety margin against slip. With different contact surfaces subjects adapted the F_n:L ratios at the individual digits to the local friction with only small influences by the friction at the other two digits. They accomplished this by scaling the normal forces similarly at all digits and changing the distribution of load among the digits. The surface combination did not, however, influence digit position, tangential torque, or object tilting systematically. The change in load distribution, rather, resulted from interplay between these factors, and the nature of this interplay varied between trials. That is, subjects achieved grasp stability with various combinations of fingertip actions and appeared to exploit the many degrees of freedom offered by the multidigit grasp. The results extend previous findings based on two-digit tasks to multidigit tasks by showing that subjects adjust fingertip forces at each digit to the local friction. Moreover, our findings suggest that subjects adapted the load distribution to the current frictional condition by regulating the normal forces to allow slips to occur early in the lift task, prior to object lift-off.

INTRODUCTION

In common manipulatory tasks the loads that potentially destabilize the grasp include time-varying forces and torques tangential to the grasped surfaces. These tangential loads develop as a consequence of the subject's actions on the object. Linear load forces counteract gravitational and inertial forces and occur, for instance, whenever we lift an object from a support. Torque loads develop when we tilt an object or accelerate the hand-held object with the center of mass (CM) off the grip axis (e.g., the line joining the tips of the thumb and the index finger in a precision grip task). Several studies during the last 15 yr have examined the control of grasp stability under tangential force loads (for recent reviews see Johansson 1996, 1998; Wing 1996) and more recently under loads that include tangential torque (Goodwin et al. 1998; Johansson et al. 1999; Kinoshita et al. 1997; Wing and Lederman 1998). A number of sensory-motor mechanisms involved in the control of grasp stability have been identified. These mechanisms serve to prevent linear and rotational slips and excessive forces by automatically regulating forces normal to the grasped surfaces to match the tangential load. Furthermore, to cope with different frictional conditions between digits and objects, subjects use tactile information about friction to adapt the ratio between normal force and tangential load to the prevailing frictional conditions of the grasp. Importantly, in two-fingered lifting tasks performed unimanually, bimanually, or by two cooperating subjects, subjects tune this ratio independently at each digit to the local frictional condition at that digit (Burstedt et al. 1997b; Edin et al. 1992). When subjects lift objects with parallel vertical contact surfaces covered with different materials, they achieve different ratios at the two digits by applying a lower tangential force at the more slippery side. This strategy typically results in some object tilt (toward the more slippery side) after the tangential lift forces overcome gravity and the object lifts off. Similarly, when subjects restrain active objects they also adjust the distribution of tangential forces such that the force coordination at individual fingers is adapted to the local frictional conditions (Birznieks et al. 1998; Burstedt et al. 1997a). Thus whenever the mechanical constraints imposed by the task and the object permit, subjects appear to adjust the force coordination at the individual digits for grasp stability.

The control of grasp stability has until recently been studied primarily in tasks involving two digits only, typically the thumb and index finger. Yet, most motor skills we associate with dexterous manipulation involve more than two digits. Although a multidigit grasp is inherently more stable than a two-digit grasp, it presents the sensorimotor systems with an added challenge. That is, because the orientations of the force vectors applied by the separate digits are less constrained in multidigit grasps, the motor controller has to choose from a number of possible solutions, i.e., grasp stability can be achieved with many different combinations of fingertip forces

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(Flanagan et al. 1999). The search for rules employed by the nervous system for force sharing among digits under various experimental conditions has been a topic of several previous investigations (Amis 1987; Imrhan and Sundararajan 1992; Kinoshita et al. 1995, 1996; Latash et al. 1998; Li et al. 1998; Radhakrishnan and Nagaravindra 1993; Radwin et al. 1992). However, these studies analyzed neither the coordination of normal and tangential forces applied by individual digits nor the distribution of fingertip force among the digits in the context of control of grasp stability or specified task constraints. To our knowledge, our prior study (Flanagan et al. 1999) is the only previous study in which mechanisms supporting grasp stability have been explicitly addressed during multidigit manipulation. We examined in that study the control of fingertip forces when subjects lifted an object with unimanual and bimanual three-digit grasps that engaged the tips of the thumb and two fingers. The grasp resembled those used when lifting a cylindrical object from above. We found that many of the principles for coordination of fingertip forces originally demonstrated for two-digit grasping (see Johansson 1996) also apply to this multidigit manipulatory task. First, the normal forces generated by each digit increased in parallel with the vertical tangential force applied to lift the object (subjects tended to avoid horizontal tangential forces). The vertical lift forces (and normal forces) were synchronized across the digits, and the contribution by each digit reflected intrinsic object properties, i.e., geometrical relationship between the grasp sites and the center of mass of the object. Second, the development of normal forces and load forces before object lift-off reflected the object's weight (and mass distribution) and was thus based on sensorimotor memory built up from experience of object mass in previous lifts. Third, the sensorimotor mechanisms engaged in the control of normal force appeared to take into account the combined effect of linear (tangential force) and rotational (tangential torque) and load components (see Goodwin et al. 1998; Johansson et al. 1999; Kinoshita et al. 1997; Wing and Lederman 1998).

In the present study, we extended the analysis of three-digit manipulation by examining the control of grasp stability under various frictional conditions between the digits and the object. First, we wanted to investigate whether the frictional conditions influenced the magnitudes of the fingertip forces and the distribution of forces among the digits. Second, we wanted to know the extent to which the coordination of fingertip forces at the individual digits is tuned to the local frictional conditions at the separate grasp sites; that is, if the ratio between the normal force and the tangential load is adapted to the local frictional condition. Finally, in light of the fact that subjects should be able to achieve grasp stability with many combinations of fingertip actions in multidigit manipulation, we wanted to identify the ways in which they preferred to implement the grasp.

METHODS

Subjects and general procedures

Seven healthy subjects (3 men and 4 women between 19 and 45 yr of age) participated in this study after giving their informed consent. All subjects were naive concerning the specific purpose of the study. Subjects sat in an ordinary chair with their upper arms parallel to the trunk and the forearms extended anteriorly. An instrumented test object (Fig. 1*A*) was located on a small table in front of the subject. On instruction, the subject lifted the object to a height of ~6.5 cm by grasping the object from above using the tips of right thumb, index finger, and middle finger (Fig. 1*A*). No explicit instructions were given regarding the speed of lifting, forces to apply, or the orientation of the object in space, but the experimenter demonstrated the task. In addition, to familiarize the subject with the task, they lifted the object once with the contact surfaces covered with sandpaper before the experiment. Throughout the trials, subjects could see their hand and the test object. Before the experiments, subjects washed their hands with soap and water.

Test object

The instrumented test object (Fig. 1, *A* and *B*) has been described in detail in an earlier report (Flanagan et al. 1999). Briefly, each digit contacted a separate vertically oriented contact disk (30 mm diam). Each contact disk was exchangeable, and the surface facing the digits was covered either by rayon or fine grain sandpaper (no. 320). The distance between the center of each disk and the center of mass (CM) of the object was 30 mm in the horizontal plane. The mass of the object was 0.4 kg, and its center was located ~2 cm below the contact surfaces when the object was level. Each contact disk was mounted on a six-axis force-torque sensor (Nano F/T transducers, ATI Industrial Automation, Garner, NC) that measured the normal force (F_z) perpendicular to the disk and two orthogonal forces tangential to the contact disks (Fig. 1*C*). Tangential forces were measured in the vertical (F_y) and horizontal (F_x) directions when the object was level, i.e., F_y directly measured the vertical lift force unless the object was tilted. The sensor likewise measured torques about these three force axes at the center of the contact surface (Fig. 1*C*). An electromagnetic position-angle sensor recorded the linear position and angular orientation of the object in three dimensions independent of the subject ("world" coordinates; Fig. 1*A*; 3SPACE, FASTRAK, Polhemus, Colchester, VT). The angular orientation of the object was represented in Euler angles (azimuth, elevation, and roll). These were all zero when the object was located on the table before lift-off. Notably, any tilting of the object out of the horizontal plane was gauged by changes in the elevation and roll angles. Subjects primarily moved the object along the *y*-axis in the present lifting task.

Lifting trials

The frictional condition of the grasp was varied experimentally by letting the subjects lift the object under five different *surface combinations*: *1*) all disks covered with sandpaper, *2*) rayon at the index finger only, *3*) rayon at the middle finger only, *4*) rayon at both the index and middle fingers, and *5*) all three disks covered with rayon. Each subject completed eight consecutive lifting trials with each of the five combinations of surface materials.

Three different auditory cues paced the subject through each lifting trail (Fig. 1*D*). The first auditory cue notified the subject to grasp the object, lift it and hold it steady in air (*hold phase*). Four seconds after the first cue a second auditory cue prompted the subject to perform a *fiddling procedure*. By this procedure, we obtained estimates of the coefficient of static friction for each digit on a trial-by-trial basis as previously described (Flanagan et al. 1999). During the fiddling procedure, the subject slid the tip of each digit, in any order, across the contact surface while holding the object in air. For each digit, the subjects typically chose to generate the slip by simultaneously decreasing the normal force slightly and increasing the vertical force (Fig. 1*D*). The decrease in vertical force at a given digit was associated with object tilting and changes in tangential torque and vertical force at the other digits (see fluctuations in elevation and roll angles and in tangential torques in Fig. 1*D*). Although all subjects generated three intentional slips in all trials, one for each digit, only once did a subject drop the object. A new period of stable holding commenced after the fiddling procedure. A third auditory cue that appeared ~3 s later prompted the subject to replace the object on the tabletop and release it.

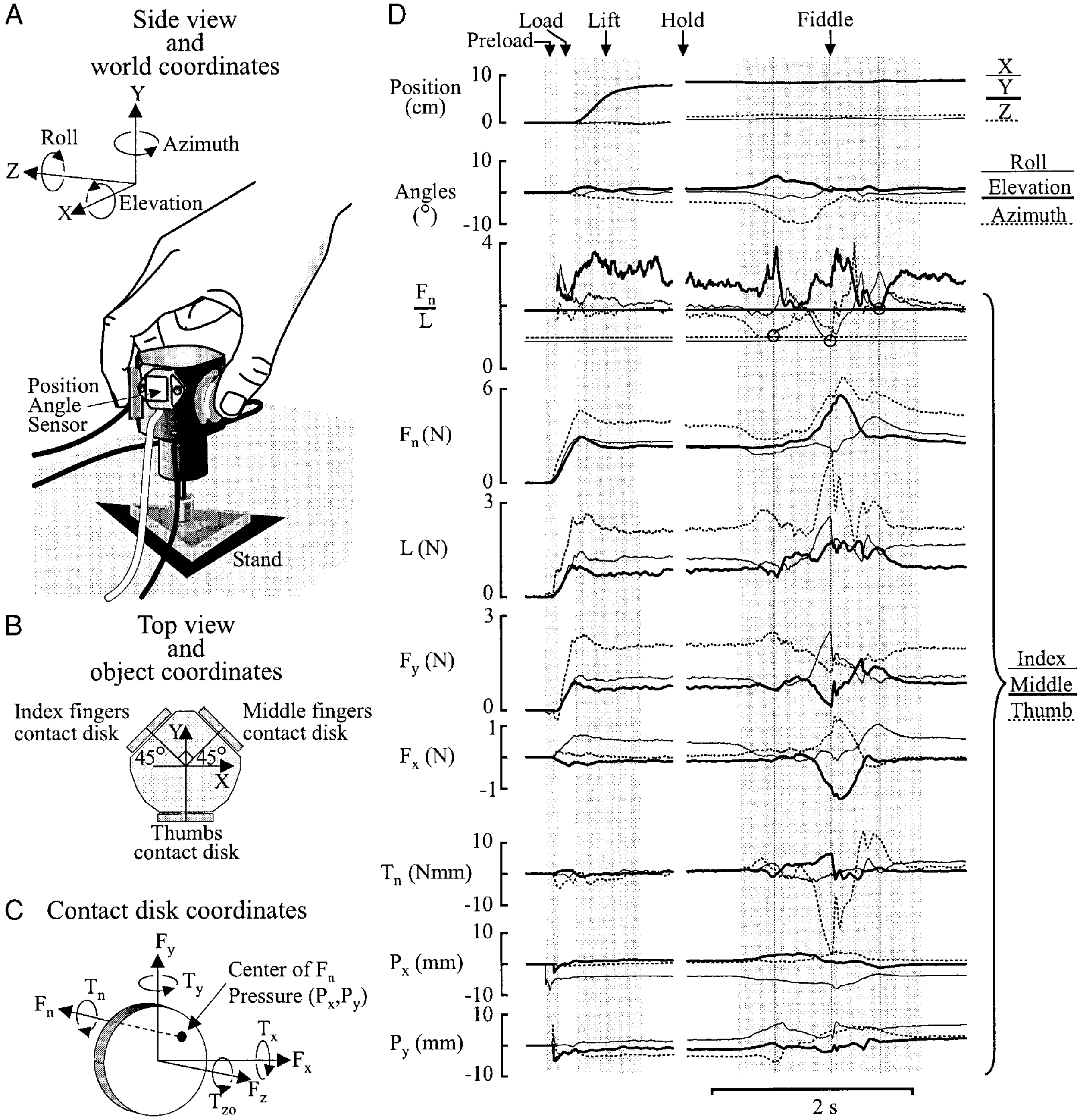

FIG. 1. Apparatus and task. *A*: side view of the instrumented test object. A 6-axis position-angle sensor measured the position and orientation of the object in world coordinates. *B*: orientation of the 3 contact disks in the horizontal plane of the object. *C*: contact disk coordinates and measured forces and torques from which F_n, T_n, and the center of F_n pressure were derived. *D*: kinematic and kinetic records as a function of time from a single trial performed with rayon at the middle finger and sandpaper at the other digits (L denotes the overall fingertip load in linear force equivalents as described in METHODS, F_n:L ratio is the ratio between the normal force and load, and P_x and P_y give the position of the center of F_n pressure in contact disk coordinates). Gray bars delineate the trial into different phases. Subjects were instructed to grasp and lift the object, hold it level, perform a "fiddling procedure," hold the object level again before replacing it (not shown). During the fiddling procedure, subjects slid each digit across the contact surface. Vertical dashed lines mark the times when each digit slid (1, thumb; 2, index finger; 3, middle finger). These times coincide with minima in the F_n:L ratios (circles) which, in turn, correspond to the inverse of the coefficients of linear friction because the tangential torques (T_n) at the slipping digit is close to zero. Note the interrupted time scale.

Data analysis and statistical procedures

A flexible data acquisition and analysis system (SC/ZOOM, Department of Physiology, Umeå University) was used to sample signals from the force-torque sensors (400 samples/s; 12-bit resolution) and the position-angle sensor (120 samples/s; 14-bit resolution). The sampling program transferred the origin of the forces and torques from the surface of the transducers to the contact surfaces (Fig. 1*C*). The force tangential to the contact surface (F_t) was computed as the vector sum of the two tangential force components, and the force normal to the contact surface (F_n) was defined simply as $-F_z$. The position of a digit at its contact surface (P_x and P_y) was defined as the equivalent point of normal force pressure calculated from the torques about the *x*- and *y*-axes of the contact disks (T_x and T_y) and F_z as described in Kinoshita et al. (1997).

If the positions of the digits deviated from the *z*-axis intersecting the centers of the contact surfaces, the measured torque (T_{zo}) could have differed from the true tangential torques at the fingertips. That is, off-axis torques caused by forces tangential to the contact surface could have contributed to the measured torque. To determine the true tangential torque, we subtracted the off-axis torques as follows: $T_z = T_{zo} - F_y \cdot P_x + F_x \cdot P_y$. We then defined the true torque about the normal force vector as $T_n = -T_z$. The arrows representing torques in Fig. 1*C* indicate positive directions of torque measurements at each contact disk.

Kinoshita et al. (1997) have recently shown that the minimum normal force, or slip force (F_s), required by a human fingertip to prevent any slip, linear or rotational, in the face of a tangential force (F_t) and tangential torque (T_n) can be estimated by the following equation

$$F_s = \frac{F_t + a|T_n| + bF_t|T_n|}{\mu_{lin}} = \frac{L}{\mu_{lin}} \quad (1)$$

where μ_{lin} is the coefficient of linear friction, $a = 0.133\ \mathrm{mm}^{-1}$ and $b = -0.011\ (\mathrm{Nmm})^{-1}$. We used the variable L to represent a generalized load that was defined by the nominator in *Eq. 1*. The variable L thus represents the overall destabilizing tangential load expressed in linear force equivalents. Notably, to prevent slips between a digit and its contact surface, the ratio between normal force and load (F_n:L ratio) coordinated by the subject has to be greater than a minimum ratio determined by the slip force (i.e., the F_s:L ratio), termed the slip ratio. This critical normal-force-to-load ratio coincides with the inverse of the coefficient of linear friction (${\mu_{lin}}^{-1}$). We measured the coefficient of linear friction, μ_{lin}, as the inverse of the slip ratio observed during the fiddling period as previously described in Flanagan et al. (1999). This minimum coincided with the moment at which the digit began to slip. For each of the 35 subject ($n = 7$) and surface combinations ($n = 5$), an average coefficient of friction was estimated for each digit based on the slip measurements obtained in single trials. As expected, the estimated μ_{lin} was significantly lower when the digits contacted rayon than when did they contacted sandpaper (0.66 ± 0.13 and 1.01 ± 0.14, respectively; mean ± SD). The ratio between the μ_{lin} measurements for rayon and sandpaper was on average 1.6 and ranged between 1.2 and 2.8 across subjects and digits.

We defined the phases of the lifting trial as in Flanagan et al. (1999). Accordingly, we defined the *preload* phase as the period between the moment the leading digit contacted the object and the onset of the *load phase*. The latter began when the first time derivative of the total vertical force generated by the three digits last exceeded 0.5 Ns^{-1} before reaching its maximum value, i.e., when the vertical force began to increase steadily. The time at which the total vertical force reached the mean total vertical force employed during the hold phase was the end of the load phase and closely matched the time of lift-off. Force, torque, position, and angle measurements determined for the hold phase were computed as averages of the values recorded during the last 0.5 s before the delivery of the auditory cue that prompted the subjects to perform the fiddling procedure. As a measure of the safety margin against slips during the hold phase, we used the relative safety margin defined as $\mathrm{SM} = (F_n - F_s)/F_n$.

We used linear regression and correlation analysis to examine relations among variables and repeated measures ANOVA to assess effects of surface combination and digit (unless otherwise indicated in the text). We considered a P value of 0.05 statistically significant. Values reported in the text for data pooled across trials refer to means ± SD based on one mean value obtained for each digit and each series of lifting trials (unless otherwise indicated in the text). We ignored the first trial in each of the series in the analysis because initial adjustments to new frictional conditions were not the focus of the study (cf. Birznieks et al. 1998; Edin et al. 1992). Furthermore, we focused on the hold phase before the fiddling procedure. In this phase the grasp conditions represented those initially chosen by the subjects, whereas the second hold phase occurred after the fiddling procedure during which the grasp was reorganized. Likewise, we did not consider the replacement and release of the object in this study.

RESULTS

We first provided a general description of the subjects' behavior during the three-digit lifting task based on data pooled across the various combinations of materials at the contact surfaces. We then analyzed the influence of changes in frictional conditions at the digit-object interfaces. We focused on how subjects control the fingertip forces to obtain grasp stability. We specifically asked to which extent, and how, the ratio between the normal force and the overall load (F_n:L ratio) at each fingertip was adapted to the local frictional condition assessed as the minimum ratio required to prevent slip, i.e., the slip ratio.

General performance

The subjects' behavior corresponded to that described for the "standard" grip in our previous study of the three-digit lifting task (Flanagan et al. 1999). Figure 1*D* shows a single trial that illustrates the task and its phases. In this trial, one digit (middle finger) contacted the slippery material rayon, and the cooperating digits (thumb and index finger) contacted sandpaper.

PRELOAD AND LOAD PHASES. After contacting the object, all subjects exhibited a *preload phase* during which they applied normal forces (F_n) before they reliably applied vertical "lifting" forces (F_y). During this phase, the digits were also subjected to some tangential load (Fig. 1*D*) reflecting small vertical forces, forces tangential to the contact surfaces in the horizontal direction (F_x), and/or small tangential torques (T_n).

During the subsequent *load phase*, the normal force increased in parallel with the vertical force and the load at each contact surface (Figs. 2, *A–D*). This type of "parallel" coordination has previously been demonstrated for grasps involving two digits (Johansson and Westling 1984a) and three digits (Flanagan et al. 1999). The median coefficient of correlation between the normal force and vertical force in single trials was 0.94 ($Q_1 = 0.85$ and $Q_3 = 0.98$; data pooled across digits and surface combinations). The correlation coefficient relating normal force and overall load (L) was slightly higher (0.97, $Q_1 = 0.93$ and $Q_3 = 0.99$) than that between normal force and vertical force ($P < 0.001$; Wilcoxon signed ranks test). Furthermore, changes in normal force (F_n), vertical tangential force (F_y), and load (L) were well synchronized among the digits (Fig. 2, *E* and *F; F_y* not shown). The correlation between the normal forces at the three contact surfaces were 0.99 ($Q_1 = 0.98$ and $Q_3 = 1.00$), 0.99 ($Q_1 = 0.99$ and $Q_3 = 1.00$) and 0.99 ($Q_1 = 0.99$ and $Q_3 = 1.00$) for the three possible combinations, i.e., thumb versus index finger, thumb versus middle finger, and index versus middle finger. The corresponding correlation values for the vertical forces at the three contact surfaces were 0.91 ($Q_1 = 0.84$ and $Q_3 = 0.96$), 0.92 ($Q_1 = 0.86$ and $Q_3 = 0.96$), and 0.92 ($Q_1 = 0.89$ and $Q_3 = 0.96$) and for the loads at the three contact surfaces were 0.92 ($Q_1 = 0.81$ and $Q_3 =$

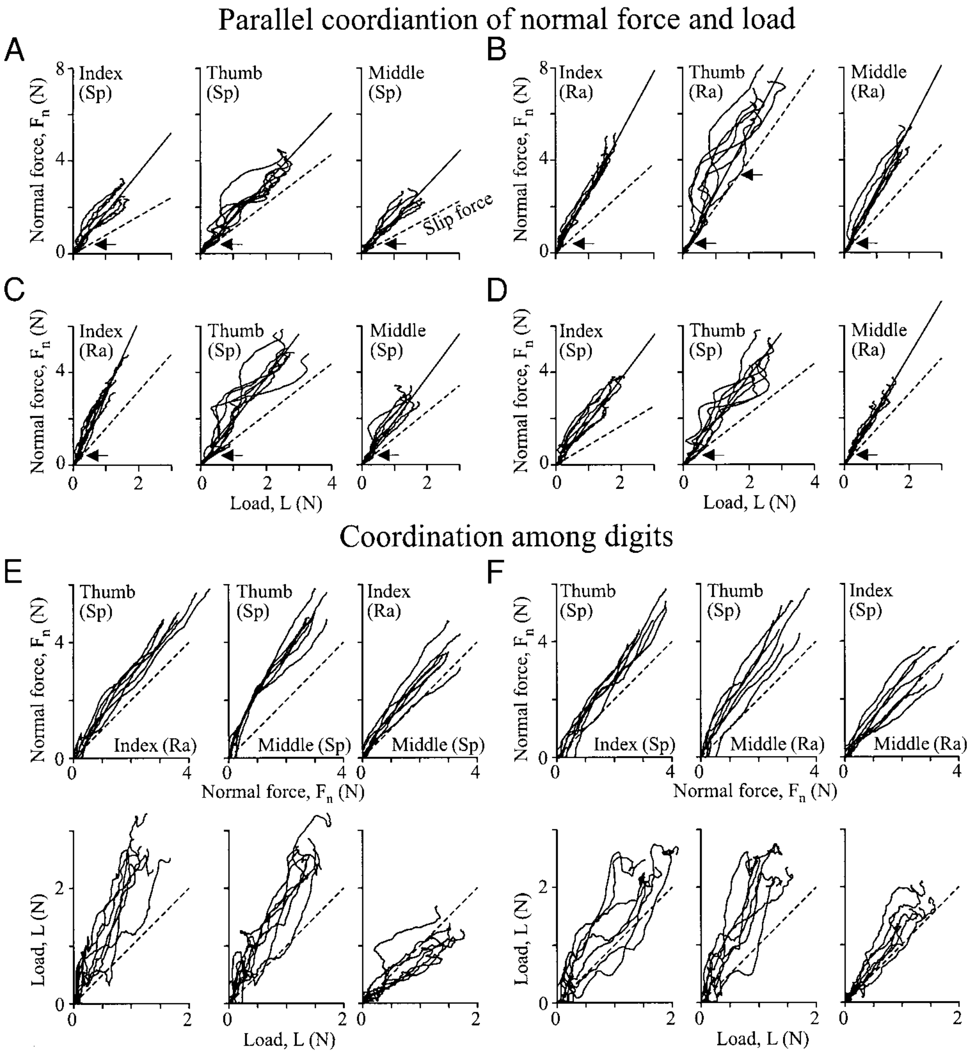

FIG. 2. Coordination of fingertip actions during the load phase represented by single trial data from a single subject (*AWA*). *A–D*: relationship between the normal force (F_n) and the load (L) applied by each single digit. Dashed line indicates the estimated minimum normal force required to prevent slips (slip force), and the solid line provides an average of the slopes coordinated by the subject as determined by eye. Note that at low loads and normal forces, the normal force was often very close to the slip force (arrows). This suggests that slips easily occurred during this period of the load phase. *E–F*: coordination of fingertip forces among digits. *Top panels*: coordination between normal forces (F_n) applied at the 3 contact disks. *Bottom panels*: coordination between loads (L). The *left, middle,* and *right columns* show the coordination between the thumb and the index finger, the thumb, and middle finger, and the index and the middle finger, respectively. Dashed line indicates equal F_n or L at both digits. In *A* and *B* all digits contacted sandpaper and rayon, respectively. In the other graphs one of the fingers alone contacted rayon: in *C* and *E* the index finger and in *D* and *F* the middle finger.

0.97), 0.94 ($Q_1 = 0.88$ and $Q_3 = 0.97$), and 0.96 ($Q_1 = 0.90$ and $Q_3 = 0.98$).

HOLD PHASE. During this phase, as well as in the preceding load and lift phases, the thumb applied stronger vertical and normal forces than the cooperating fingers, which applied about equal amounts of force (Fig. 1*D;* also see Figs. 5). This overall distribution of force was expected based on the geometric relationship between the contact surfaces of the object and its mass distribution (for details see Flanagan et al. 1999). Indeed, these object properties would fully determine the distribution of normal and vertical forces among the digits if subjects applied the forces at the centers of the contact surfaces, applied no horizontal force or torque tangential to the disks, and held the object level. Thus deviations from this nominal force distribution could depend on the positions of the digits, application of tangential horizontal forces and torques, and on object tilt.

As found in previous studies, subjects typically applied forces to the contact surfaces that were slightly off-center (see standard grip in Flanagan et al. 1999). First, in the horizontal plane of the object, the positions of the fingers were shifted away from the thumb and the position of the thumb was closer to the index than the middle finger. Because of the positions of the digits in the horizontal plane, the thumb would be expected to apply greater normal and vertical forces than predicted by centered digit positions, and greater forces would be expected at the middle finger than at the index finger. This was indeed the case (see Figs. 4*B* and 5). Second, the digits also applied force at different vertical positions on the contact surfaces. On average, the thumb applied force 1.3 mm below the index finger but 0.6 mm above the middle finger. To prevent the object from spinning due to application of normal forces at different heights, subjects needed to alter the vertical tangential forces applied by the digits to counterbalance the moment produced by the normal forces. Thus the observed vertical digit positions would also have fostered a difference between the vertical forces applied by the middle and index fingers.

Subjects typically held the object close to level during the hold phase. In 75% of the trials, the elevation and roll angles were <1.6 and 3.4° (absolute values). The mean roll angle, $2.7 \pm 1.3°$, was significantly different from zero, but the elevation angle ($0.3 \pm 1.4°$) was not. The positive roll angle implies that, on average, subjects tilted the object slightly toward the middle finger during the hold phase (see Fig. 1*A*).

The distribution of loads (L) among the digits resembled that of the vertical tangential force because the contribution by torques (T_n) and, in particular, horizontal forces (F_x) tangential to the contact surfaces were comparatively small (see Fig. 5).

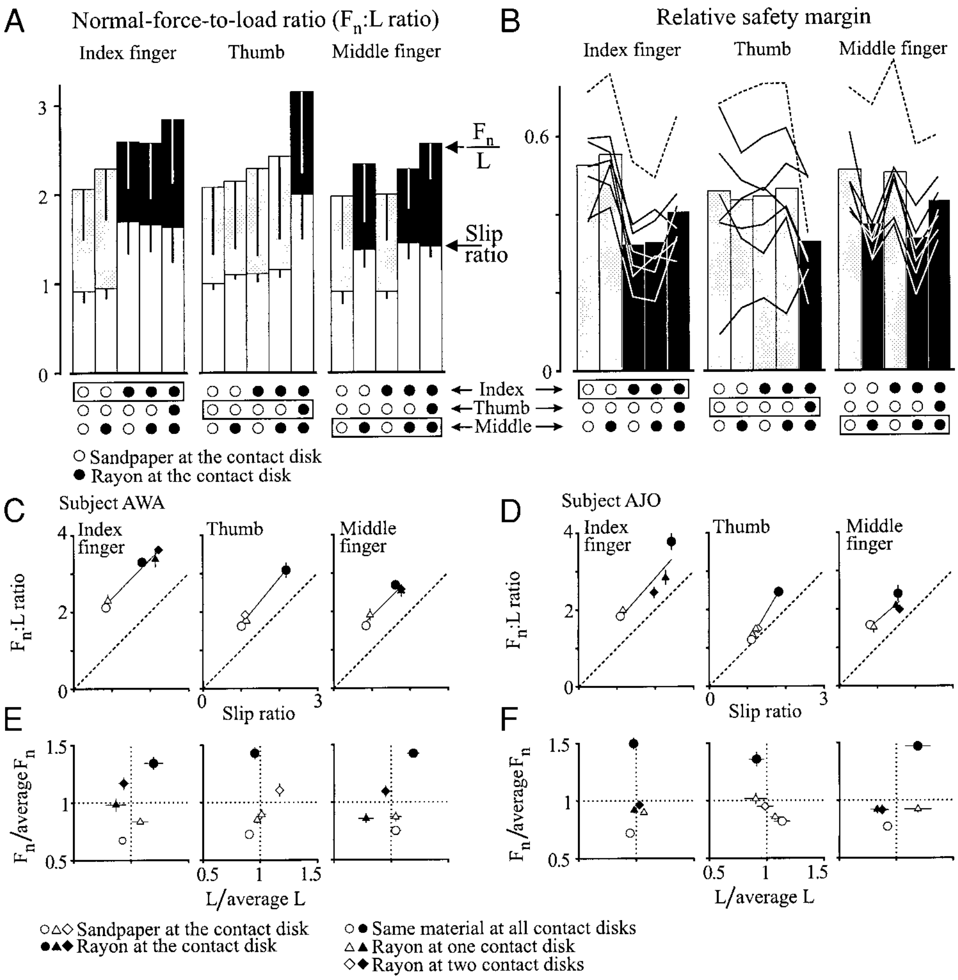

FIG. 3. Coordination of normal force and load for each digit and surface combination during the hold phase. *A*: ratio between normal force and load (F_n:*L* ratio) and the corresponding slip ratio. Filled columns represent the employed F_n:*L* ratio, and the superimposed open columns represent the slip ratio. *B*: columns represent the average safety margin against slips as a fraction of the employed normal force, data pooled across subjects, and the lines represent single subject data. *A–B*: averages based on subject means and vertical lines unilaterally represent standard deviations. Gray and black columns represent data obtained when the digit contacted sandpaper and rayon, respectively. *C–D*: employed F_n:*L* ratio plotted against the estimated slip ratio. Solid lines give the linear regression lines (based on single trial data), and dashed lines indicate the minimum F_n:*L* ratio required to prevent slip (F_n:*L* ratio = slip ratio). *E–F*: relative change in normal force and load with changes in surface combination for the individual digits. For each surface combination the applied normal force or load was divided by the average of the 5 surface combinations. *C–F*: symbols represent mean values for each of the 5 surface combinations, and vertical and horizontal error bars give standard errors. Open and filled symbols represent data obtained when the digit contacted sandpaper and rayon, respectively, and symbol shape denotes surface materials contacted by the cooperating digits. Data shown for 2 individual subjects.

The total tangential force (F_t) was only 4% larger than the vertical tangential force (F_y). However, the estimated total load (*L*) was on average 20% greater than the tangential force because of the tangential torque contribution. The generation of such tangential torques increases the normal force requirements for grasp stability (Kinoshita et al. 1997), but in the present three-digit task torques can also influence the distribution of vertical force among the digits.

Effects of changing surface structures

Previous work on precision grip control has shown that subjects adjust the balance between normal forces and tangential loads to the frictional conditions of the grasp in a manner that supports grasp stability (for references see INTRODUCTION). In our multidigit task, the friction between the digits and the object did indeed influence the coordination of normal forces and tangential loads from the load phase and onwards. During the load phase the surface combination influenced the slope of the relationship between normal force and load at the individual digits, whereas the parallel change in normal force and load remained regardless of surface combination (Fig. 2, *A–D*). For all five surface combinations, the median correlation between normal force and load were between 0.97 and 0.98 (data pooled across subjects and digits). Consistent with this result, the surface combination influenced the coordination of normal forces and load at the level of individual digits during the lift and hold phases. To further examine this coordination, we focused on subjects' behavior during the hold phase.

RATIO BETWEEN NORMAL FORCE AND LOAD (F_N:*L*) DURING THE HOLD PHASE. As a measure of coordination of normal force and load we calculated the ratio between normal force and load (F_n:*L* ratio) at each digit and compared this "employed" ratio to the minimum F_n:*L* ratio required to prevent slips, linear or rotational. This minimum ratio, termed the slip ratio, represents the inverse of the coefficient of linear friction at the digit-object interface (see METHODS). On average, subjects adapted the F_n:*L* ratio at each digit to the local friction (Fig. 3*A*). The thumb and the index and middle fingers employed significantly higher ratios when they contacted the slippery rayon than when they contacted sandpaper [$F_{(1,6)} = 31.43$; $P < 0.01$, $F_{(1,6)} = 7.28$; $P < 0.05$ and, $F_{(1,6)} = 13.92$; $P < 0.01$, respectively]. The slip ratios at the cooperating digits had small effects on the employed ratio in comparison to the effect of the local slip ratio (Fig. 3*A*). Subjects applied significantly higher ratios at the thumb when it contacted sandpaper and both cooperating fingers contacted rayon than when all digits contacted sandpaper [$F_{(1,6)} = 6.38$; $P < 0.05$]. The index finger applied a slight higher ratio when it contacted sandpaper and the middle finger contacted the slippery material rayon [$F_{(1,6)} = 27.93$; $P < 0.01$] and the middle finger a slightly higher ratio when all digits contacted rayon than when one of the cooperating digits or both contacted sandpaper [$F_{(1,6)} = 9.19$; $P < 0.05$]. Figure

3, *C* and *D*, shows the regulation of employed ratios to local friction for individual subjects (and digits) by plotting the relationship between the slip ratio and the employed F_n:L ratio. The two subjects chosen for illustration showed large frictional differences between the two types of surface materials and therefore a correspondingly strong adjustment of the ratios.

Safety margin against accidental slips during the hold phase. The vertical distance between a data point and the dashed line in Fig. 3, *C* and *D,* represents a measure of the safety margin against slips, i.e., the difference between the employed F_n:L ratio and the slip ratio (see also the filled part of the columns in Fig. 3*A*). This difference, if expressed as a fraction of the employed ratio, coincides with the fraction of the applied normal force that subjects use as a safety margin against slips, i.e., the relative safety margin (Fig. 3*B*). The relative safety margin did not differ among digits, but there was a significant interaction between digit and surface combination [$F_{(8,48)} = 13.73$; $P < 0.001$]. When a digit contacted the slippery rayon, the safety margin was smaller than when the same digit contacted the sandpaper surface. Thus in relative terms subjects did not fully compensate for the increase in the slip ratio by a proportional change in the employed ratio. With the index and middle fingers, the safety margin tended to decease when one finger or both contacted rayon. This was also true if the safety margin was measured as the extra normal force applied to avoid slippage (see Fig. 4*A*). Finally, Fig. 3*B* shows that the safety margins varied between subjects; the dashed lines represent the subject with the highest overall safety margin.

Subjects could have accomplished the adjustment of the F_n:L ratio to the surface combination by changing the magnitudes and the distribution across fingers of either normal forces or loads or both variables. In the remaining part of RESULTS, we examine how subjects accomplished these adjustments based on data obtained during the hold phase.

FRICTIONAL EFFECTS ON NORMAL FORCES AND DIGIT LOADS. In this section we first describe and provide statistical analysis based on all subjects behavior and then describe the results for a representative subject in some detail. The combination of surface materials at the contact disks influenced the magnitudes of the normal forces [$F_{(4,24)} = 19.29$; $P < 0.001$; main effect]. For all three digits, the normal force tended to increase as the number of digits contacting rayon increased (Fig. 4*A*). Subjects applied more normal force when one of the digits, index or middle finger, contacted rayon than when all digits contacted sandpaper [$F_{(1,6)} = 6.28$; $P < 0.05$], but they applied even more normal force when both fingers contacted rayon [$F_{(1,6)} = 6.94$; $P < 0.05$]. Likewise, subjects applied more normal force when all digits contacted rayon then when the thumb contacted sandpaper [$F_{(1,6)} = 25.03$; $P < 0.01$). Thus subjects scaled the normal forces to the frictional condition by essentially changing the forces in parallel. The common scaling of normal forces to changes in the frictional conditions is demonstrated by the fact that the proportional distribution of the normal force is relatively constant across the surface conditions (Fig. 4*B*). There was, however, a small but significant interaction between digit and surface combination [$F_{(8,48)} = 8.76$; $P < 0.001$], indicating that the surface combination did influence the distribution of normal force to some extent.

Furthermore, regardless of surface combination, the forces

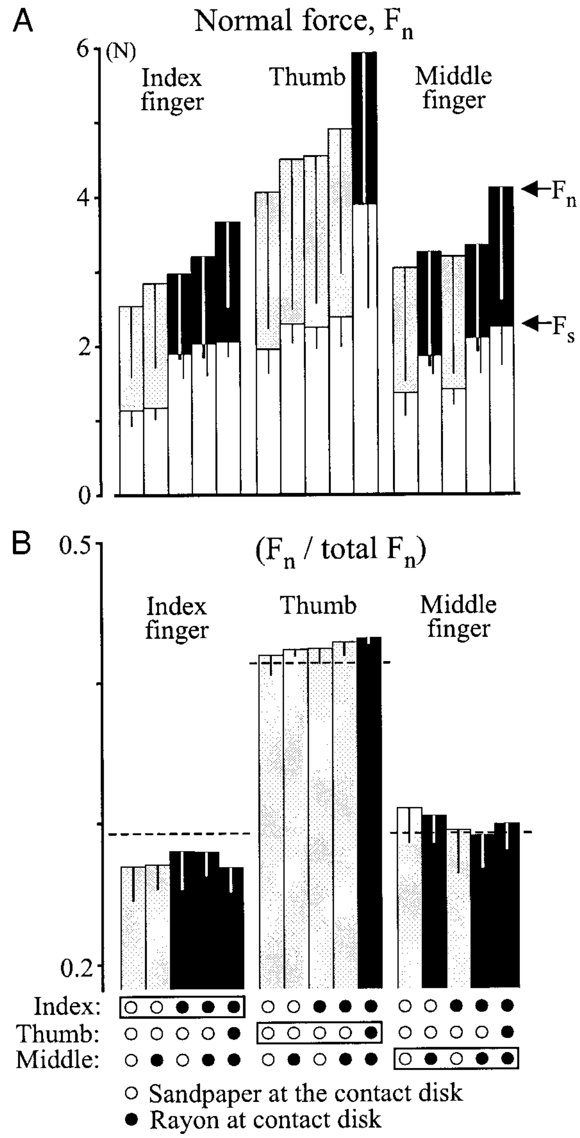

FIG. 4. Normal forces applied by the 3 digits during the hold phase shown for each surface combination. *A*: full columns represents the employed normal force and the superimposed hollow columns represents the slip force. *B*: fractional contribution by each digit to the total normal force. Dashed horizontal lines show the expected distribution of normal forces if subjects would have *1*) applied the forces at the centers of the contact disks, *2*) held the object level, and *3*) applied no horizontal tangential forces. *A–B*: averages based on subject means. Vertical lines represent standard deviations. Gray and black columns represent data obtained when the digit contacted sandpaper and rayon, respectively.

in the horizontal plane of the object were primarily normal forces. The arctangents of the ratios of normal force to horizontal tangential force were, on average, 87.3 ± 3.9, 86.2 ± 5.7, and 90.9 ± 5.4° for the thumb, index finger, and middle finger, respectively; data pooled across surface conditions. These were not significantly different from 90° ($P > 0.2$ in all 3 cases). Thus in agreement with our previous observations, subjects tended to avoid producing tangential force horizontal to the contact surfaces and, as a result, the force vectors in the horizontal plane intersected near the center of the object (Flanagan et al. 1999).

The surface combination did not influence the sum of tangential load over the digits, but did influence the distribution of

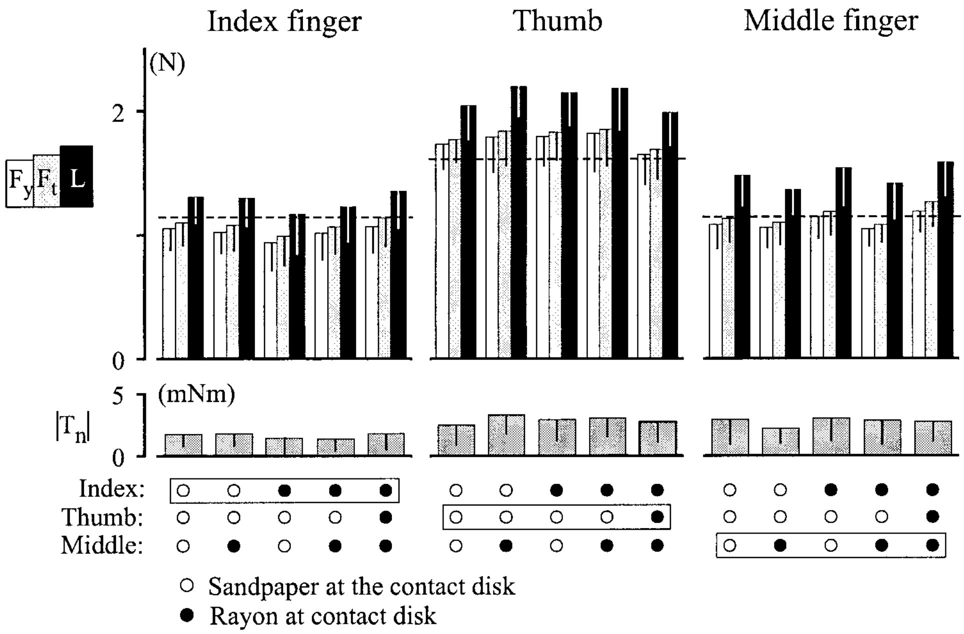

FIG. 5. Loads at the digits during the hold phase. *Top panels*: vertical force (F_y), total tangential force (F_t), and total tangential load (L) at the 3 digit-object interfaces for each surface combination, and *bottom panels* show the absolute value of the tangential torque ($|T_n|$). Values represent averages based on subject means, and the vertical error bars represent SD. The difference between F_y (open) and F_t (gray) indicates the contribution of forces tangential to the contact surfaces in the horizontal plane of the object (F_x). The difference between F_t (gray) and L (black) represents the contribution of tangential torque (T_n) to the total load. Dashed horizontal lines indicate vertical forces expected at each digit if subjects would have *1*) applied the forces at the centers of the contact disks, *2*) applied no torque tangential to the disks, *3*) held the object level, and *4*) applied no horizontal tangential forces.

loads among the digits [$F_{(8,48)} = 3.08$; $P < 0.01$; Fig. 5]. Subjects unloaded the finger or fingers that contacted the slippery rayon [$F_{(1,6)} = 8.66$; $P < 0.05$] and increased the load of the thumb [$F_{(1,6)} = 8.49$; $P < 0.05$] when the digits contacted different surface materials.

Taken together, these observations suggest that subjects primarily changed the magnitude of normal forces and the distribution of loads among the digits to adjust the F_n:L ratios to the local frictional conditions. We illustrate this for a single subject (same subject as in Figs. 2 and 3, *C* and *E*). Symbols in Fig. 6 show, for individual trials, the F_n:L ratio (*top panel*), the normal force (*middle panel*), and the load and vertical force (*bottom panel*). Although there was substantial variability in F_n:L ratios between trials, the mean ratio at each digit clearly reflected the frictional condition at the digit as represented by the slip ratio (dashed horizontal lines in *top panels*). On average, the largest normal forces were observed when all digits contacted rayon, and the smallest were observed when they all contacted sandpaper. For the other three surface combinations, the normal forces were on average greater when both fingers contacted rayon than when only one contacted rayon. As for the load, a finger was loaded less when it contacted rayon compared with when it contacted sandpaper or when all digits contacted the same surface material. When the thumb contacted sandpaper, its load tended to increase as the number of cooperating digits contacting rayon increased (from 0 to 2), but when all digits contacted the same material its load was similar whether the material was sandpaper or rayon. It is obvious that this subject accomplished the adaptation of the F_n:L ratio to the local frictional condition in different manners for the different digits. For instance, the change of the ratio at the middle finger when it alone contacted rayon and the index finger contacted sandpaper compared with the reverse surface contact pattern was essentially accounted for by an unloading of the middle finger. In contrast, a combined effect of unloading and an increase in the normal force accounted for the corresponding adaptation of the index finger. Figure 3*E* summarizes the interactions between normal force and load that contributed to adjust the F_n:L ratio to changes in surface combination in this subject, whereas Fig. 3*F* illustrates corresponding data from another subject. The graphs show relative changes in load against relative changes in normal force at the separate digits (means for each digit data normalized to the mean values across all surface combinations). It is obvious that changes occurred in both normal force and load in response to changes in surface combination and that the pattern of changes differed across the subjects (cf. Fig. 3, *E* and *F*). Indeed, we observed more or less different patterns of changes in normal forces and loads for all seven subjects.

Changes in load distribution. Subjects could have used several strategies to change the distribution of loads among the digits with changes in the frictional conditions of the grasp. They could have redistributed vertical force among the digits and/or changed the size and distribution of tangential torques. (The tangential forces in the horizontal plane of the object were negligible in this context.) A change in the distribution of vertical forces would have altered the orientation of the object unless counterbalanced by changes in the contact positions of the digits or by application of tangential torques or both. Indeed, the surface combination influenced the elevation angle [$F_{(4,24)} = 2.88$; $P < 0.05$; surface combination as repeated measure] but not the roll angle. Subjects tilted the object slightly toward the fingers when the index finger, middle finger, or both fingers contacted rayon, but not when all digits contacted the same surface material. This tilt would have contributed to a decrease in vertical force (and hence load) at the fingers; however, changes in object orientation would not have influenced the load distribution between the two fingers.

The digits contact positions had prominent effects on the distribution of vertical force. Across subjects and surface combinations, the locations of the digits explained 89% of the variability in the vertical force at the thumb and 64 and 55% for the index and middle fingers, respectively (based on adjusted R^2 values). To demonstrate this, we used a multiple linear regression model with F_y as the dependent variable and the location of the center of normal force pressure (P_x and P_y) as

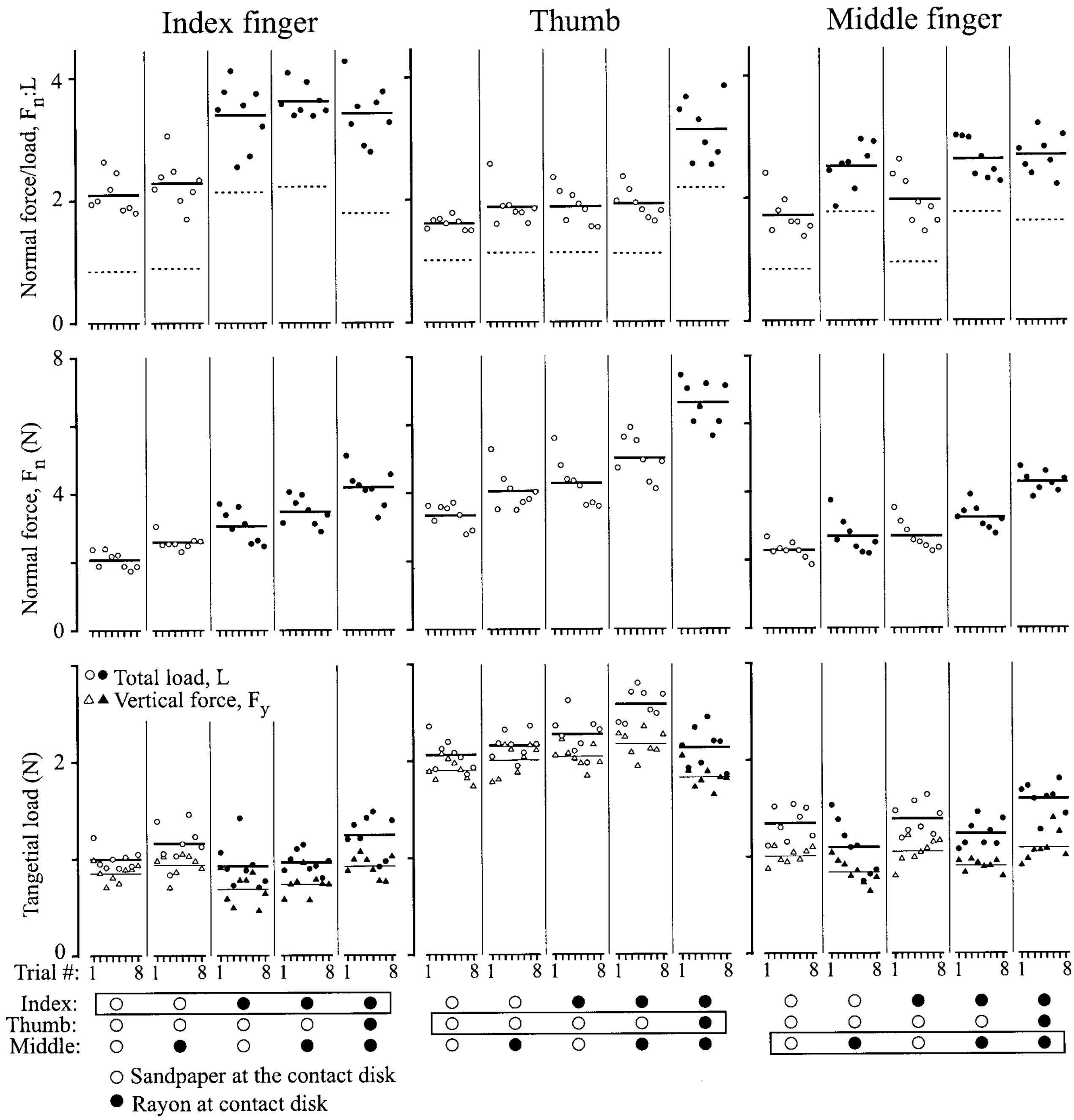

FIG. 6. Ratio between normal force and load (F_n:L ratio; *top panels*) for each of the 3 digits together with normal force (F_n; *middle panels*), total load (L; *bottom panels*) and vertical force (F_y; *bottom panels*). Data shown for consecutive trials from one subject carried out during each of the 5 surface combinations, indicated by the key at *bottom*. ○ and ●, data obtained when the digit contacted sandpaper and rayon, respectively. Horizontal solid lines give the mean values during each lift series, and dashed lines in the ratio plots gives the estimated slip ratio. Triangles in the *bottom panel* show the vertical force for individual trials, and the thin solid horizontal line gives the mean vertical force.

independent variables (regression based on single trial data pooled across surface combinations). We obtained similar results at the level of individual subjects. Figure 7 exemplifies, for three subjects, the strong impact of the vertical location of the digits on their vertical forces. Despite this strong effect of contact position on the distribution of vertical force, the surface combinations influenced neither the horizontal nor the vertical positions reliably across subjects [$F_{(4,24)} = 1.15$; $P = 0.36$ and $F_{(4,24)} = 1.05$; $P = 0.40$]. We therefore conclude that the subjects did not control digit positions in a systematic manner to adjust the F_n:L ratios to the prevailing frictional conditions.

Changes in torques tangential to the contact surfaces may have influenced the load distribution even though the relative contribution of the torque to the load was small compared with that of the vertical force. The surface combination, however, did not influence the magnitude of the torque at any digit in a systematic manner [$F_{(4,24)} = 0.81$; $P = 0.53$; Fig. 5]. Rather, the tangential torques at the three contact surfaces varied across

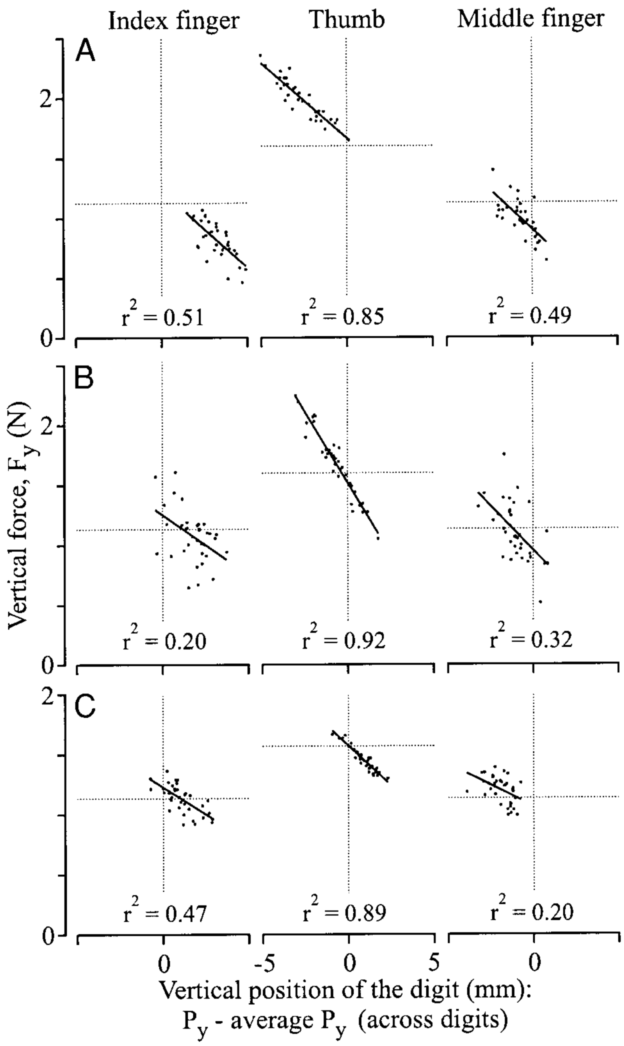

FIG. 7. Influence of vertical digit position on vertical force where digit position is represented by the location of the center of normal force pressure. Vertical force plotted against the relative vertical position of the digit (digit P_y − average P_y across all digits). Single trial data shown for 3 separate subjects (*A–C*); data pooled across surface combinations. Solid lines give the linear regression line for the data points. Dotted horizontal lines show the vertical tangential forces for each digit that would be expected if the subject *1*) applied the forces at the centers of the contact disks, *2*) applied no torque tangential to the disks, and *3*) held the object level.

subjects in both magnitude and direction, and they could vary among trials within the separate lift series.

Despite the absence of a systematic effect of surface combination across subjects on tangential torques and digit positions, these factors must have influenced digit loads and thereby the F_n:L ratios at the individual digits. Therefore there are good reasons to believe that the importance of each of these factors varied across subjects and perhaps across trails. If so, they would explain the variation in vertical forces as well as in load on a single trial basis. We demonstrated this by linear regression for each digit using single trial data (n = 244) pooled across all subjects. We used, as independent variables, the torque at the three digits (3 variables) and the positions of the digits on the contact surfaces (6 variables). On the basis of adjusted R^2 values, we found that these variables explained 91, 87, and 84% of the variance in vertical force for the thumb, index finger, and the middle finger, respectively. The corresponding values for the loads were 92, 89, and 91%. Interactions among these independent variables and mechanical influences on the test object by the cables of the transducers may have accounted for the unexplained variance, as well as object tilt. If the elevation and roll angles of the object were included as independent variables, the linear model explained 93, 93, and 91% of the variance in vertical force for these three digits, respectively, and 94, 93, and 92% of the variance in load.

DISCUSSION

In the present thee-digit manipulatory task, subjects either lifted an object with the same surface material at all three contact disks, one slippery and one less slippery material, or with a different material at one of the three contact surfaces. First, when the digits contacted the same surface material, subjects adjusted the fingertip forces at all digits such that the ratio between the normal force and load (F_n:L ratio) was similar across digits and adapted by an adequate safety margin to the minimum ratio at which slips would have occurred. This control policy, which supports grasp stability, was originally demonstrated for precision grip tasks engaging two digits (Johansson and Westling 1984b; also see Cadoret and Smith 1996; Flanagan and Wing 1997b; Flanagan et al. 1995; Forssberg et al. 1995; Kinoshita and Francis 1996; Smith et al. 1997). Second, with different materials at the three contact surfaces, subjects adapted the F_n:L ratios at the separate digits to the local frictional conditions. Again, this behavior has previously been demonstrated in two-digit manipulatory tasks carried out by digits belonging to one hand, two hands, or to two subjects (Birznieks et al. 1998; Burstedt et al. 1997a,b; Edin et al. 1992). Thus the present findings strongly suggest the control for grasp stability by adjustments of the F_n:L ratios at individual digits to the local frictional condition is a general control policy that supports grasp stability in manipulation. As previously demonstrated for two digit grasps, subjects principally adjusted the F_n:L ratios by collectively scaling the normal forces to the "average" slip ratio across the grasp sites and by partitioning the load among the digits. However, it must be stressed that adjustments of the F_n:L ratios at all digits engaged is overruled in many manipulatory tasks by mechanical constraints imposed by the task, the object, and the grasp configuration. For instance, when subjects rotate an object held between the thumb and the index finger by pronation and supination movements, the F_n:L ratio is regulated to the slip ratio with an adequate safety margin at only one of the digits, whereas the ratio of the opposing digit that will support the object from underneath may be very high (Johansson et al. 1999).

In the present study and our previous study dealing with three-digit manipulation (Flanagan et al. 1999), we observed that subjects change the normal forces in parallel with changes in tangential loads during the load phase. Likewise, for a number of two-fingered manipulative tasks, in which the load was primarily tangential force, it has been demonstrated that the normal force is controlled to increase and decrease in parallel with changes in tangential load (for reviews see Johansson 1996; Wing 1996). More recently, we have demonstrated that this type of coordinative constraint also applies when the load is composed of combinations of tangential force and tangential torque (Goodwin et al. 1998; Johansson et al.

1999; Kinoshita et al. 1997). Because this coordinative constraint appears to be expressed in all types of manipulatory tasks requiring grasp stability, it seems to represent a general rule in dexterous manipulation. Given that the F_n:L ratios at the relevant digits are adjusted to local frictional conditions, this coordinative constraint effectively supports grasp stability in skilled manipulation by ensuring that the normal force is above the minimum required to prevent slip at any tangential load.

Coordination of forces among digits

The distribution of normal and vertical forces among digits strongly reflected constraints imposed by the task (i.e., to grip the object at the contact disks and lift it vertically) and by certain properties of the test object (the geometric relationship between the object's center of mass and the contact surfaces) (Flanagan et al. 1999). The adjustments of the F_n:L ratios to the changes in the frictional conditions took place on top of this distribution and involved changes in the magnitude of normal forces as well as redistributions of load among the digits.

Previous work on precision grip control suggests that the controller attempts to reduce fingertip forces, but without compromising grasp stability. First, subjects regulate the normal forces both to tangential load (Flanagan and Wing 1993, 1997a; Johansson and Westling 1988; Westling and Johansson 1984) and to frictional aspects of the grasp (Goodwin et al. 1998; Jenmalm and Johansson 1997; Johansson and Westling 1984) in a manner that results in a reasonably small safety margin against slips over a wide parameter space, i.e., they avoid excessive normal forces. Second, in two-fingered manipulatory tasks with different friction at the two contact surfaces, when the tasks admits, subjects distribute the load between digits in a manner that decreases the normal force required to maintain grasp stability (Burstedt et al. 1997a,b; Edin et al. 1992). Because this behavior also applied to the subjects' performances in the present multidigit manipulatory task, we propose that attempts to reduce fingertip forces represent one general control role in dexterous manipulation. As one alternative, subjects could have scaled the normal forces to the friction at the most slippery contact while not changing the distribution of load among the digits. However, this would require greater normal forces also at the less slippery contact sites resulting in inflated safety margins.

CONTROL OF NORMAL FORCES. Subjects changed the magnitude of normal force with changes in the frictional conditions of the grasp, whereas the distribution of normal forces among the digits was modestly influenced. This behavior agrees with that observed in previous studies of lifting tasks involving two digits (Burstedt et al. 1997b; Edin et al. 1992). In these two-digit tasks, however, the digits were bound to apply similar normal forces, whereas in the present three-digit task, the distribution of normal force among the digits was less constrained (Flanagan et al. 1999). In fact, in our three-digit task, subjects could have chosen quite different distributions of normal force and still have been able to lift and hold the object. This occurred during the fiddling procedure in which the normal force often reached quite low values at an individual digit without the subject losing the object. Yet, during the ordinary load and hold phases, regardless of surface combination, subjects maintained a force distribution that largely reflected the position of the digits in relation to the center of mass of the object. Interestingly, we also recently observed a parallel scaling of the normal forces to the "average" friction at the engaged digits in a two-fingered restraint task in which subjects were free to apply any force combination (Birznieks et al. 1998; Burstedt et al. 1997a). Thus these findings suggest that a default control strategy in manipulation is to changes normal force in parallel at all digits engaged.

Sensory information obviously controlled the scaling of normal forces to the prevailing frictional conditions. There is evidence that signals in digital tactile afferents obtained when subjects initially grasp an object provide information about the frictional conditions at the contact surfaces (Cole and Johansson 1993; Johansson and Westling 1984b, 1987). The "global" effect on normal force by local changes in the frictional conditions implies that subjects integrate such fictional information across all digits engaged in the task. Moreover, because the combination of surface materials was constant across eight consecutive trials in the present study, anticipatory control strategies pertaining to the frictional conditions could have been used efficiently. Indeed, subjects use as a default strategy in two-digit manipulatory tasks frictional information from previous trials to scale the force output in anticipation of the frictional conditions (Birznieks et al. 1998; Burstedt et al. 1997b; Edin et al. 1992; Johansson and Westling 1984b).

DISTRIBUTION OF LOAD AMONG DIGITS. In addition to a global scaling of the normal forces, an important factor for the adjustment of F_n:L ratios in response to changes in the frictional condition were changes in the distribution of load across digits. Although the position of the digits on the contact surface strongly influenced the distribution of vertical force among the digits, subjects did not systematically vary the position of digits to adapt the force coordination to changes in the frictional conditions. Rather, the position of the digits appeared to be poorly controlled in this respect. Likewise, the surface combination did not systematically effect the tangential torques at the digit-object interfaces. Because the load component accounted for by the tangential torque was of similar magnitude regardless of surface combination (on average ~20% of total load), we can safely conclude that subjects did not rely solely on a "torque strategy" to adapt the F_n:L ratios to local frictional conditions. Changes in object orientation would also be a helpful strategy for changing the distribution of load across digits, but the results indicate that object tilt could not fully explain the observed changes in load distribution. Object tilt appears to be secondary to redistributions of vertical forces among the digits in response to local frictional changes (Burstedt et al. 1997b; Edin et al. 1992). Thus the frictional conditions of the grasp did not appear to systematically influence any of the above factors (i.e., digit position, tangential torque, and object tilt). However, the frictional conditions had a systematic effect on the load distribution, and together these factors explained nearly all of the variability in load observed across trials at the level of individual digits. These results indicate that the changes in load distribution resulted from interplay of these factors and that the nature of this interplay varied between subjects and across trials within subjects.

Compared with two-digit grasps, a multidigit grasp seems to present the sensorimotor systems with an added challenge in the sense that grasp stability can be achieved with many different combinations of fingertip forces. Indeed, Bernstein

(1967) formulated the main problem of control of voluntary movement as the elimination of redundant degrees of freedom. It is widely believed that the brain operates with task-related coordinative constraints to reduce the number of degrees of freedom of the musculoskeletal apparatus that have to be explicitly controlled (Bernstein 1967; Sporns and Edelman 1993; Turvey et al. 1978). There are several examples of coordinative constraints expressed in manipulation (for overviews see Johansson 1996, 1998; Wing 1996). In the present experiments, however, no clear strategy could be identified that could account for the robust influences by the frictional condition on the load distribution among digits. This observation reflects "motor equivalence," a term used by Lashley to denote invariant goal achievements with variable means (Lashley 1930, 1951). At one level, motor equivalence allow humans and animals to flexibly employ various effectors or combination thereof to carry out defined tasks. This type of motor equivalence certainly characterizes subjects' behavior when they lift and transport objects using a variety of unimanual and bimanual grasp configurations (Flanagan and Tresilian 1994; Flanagan et al. 1999). At another level we can observe neurally mediated compensations in individual finger and hand actions that reduce endpoint variability (Cole and Abbs 1986; Cole et al. 1984; Paulignan et al. 1991). Indeed, even at the muscular level there is no fixed activation pattern during grip actions despite behavioral invariance in terms of force generation (Maier and Hepp-Reymond 1995). In our multidigit lifting task, the variability in load redistributions associated with changes in the frictional conditions probably reflects a third level motor equivalence. This level would relate to the overall organization of the control of the task and how this control interacts with the manipulated object and the biomechanical properties of the hand. That is, the requested behavior in terms of F_n:L ratio adaptation may emerge without the necessity of explicitly controlling the positions of the digits, tangential torques or object tilt. An adaptation of the normal force to the "average" friction so as to allow "controlled" frictional slips would have been the only necessary control function required.

Birznieks et al. (1998) recently showed that subjects use controlled frictional slips to adjust the load distribution across two digits engaged in restraint of a linear load. That is, the distribution of load among the digits was determined by sliding events at one of the digit-object interfaces and which took place early during the load phase. Importantly, this strategy implies that subjects finely adjusted the normal force to allow slips only at the more slippery digit-object interface(s). To this end, the subjects scaled the normal force to the average friction at the two contact surfaces as in the present experiment. We believe that subjects employed a similar slip strategy in the present task and that both rotational and linear slips could have played a part. Small rotational and linear slips probably occurred primarily during the early part of the load phase. During the early load phase, when normal forces and loads are small, the F_n:L ratio coordinated by the subjects was relatively low and the normal forces were very close to the estimated slip forces (see arrows in Fig. 2, *A–D*). In fact, it seemed as if the slip force often limited the normal force as if sliding occurred. Furthermore, in many trials there were marked redistributions of load among the digits at these low load levels (Fig. 2, *E* and *F*). We emphasize, however, that our slip ratios, estimated using *Eq. 1* in METHODS, may be uncertain at these low force levels (see Kinoshita et al. 1997).

A load distribution resulting from the proposed slip strategy would provide an explanation to the apparent lack of robust systematic effects across subjects by the surface combination on the positioning of the digits, torques, and object tilt. That is, depending on variability in how the object was initially grasped in terms of digit positions, initial torques, and normal forces, etc., the relative contribution of these factors could vary between subjects as well as between trial within subjects. This strategy would also explain why subjects employed smaller safety margins at the most slippery contact surfaces when at least one of the other digits contacted a less slippery material. That is, the postulated slip events, occurring early during the load phase, would tend to unload digits with rayon when the load is low, but not later during the load phase when F_n:L ratio increases due to the normal force drive. As pointed out by Birznieks et al. (1998), successful use of slips to distribute the load requires fine regulation of normal forces. To avoid movements of the object in the horizontal plane in the present task, the changes the normal forces at three digits must take place in parallel regardless of frictional condition. Accordingly, normal force adjustments in response to changes in the frictional condition must act on all digits, which indeed was the case.

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