INTRODUCTION

Most manipulative tasks require precise coordination of fingertip actions for grasp stability. To avoid accidental slips, subjects apply large enough grip forces normal to the grip surfaces in relation to destabilizing tangential loads, while they avoid excessive grip forces. Potentially destabilizing loads include time-varying linear load forces but also torque loads, i.e., torque tangential to the grip surfaces. Due to gravitational and inertial reaction forces, torque loads typically develop in manipulation of objects whose center of mass does not lie on the grip axis, i.e., the axis between the centers of the grip surfaces of the tips of the thumb and the index finger during a precision grip. These torque loads tend to rotate the object around the grip axis. The grip forces required to prevent rotational slips increase linearly with the torque load with a slope that depends on the friction of the grasp (Kinoshita et al. 1997). Subjects automatically increase and decrease the grip force in parallel with the changes in torque load (Goodwin et al. 1998; Johansson et al. 1999; Wing and Lederman 1998) just as they do for linear loads (Flanagan and Wing 1993; Johansson and Westling 1984). Thus the sensorimotor mechanisms that control the grip force in manipulatory actions predict the destabilizing effects of self-generated linear and torque loads tangential to the grip surfaces.

Most objects that we handle have curved surfaces. We have recently demonstrated that the surface curvature has modest effects on grip force requirements for grasp stability under linear load forces (Jenmalm et al. 1998), whereas the effects are profound under torque loads (Goodwin et al. 1998). With spherically curved convex surfaces, the minimum grip force required to prevent rotational slip under torque load increases with curvature. In agreement with established principles concerning the adaptation of fingertip forces to other object properties (for overviews, see Johansson 1996, 1998), adaptation to surface curvature for grasp stability under torque load is achieved by parametric adjustments of the balance between the grip force and the fingertip load (Goodwin et al. 1998). That is, for a given torque load, subjects scale their grip force to curvature, keeping an adequate safety margin against rotational slips. However, the sensory information that underlies this parametric adaptation to surface curvature is unknown, both concerning sensory modality and use of sensory information for possible anticipatory control of force-torque coordination and for compensatory adjustments (cf. Johansson 1996; Wing...
In the study by Goodwin et al. (1998), the subjects grasped, lifted, and held an object in air under linear load forces before rotating it such that torque load developed. That is, subjects could have used visual as well as tactile cues related to surface curvature during any phase of the trial according to any control policy.

When subjects lift objects with flat grip surfaces that are tapered upward or downward, they use visual cues for feedforward control such that the ratio between the grip force and the linear load force is adapted to object shape before the execution of the motor commands (Jenmalm and Johansson 1997). When vision is not available, subjects use tactile information obtained at touch to update parametrically the coordination to a change in object shape. However, this scheme may not necessarily apply for the adaptation of the motor output to object curvature under torque loads. Objects that have tapered flat grip surfaces may be particularly suitable for forward control based on visual geometric cues because the surface angle directly relates to the required coordination of grip and load forces. Moreover, the fact that the effects of surface curvature on the grip force requirements strongly depend on the type of load suggests a different control scheme. With curved surfaces under torque load, tactile information may be critical despite visual cues. High-fidelity tactile information about surface curvature is indeed available once the object is contacted, i.e., at very low contact forces (Goodwin et al. 1991, 1997). Furthermore when the torque load develops, tactile information related to localized and overt rotational slips may update memory systems for parametric control of force-torque coordination, similar to the manner by which subjects use tactile signals for adaptation of the grip-load force coordination to the frictional condition of the grasp under linear load (Johansson and Westling 1984, 1987).

Apart from rotational slips, torsional viscoelasticity of the fingertip pulps may tend to destabilize precision grips in tasks that involve tangential torque load. Although little is known about fingertip mechanics in relation tangential torque load, the fingertip pulp shows viscoelastic properties both when compressed (e.g., Pawluk and Howe 1999; Serina et al. 1997, 1998; Srinivasan 1989; Srinivasan and Dandekar 1996) and when subjected to tangential shear forces (Nakazawa et al. 2000). It seems therefore reasonable that viscoelasticity of the fingertip pulp would account for rotational compliance and creep that subjects would need to control for if required to precisely orient objects in space under torque load. Furthermore we hypothesized that any changes in surface curvature would influence this control. This is because the rotational yield of the grasp increases with surface convexity since the contact area between the fingertips and the object decreases, i.e., the fingertips only partially mold to a highly curved surface.

We devised a prototypical manipulatory task that involved dexterous application of torques around the grip axis to examine how subjects adapt the fingertip actions to changes in object curvature and which sensory information they use. The subjects were asked to use a precision grip to grasp an elongated object at one end and lift it such that torque load developed. That is, the object was tilted such that its anterior end was elevated. The connecting cable to the position-angle sensor attached to the nail was taped to the index finger. The cables delivered with the force-torque and position-angle sensors were substituted with custom-made light flexible cables to practically eliminate the contribution by the cables to the mass and mass distribution of the object. C. circles in table indicate the different sensory conditions that the subjects experienced.

**METHODS**

**Subjects and general procedure**

Eight healthy women and men between 21 and 32 yr participated in the study. All gave their informed consent, and the local ethics committee had approved the experimental protocol. The subjects sat in a chair with the right upper arm parallel to the trunk and the forearm extending anteriorly. In this position, they were asked to grasp an elongated object at one end and lift it (Fig. 1). The test object was located on a tabletop about 8 cm below the hand. The length axis of the object was oriented in a sagittal plane, and the proximal end of the object, grasped by the subjects, was located about 10 cm in front of the hand. The object was grasped between the tips of right index finger and thumb, and subjects were instructed to lift the object vertically.

![FIG. 1. Test object and sensory conditions that the subjects experienced.](http://jn.physiology.org/)

- **With vision (vision of surface curvature and object motion)**
- **Without vision (no vision of surface curvature and object motion)**
- **Restricted vision (no vision of surface curvature but of object motion)**

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about 8 cm while keeping it level and maintaining its orientation in the horizontal plane. During the lift, the grasp was subjected to a torque load because the center of mass of the object was located distal to the grasped surfaces. That is, the line between the centers of the grasped surfaces, the grip axis, was horizontal and perpendicular to the length axis of the object. About 5 min before the experiments, the subjects washed their hands with soap and water.

**Apparatus**

The test object was built of balsa and its total weight was 50 g (Fig. 1). It was equipped with two grasping surfaces whose lateral parts were separated by 25 mm. The center of mass of the object was located 21 mm in front of the grip axis, which resulted in a nominal torque load of 10.3 milli-Newton-meters (mNm) when the object was held level in air. An electromagnetic position-angle sensor (FASTRAK, Polhemus, Colchester, VT) was attached to the object to measure its vertical position referenced to the midpoint between the centers of the grasped surfaces. This sensor also measured the elevation angle of the object in relation to the horizontal; elevation of the distal end of the object provided positive angles (Fig. 1B). Another sensor was attached to the nail to measure the elevation angle of the right index finger to assess possible rotations of the grasp about the horizontal grip axis during the lifting trials. That is, one likely way to compensate for rotational yield of the grasp under torque loading would be that subjects employed a radial flexion of the wrist to rotate the fingertips around the grip axis when holding the object. Furthermore by comparing the difference between the elevation angles of the finger and the object, we assessed the rotational yield of the grasp under tangential torque load. In the environment of the sensors, the accuracy of the position measurement was better than 0.5 mm (resolution: 0.12 mm), and the accuracy of the angle measurement was better than 1° (resolution: 0.025°).

The grasped surfaces were coated with silicon carbide grains (50–100 μm) covered by a thin layer of cyanoacrylate. The surface contacted by index finger could be changed between lifting trials. It was either flat or spherically curved with a radius of 10 or 5 mm, i.e., the convex curvature defined as the inverse radius was 0, 100, or 200 m⁻¹. This grip surface was connected to the rest of the object via a six-axis force-torque sensor (Nano F/T transducer, ATI Industrial Automation, Garner, NC) that measured forces and torques applied by the index finger. We measured the grip force along the grip axis (resolution of 0.05 N) and the component of the load force orthogonal to the grip axis that was vertical when the object was supported by the table (resolution of 0.025 N). These measurements provided an adequate estimate of the vertical load force during the lifting trial because the deviations in object elevation from level was relatively small (see RESULTS). The time-varying torque load was measured as the tangential torque about the grip axis (resolution: 0.125 mNm). Because the surface contacted by the thumb was equipped with a ball bearing mechanism, the index finger took up the entire torque load during the lifting task. The curvature contacted by the thumb was constant at 200 m⁻¹.

There were several reasons for the design of the test object: first, by focusing the torque load of the grasp to one of the two digits, we could directly relate the employed grip force to the torque load. We have previously demonstrated that the partitioning of torque can vary widely between the index finger and thumb when humans manipulate objects with fixed grip surfaces (Goodwin et al. 1998; Johansson et al. 1999). Second, by using a strongly curved surface at the thumb, we promoted the use of grasp sites that were close to the centers of the grasped surfaces. This is important because otherwise subjects could have generated substantial coupled tangential forces at the two digits to prevent the object from spinning. Third, by keeping the mass of the object low we could safely assume that the linear force loads observed in our experiments (less than 1 N) had negligible influences on grip force requirements compared with those imposed by the torques (Kinoshita et al. 1997). Finally, with low load forces and the grasp sites centered on the grasped surfaces, we reduced errors in torque measurements because otherwise linear load forces (tangential to the grip axis) could have contributed significantly to the measured torque.

In control experiments carried out on two subjects, we compared the behavior with the present configuration of the test object and the behavior with a similar object that had matching pairs of grip surfaces that were both fixed. The pattern of the time-varying fingertip forces and torques were the same across the two objects for all surface curvatures. The only differences that we observed concerned the distribution of the torque load between the two digits and the magnitude of the grip forces. As expected, the partitioning of the torque load varied between the two digits across trials (see Goodwin et al. 1998). Furthermore the magnitude of the grip force was adapted to the torque load of the digit that showed the greater of the two torque loads.

**Lift series**

Each subject performed two different types of lift series. In the first kind of series, we wanted to stress the need of adapting the fingertip actions to changes in surface curvature. This series consisted of 37 lifts with unpredictable changes of the surface curvature between lifts. To facilitate analysis of possible effects of surface curvature in the previous lift, each of the three curvatures (0, 100, or 200 m⁻¹) was preceded by one of the other two curvatures or the same curvature at least four times during a single series. Five seconds after the object was initially touched, an auditory cue (1 kHz, 0.1 s) told the subjects to replace the object on the table while maintaining the object level. The interval between trials was 5 s. To assess the importance of vision and digital sensibility, all eight subjects carried out this lift series under normal sensory conditions, i.e., with vision and normal digital sensibility; with normal digital sensibility but without vision; with normal vision but with digital anesthesia; and when both vision and digital sensibility were removed (see table in Fig. 1C). To block vision, the subjects wore electronic shutter glasses that occluded vision at grip forces above 0.1 N. Thus the subject could reach for the object guided by vision but once the object was touched vision was removed. Furthermore we prevented the subjects from ever seeing the surface contacted by the index finger by using a small horizontally oriented paper shield attached to the top of object (see Fig. 1A, dashed rectangle). We removed digital sensitivity by blocking the digital nerves of the index finger by injecting a mixture of bupivacain (3 ml 5% solution) and prilocain (1.5 ml 10% solution) about 2 cm distal to the metacarpophalangeal joint. We considered the procedure successful when the subjects failed to report light touch, heavy touch, pinprick and squeezing of the distal phalanx of the index finger. Four of the subjects completed the same lifting series one additional time during digital anesthesia. This time we prevented the subjects from seeing the right grip surface by using the shield, but they could see the test object (and the hand) throughout the lifting trials (“Restricted vision” in Fig. 1C). If the manipulandum accidentally rotated due to slippage during any lift series, the subject resumed the series by repeating the current trial.

The second type of lift series was designed primarily for measurements of rotational friction of the grasp. Rather than replacing the manipulandum while keeping it level, the subjects ended the trials by decreasing the grip force when the object was held in air to allow it to rotate under the influence of gravity until its distal tip touched the table (cf. Goodwin et al. 1998). An auditory cue (1 kHz tone for 0.1 s) that occurred 5 s after the object was initially touched (defined at a grip force level of 0.1 N) signaled the commencement of this “rotational slip test.” Following the rotational slip, the subjects fully replaced the object on the table. This lift series consisted of 24 trials delivered in six blocks of 4 trials in which the curvature of the right grip surface was held constant. We varied the curvature of the grasped surface between blocks and the sequence of presentation of curvatures varied among the subjects. The subjects were free to use vision of the object and its surface curvature. To analyze whether rotational friction
of the grasp was influenced by digital anesthesia, we ran this series with normal digital sensibility and after we had anesthetized the right index finger.

INSTRUCTIONS TO THE SUBJECTS. Before data collection started, the experimenter demonstrated the task and the subject performed four practice trials with each of the three different surface curvatures (0, 100, and 200 m$^{-1}$). We specifically instructed each subject to grasp the surfaces at their centers, which we pointed out, and to lift the object vertically while avoiding any tilt. We carefully observed the subject during the practice trials to ensure that they complied with the instructions. Importantly, the subjects were given no instructions regarding which fingertip forces to use, and they always lifted the object at their own preferred speed.

Data collection and analysis

A flexible data-acquisition and -analysis system (SC/ZOOM, Section for Physiology, IMB, Umeå University) was used to digitize and store the transducer signals. Signals were recorded with a resolution of 12 bits and at 400 samples/s from the force-torque sensor and 14 bits and at 60 samples/s from the two position-angle sensors. Rate of change in grip force was assessed from the first time differential of the force signal using a ±5-point numerical differentiation (±12.5-ms window).

All measurements obtained for quantitative analyses were taken from single trials. We defined the torque-loading phase as the period during which the torque load increased until object liftoff. The start, midpoint, and end of this phase were defined as the times at which the torque load reached 10, 50, and 90% of the static torque load recorded during the hold phase when the subjects held the object still in air (see Fig. 2A). Measurements taken during the hold phase are referred to as “static” measures and were obtained by averaging the relevant signals during a 1-s interval that commenced 4 s after the object was first contacted. We defined the point of initial contact with the object as the time when the grip force exceeded 0.1 N.

ROTATIONAL SLIP COEFFICIENT. The onset of the slips evoked in the rotational slip test was determined off-line by visual inspection of the object elevation, grip force, and torque load records as described by Kinoshita et al. (1997). Thus the onset of a rapid decrease in torque load followed by a decrease in object elevation indicated the commencement of the rotational slip. The rotational slip force, i.e., the minimum grip force required to prevent rotational slip, was defined as the grip force value at the onset of such rapid decreases in torque. The difference between the static grip force and the rotational slip force represented the safety margin against rotational slips. We also computed the rotational slip coefficient, i.e., the ratio between the grip force and torque load at the onset of rotational slip. With normal finger sensibility this coefficient was $0.22 \pm 0.03$ (SD) mm$^{-1}$ (for all subjects and trials) for the flat surface and $0.31 \pm 0.07$ and $0.63 \pm 0.14$ mm$^{-1}$ for the 100 and 200 m$^{-1}$ surfaces, respectively. These coefficients are similar to those reported in a previous study for the same curvatures (Goodwin et al. 1998). Anesthesia of the index finger did not appreciably influence the rotational slip coefficients. They computed the rotational slip coefficient, i.e., the ratio between the grip force and the rotational slip force, i.e., the opposite of the safety margin against rotational slips. We also computed the rotational slip coefficient, i.e., the ratio between the grip force and torque load at the onset of rotational slip. With normal finger sensibility this coefficient was $0.22 \pm 0.03$ (SD) mm$^{-1}$ (for all subjects and trials) for the flat surface and $0.31 \pm 0.07$ and $0.63 \pm 0.14$ mm$^{-1}$ for the 100 and 200 m$^{-1}$ surfaces, respectively. These coefficients are similar to those reported in a previous study for the same curvatures (Goodwin et al. 1998). Anesthesia of the index finger did not appreciably influence the rotational slip coefficients. They computed the rotational slip coefficient, i.e., the ratio between the grip force and the rotational slip force, i.e., the opposite of the safety margin against rotational slips.

TWIST OF GRASP, ROTATIONAL YIELD, ROTATIONAL COMPLIANCE, AND ROTATIONAL CREEP. We estimated the twist of the grasp around the grip axis as the change in fingertip elevation from the start of the torque-loading phase until the end of the hold phase. (In illustrations including the twist of the grasp, it has been set to 0 at the start of the torque-loading phase.) We also assessed the amplitude of the twist during the first 200 and 400 ms after the start of the torque-loading phase measured as the change in fingertip elevation over these intervals. Rotational yield of the grasp was computed as the time varying difference between twist of the grasp and object elevation angle that occurred after the start of the torque-loading phase.
actions were analyzed and, unless reported in RESULTS, they were
to evaluate the possible influence of surface curvature (0, 100, 200 m\(^{-1}\)), lift series (2 levels; e.g., normal and impaired digital sensibility or sighted and blindfolded) and surface curvature in the previous trial (0, 100, 200 m\(^{-1}\)). Details are provided in RESULTS. One-way interactions were analyzed and, unless reported in RESULTS, they were insignificant. The level of probability selected as statistically significant was \( P < 0.05 \). Unless otherwise stated, the following procedure was used when pooling data across subjects: for each subject, the trials in which the experimental parameters were identical were combined providing a subject mean for each measurement. These average values were used in the ANOVA analyses, and in many figures subject means and SE \(( n = 8 \) ) are presented.

**RESULTS**

We first describe principal features of our prototypical lifting task that were common for trials in all experimental conditions. Second, we explore effects of the curvature of the grasped surface on the development of the grip force, on the torque load, and on the twist of the grasp that subjects performed to counteract rotational yield of the grasp. We based these analyses on lifts performed under optimum sensory conditions, i.e., with vision and normal digital sensibility. Finally, we study the importance of somatosensory and visual information for the adaptation of fingertip actions by analyzing the performance of the subjects during restriction of vision and of digital sensibility.

**General structure of the trials**

Figure 2A shows an example trial that illustrates the general features of subjects’ behavior when asked to lift and hold the test object in air while keeping it level. The subject had vision available and had normal digital sensibility, and the surface curvature was 200 m\(^{-1}\). At the start of the trial, there was a brief increase in grip force as the grasp was established. After this initial “preload phase” (Johansson and Westling 1984), the vertical load force and grip force increased together when the vertical load force became large enough, the proximal end of the object lifted off while the distal end of the object remained on the table. Thus the moment of proximal liftoff was readily observed in single trial records by a simultaneous onset of the grip force rate and grip force was quite high. Because of the sequential development of grip force and torque load, these variables showed a markedly curved relationship rendering high grip force-to-load ratios at low torques and the lowest ratios when the object was in the air (Fig. 2C). Importantly, the high grip forces early during the trial could not be explained by stability requirements imposed by the linear load force; throughout the trial, the grip force was at least an order of magnitude larger than the load force. The grip force development instead anticipated requirements induced by the upcoming torque load. Although the vertical load force contributed only to a minor degree to the total fingertip load, it played a crucial role for the kinematic structure of the task. The smooth vertical lifting movement of the object indicated that the development of the vertical load force was adequately programmed for the mass of the object (Johansson and Westling 1988a) as well as for the desired height and speed of the lift (Kinoshita et al. 1993). Furthermore the increase in load force determined the onset of the torque load increase (proximal lift-off) and together with the twist and rotational compliance of the grasp, it determined the further development of the torque load. When the subjects replaced the test object on the tabletop, the motor output largely mirrored that observed during the lifting phase illustrated in Fig. 2A.
Adaptation of fingertip actions to changes in surface curvature during normal sensory conditions

In this section, we describe the adaptation of the fingertip actions to changes in the curvature of the grasped surface based on lifts performed with vision and normal digital sensibility. Unless stated otherwise, the analyses are based on the first lift series in which we changed the surface curvature (0, 100, or 200 m⁻¹) in an unpredictable order between lifts. Because object mass and mass distribution were constant, changes in surface curvature influenced neither the final torque load nor the vertical load force.

Coordination between grip force and torque load

Surface curvature strongly influenced the grip force throughout the trials. Figure 3, A and B, shows examples of single trials with the three surfaces performed by two subjects (aligned in time on touch), and Fig. 7A shows data averaged across all subjects (trials synchronized at the start of the torque-loading phase). Right from the beginning of the trial, the grip force was higher with a more curved grip surface. The peak rate of grip force increase was scaled to the curvature (P < 0.0006; Figs. 3, A and B, and 7A), and so were the grip forces at both the start of the torque-loading phase (P < 0.0007; Fig. 4A) and at the end of the hold phase (P < 0.0001; Fig. 5). The surface curvature also influenced the rate of the torque load increase (Fig. 3, A and B), i.e., the curvature influenced the duration of the torque-loading phase (Fig. 4B; P < 0.0001). With the flat contact surface, the rate of torque increase was very fast with a typical duration of the torque-loading phase of less than 0.1 s. The duration increased with increasing surface curvature. Due to the effects of surface curvature on the grip force and the rate of torque load increase, changes in surface curvature efficiently changed the balance between the grip force and the torque load during the trial; the grip force subjected used at any given torque load increased with the surface curvature (Fig. 3, C and D).

The surface curvature, however, only modestly influenced the temporal coordination of force and torque development before the torque-loading phase. Curvature did not influence the time between the peak grip force rate and the start of the torque-loading phase, but it did influence the time between object contact and the start of the torque-loading phase (P < 0.003), which increased with a more curved surface (Fig. 4C).

SAFETY MARGINS AGAINST FRICTIONAL SLIPS. All subjects maintained an adequate safety margin against accidental rotational slips in the sense that there were no discernible slips during any phase of any trial even though we changed the surface curvature between trials in an unpredictable order. We estimated the subject’s grip force safety margin against rotational slips defined as the difference between grip force measured in the hold phase and the corresponding minimum grip force required to prevent rotational slip (“rotational slip force”). For this estimation, we used data from the lift series with slip force measurements. The behavior of the subjects in this series was essentially indistinguishable from that observed during the lift series with unpredictable changes in surface curvature. Indeed, a repeated-measures ANOVA with surface curvature and lift series (3 × 2) as factors failed to indicate an effect by lift series on the static grip forces. Both the grip force and the rotational slip force during the

FIG. 3. Fingertip actions and object movements during the initial part of single trials by 2 subjects carried out with 3 different surface curvatures (0, 100, and 200 m⁻¹) during optimum sensory conditions, i.e., with vision and normal digital sensibility. A and B: time traces of grip force and torque load, object position and elevation, twist of grasp, and rotational yield for 4 superimposed trials with each surface curvature. The trials were aligned in time on touch, i.e., when the grip force exceeded 0.1 N, which is indicated by the vertical line. Data in A and B refer to 2 different subjects. C and D: coordination between the grip force and torque load is illustrated in a phase plan plot for the same trials as in A and B, respectively.

FIG. 4. Influences of surface curvature on fingertip actions in trials with vision and normal digital sensibility. Effect by curvature on grip force at start of torque-loading phase (A), duration of torque-loading phase (B), the time period from touch until start of torque loading phase (C), twist of the grasp during the epoch 0–200 ms (D) and 0–400 ms after start of the torque-loading phase (E), and overall twist during the trial (F). —, the subjects’ mean ± 1 SE (n = 8).
TWIST OF GRASP. The surface curvature also influenced the twist of the grasp (Figs. 3, A and B, and 7A). This curvature effect on the twist was significant during the initial 200-ms epoch following the start of the torque-loading phase (P < 0.0001; Fig. 4D), and it increased during the progress of the trial (Fig. 4E), being most pronounced at the end of the trial (Fig. 4F). Although subjects actively generated a stronger twist, the dip in object elevation angle was deeper with a more curved surface despite an increased twist indicates that surface curvature markedly influenced the rotational yield of the grasp. Indeed surface curvature reliably influenced the rotational compliance measured as the slope of the relationship between the rotational yield and the torque load during the torque-loading phase (Fig. 6, A and C; P < 0.0001). Furthermore there was a slow rotational yield when the subjects held the object in air under constant torque load. Regardless of curvature, this “rotational creep” occurred at an approximately constant angular velocity (Fig. 6B). The rotational creep was influenced by surface curvature (P < 0.0001), and it increased with curvature in a manner similar to the rotational compliance (Fig. 6D). Although there was a statistically significant positive correlation between the rotational compliance and the rotational creep, the correlation was not impressive (r values ranged between 0.32 and 0.80 for individual subjects). This suggests that the underlying mechanical factors differed. The rotational creep that took place during the hold phase accounted for 35 ± 20, 32 ± 10, and 33 ± 10% (mean ± SD for all subjects and trials) of the overall rotational yield with the 0, 100, and 200 m⁻¹ surface curvatures, respectively. Because the effect of curvature on object elevation declined during the course of the trial, we conclude that the twist of the grasp that occurred after the torque-loading phase was scaled by the effect of surface curvature on the rotational compliance as well as the rotational creep.

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FIG. 5. Grip forces at the hold phase (thick lines) and slip forces (thin lines) as a function of surface curvature for all individual subjects given as mean ± 1 SD. The shaded area indicates the grip force safety margin against rotational slip, i.e., the difference between the grip force and the corresponding slip force. Each surface curvature was presented in blocks of four consecutive trials with vision and normal digital sensibility.

FIG. 6. Influences of surface curvature on rotational yield of the grasp. A: superimposed single trial data from 1 subject showing rotational yield of the grasp (computed as the difference between twist of the grasp and object elevation angle) as a function of torque load. The black segment of the curves represents data from the torque-loading phase to which we applied linear regression to assess rotational compliance (see METHODS). B: time traces of rotational yield of the grasp for superimposed single trials by the same subject as in A. Data aligned at the end of the hold phase. The 2 black segments of the curves show rotational compliance during the torque-loading phase and rotational creep during the last 3 s of hold phase, respectively. C and D: histogram plotting rotational compliance and rotational creep, respectively, against surface curvature for all individual subjects (mean ± 1 SD). Dotted lines show mean data for individual subjects.
Sensory factors in adaptation of fingertip actions to changes in surface curvature

We have demonstrated that the curvature of grasped surfaces scales the coordination between grip force and torque load for grasp stability as well as the twist drive that helped to keep the object reasonably level. Thus subjects used sensory information pertaining to surface curvature to control the fingertip actions. In this section, we investigate the contribution of vision and digital sensibility by analyzing the behavior of the subjects when vision, digital sensibility, or both were removed. Importantly, the basic coordination of the grip force, vertical load force, torque load, and twist of the grasp in all experimental conditions was similar to that observed with vision and normal digital sensibility. Furthermore with the exception of the condition in which we impeded both vision and digital sensibility, subjects maintained a robust safety margin in the sense that there were no noticeable accidental slips during any phase in any of the trials. Importantly, we observed no effect of digital anesthesia on rotational compliance ($P = 0.15$), rotational creep ($P = 0.27$) or the rotational slip coefficient ($P = 0.24$; ANOVA with curvature and digital sensibility as factors).

Without both vision and digital sensibility

In the absence of visual and digital sensory information, the adaptation of fingertip actions—including grip force and grasp twist—to surface curvature was disrupted. The curvature no longer influenced the grip force development during the dynamic phase of the trial (Fig. 7B). Neither the peak rate of grip force nor the grip force at the onset of the torque-loading phase was influenced by curvature (Fig. 8A). Subjects applied a grip force that was strong enough for lifting the most curved surface (200 m$^{-1}$) regardless of the actual surface curvature. It seemed likely that these high grip forces were the result of the subjects’ experiences from rotational slips that occurred with the most curved surface during the torque-loading phase. During such slips, which were neither felt nor seen by the subjects, the distal end of the object remained on the table while it rotated around the grip axis during lifting attempts. When made aware of the slips by the experimenter, subjects increased the grip force during subsequent lifting attempts until they successfully lifted the object. The subjects then continued to use the upgraded grip force regardless of surface curvature. The magnitude of this aftereffect, however, tended to decay over time; this, in part, may explain a tendency to lower grip forces during the hold phase in trials with 0 and 100 than with 200 m$^{-1}$ (Fig. 8B). This decay could eventually lead to a new episode of rotational slips with the most curved surface and a new voluntary upgrading of the grip force.

Concerning temporal aspects of fingertip actions, the duration of the torque-loading phase was the same as when the subjects had available vision and digital sensibility (Fig. 8C), whereas the period between touch and the start of the torque-loading phase was prolonged (Fig. 8D; $P < 0.01$; ANOVA with sensory condition and curvature as factors). Similar delays regarding load application have previously been explained by an impaired verification by tactile input that a stable contact with the object had been established (Johansson and Westling 1984; see also Collins et al. 1999). This delay also contributed to the overall high grip forces at the start of the torque-loading phase during blindfolding and digital anesthesia (Fig. 8A). In contrast to when subjects were sighted and had normal digital sensibility, surface curvature did not reliably influence the period from touch until start of the torque-loading phase (Fig. 8D).

The adaptation of the twist of the grasp to surface curvature was impaired in the absence of both vision and digital sensibility. The curvature did not influence the grasp twist measured during the two time bins after the start of the torque-loading phase, i.e., 0 to 200 ms and 0 to 400 ms (Figs. 7B and 8, D and E). However, the curvature did influence the overall twist from the start of the torque loading phase until the end of the hold phase ($P < 0.003$) but much less so than during the sighted condition with normal sensibility (Fig. 8G). We believe that the mechanism behind this influence was the same as that accounting for the effect of curvature on the grip forces during the hold phase as commented on in the preceding text (see Fig. 8B). Due to the impaired twist regulation, the curvature perturbed the object elevation angle during the lifting and during the hold phase (Fig. 8H) considerably more than in trials with vision and normal sensibility (Figs. 7, A and B, and Fig. 8H).

In sum, during blindfolding and digital anesthesia, subjects generated coordinated motor output, but they failed to predict the consequences of the prevailing curvature regarding both rotational friction and rotational yield. The subjects showed large errors in object elevation angle because of a poor compensation for the rotational yield of the grasp. In addition, subjects used excessive forces with flatter grip surfaces and rotational slips were common with the most curved surface.
Thus we could safely conclude that the adaptation of the fingertip actions to changes in the surface curvature depended on the sensory modalities that we experimentally manipulated. With vision but without digital sensibility. When the subjects saw the object, including the grasped surface, the curvature scaled the grip forces and grasp twist even when the digits were anesthetized (Fig. 9A). The curvature influenced grip force at all points of measurement, including the grip forces at the start of the torque-loading phase and during the hold phase as shown in Fig. 8, A and B (P < 0.001 in all instances, ANOVAs with curvature as factor). Furthermore there were no differences between the grip forces with and without digital anesthesia provided vision was available (Fig. 8, A and B; compare Figs. 9A and 7A; ANOVAs with digital sensibility and curvature as factors). Likewise, digital anesthesia influenced neither the duration of the torque-loading phase (Fig. 8C) nor the period between peak grip force rate and the start of the torque-loading phase. However, the period from touch to start of the torque-loading phase was slightly prolonged with digital anesthesia (Fig. 8D; P < 0.04).

In contrast to trials with vision and normal sensibility, when the digits were anesthetized, surface curvature did not influence grasp twist during the first 200 ms after the start of the torque-loading phase (Fig. 8E). The surface curvature did, however, influence the grasp twist at 400 ms (Fig. 8F; P < 0.0001) and later during the trial (Fig. 8G; P < 0.0001, ANOVAs with curvature as factor). Thus the sensorimotor mechanisms that controlled the twist of the grasp appeared to require digital input to mediate an early influence of curvature on the twist. During the hold phase of the trial, there was no difference in elevation angle of the object compared with lifts with vision and digital sensibility (Fig. 8H).
PERFORMANCE WITH LIMITED VISION OF THE OBJECT DURING DIGITAL ANESTHESIA. Subjects thus efficiently use visual information to adapt the motor output to surface curvature. However, we also wanted to know if vision of the grasped surface whose curvature we changed was decisive for the performance. We tested four of our anesthetized subjects when we prevented the view of this surface but not of the rest of the test object (see METHODS). The surface curvature still influenced grip force and the twist of the grasp but not until after the torque-loading phase. As can be seen in Fig. 9B, some 0.2 s after the proximal liftoff subjects used a higher grip force with a more curved surface, although the grip forces for the two smallest curvatures (0 and 100 m^{-1}) were only modestly different. Furthermore after some additional 50 ms, the surface curvature also influenced grasp twist. Thus subjects could use visual cues other than vision of surface curvature for adjusting fingertip actions. One obvious cue for the adaptation of the fingertip actions was visual information related to the dip in object elevation that occurred after the proximal liftoff. That subjects used this cue would explain why the adjustments took place later than those observed with vision and normal sensibility. Interestingly, the late influence on the twist resembled that observed during digital anesthesia when the subjects had full view of object, including the surface whose curvature we changed (cf. Fig. 9, A and B). Thus in both conditions, the subjects may have used visual cues related to object movement after its proximal liftoff to adapt the twist.

In sum, visual cues about surface curvature could be used to adapt the fingertip actions in a feedforward manner even during digital anesthesia. Furthermore without visual cues about curvature, subjects could indirectly use visual information related to object orientation after proximal lift-off for a delayed adaptation. However, regardless of the status of visual cues, digital afferent input appeared critical for an early initiation of the scaling of the twist action.

WITHOUT VISION BUT WITH DIGITAL SENSIBILITY. When the subjects were blindfolded but had normal digital sensibility, they also adapted their fingertip actions to the prevailing surface curvature (Fig. 9C). In this condition, they used sensory information from the digits obtained after the grip surface was touched. This resulted in a delayed grip force adaptation compared with trials with vision (cf. Figs. 7A and 9C). Accordingly, in the blindfolded state, the prevailing curvature did not influence the development of the grip force at the start of the torque-loading phase (Fig. 8A). However, the curvature reliably influenced the grip force at the midpoint of the torque-loading phase and later during the trial (Figs. 9B and 8B; \( P < 0.0001 \) for both the midpoint of the torque loading phase and hold phase, ANOVAs with curvature as the factor). Blindfolding did not influence the period from touch to start of the torque-loading phase (Fig. 8, C and D; ANOVA with curvature and vision as factors). The duration of the period from the peak rate of the grip force to the start of the torque-loading phase was also unaffected by blindfolding (Fig. 9C). As with normal digital sensibility and vision, the surface curvature influenced the twist of the grasp right from the start of the torque-loading phase (Fig. 8E; \( P < 0.0003 \)). The size of this influence increased during the trial (Fig. 8, F and G); the effect of the surface curvature on object elevation during the hold phase was indistinguishable from that in trials with vision (Fig. 8H).

We conclude that signals from digital mechanoreceptors provide information that can be used to adapt fingertip actions to surface curvature, including adaptation of the twist to the influences of surface curvature on rotational compliance and rotational creep of the grasp.

Influences of curvature in the previous trial

Memories pertaining to physical properties of an object, obtained during a previous interaction with it, play a central role for predictive control during manipulative maneuvers. This applies to object mass (Johansson and Westling 1988a), mass distribution (Goodwin et al. 1998; Johansson et al. 1999; Kinoshita et al. 1997; Wing and Lederman 1998), visco- and elastic properties of objects (Flanagan and Wing 1997), friction in relation to the skin (Johansson and Westling 1984), and object shape (Jennalm and Johansson 1997). To assess whether such memory systems also support predictive control for surface curvature, we analyzed whether the curvature in the preceding trial influenced grip force. For trials with occluded vision but with normal digital sensibility, the previous curvature determined the grip force until tactile information about the current curvature could be expressed in the motor output. That is, the curvature in the preceding trial had a reliable effect on the grip force at the start of the torque loading phase (\( P < 0.02; \) ANOVA with curvature and curvature in preceding trial as factors), whereas there was no effect of the current curvature at this point. Later in the trial the influence of the previous curvature diminished under the effect of the current surface curvature. In contrast, in trials with vision, the curvature in the previous trial did not reliably influence the grip force at the start of the torque-loading phase. Finally, during blindfolding and digital anesthesia, the motor output was strongly influenced by previous experience of the object in the sense that knowledge about rotational slips with the most curved surface scaled the fingertip actions as described in the preceding text. Repeated-measures ANOVAs were used to evaluate the possible influence of surface curvature in the previous trial (0, 100, 200 m^{-1}) and current surface curvature (0, 100, 200 m^{-1}) for each sensory condition.

**DISCUSSION**

We analyzed the sensory control of precision grip when subjects contact and lift, in a continuous action, an object whose curvature changed unpredictably between trials. We found that the curvature of the grasped surface efficiently scaled the grip force for grasp stability and that humans can use both vision and digital sensibility for this scaling. We also found that the fingertip actions comprised a kinematic component by which subjects automatically counteracted the effects of rotational yield of the grasp by a twist of the grasp around the grip axis. Furthermore subjects scaled the size of this twist to the influence of the surface curvature on the rotational yield, again based on visual and digital afferent information. However, the adaptation of the grip force and the grip kinematics (twist) relied on differential use of sensory information. A normal early scaling of the twist action to changes in surface curvature required digital afferent input and different visuomotor mechanisms supported the control of the grip force and the grasp twist. The grip force control appeared to have special
access to visual mechanisms that identify object shape whereas visual cues pertaining to actual movements of the object supported the control of the kinematics.

Rotational yield and twist of grasp

Our results demonstrate that rotational yield of the fingertip pulps is an important biomechanical variable that is controlled for during dexterous manipulation. That is, to obtain a desired orientation of an object under torque load, subjects’ actions of the digits included components that prevented rotational slips but also actions that compensated for rotational compliance and rotational creep at the fingertip pulps. Torsional elasticity of the fingertip pulp accounted for the rotational compliance measured during the torque-loading phase. Likewise, the decrease in effective contact area engaged with a larger curvature would explain the effect of surface curvature on rotational compliance; if the fingertip pulp is approximated by a short elastic cylinder its torsional compliance will decrease with the contact area (Cutkosky and Wright 1986). The viscoelastic properties of the fingertip pulp most probably accounted for the substantial rotational creep that we observed under constant torque load. It is well established that the fingertip pulp show rate-dependent hysteresis and creep when subjected to compression (e.g., Howe and Cutkosky 1996; Pubols 1982; Serina et al. 1998). Moreover, the fingertips show viscoelastic properties when loaded by forces in the tangential direction (Nakazawa et al. 2000), which is a loading condition that mechanically relates to that of the torque load in the present experiment. Movements of interstitial fluids within the fingertip as well as reorientation or relaxation processes of collagen fibers and their attachments are potential mechanisms of the creep that we observed (see Lanir 1987; Purslow et al. 1998; Wilkes et al. 1973). Still we cannot exclude that also frictional creep between the grasped surface and the digit could have contributed. Because the normal pressure is smallest at the edges of the contact, surface microslips presumably preferentially occur there (see Johansson and Westling 1987). Once slipping has occurred, the region of slipping spreads from the periphery toward the center such that creep would develop (see Cutkosky and Wright 1986). A full understanding of the biomechanical events that accounted for the rotational yield of the grasp in the present task would, however, require further development of analytical models of fingertip mechanics (cf. Cutkosky and Wright 1986; Howe and Cutkosky 1996; Nakazawa et al. 2000; Serina et al. 1998; Srinivasan and Dandekar 1996).

Coordination of fingertip actions

In many manipulatory tasks, the activated sensorimotor programs ensure grasp stability by maintaining an approximately linear relationship between the grip forces and self-generated linear load forces (Blakemore et al. 1998; Flanagan and Wing 1993; Flanagan et al. 1999; Johansson and Westling 1984, 1988a). Similarly, when subjects hold an object in air and then rotate it such that torque loads develops with little changes in linear force, an approximately linear coupling between the grip force and tangential torque ensures grasp stability (Goodwin et al. 1998; Johansson et al. 1999). However, in the present task, in which the subjects contacted and lifted an object in a continuous action and the dominating load was tangential torque, there was a markedly curvilinear relation between the grip force and the load. The increase in grip force greatly preceded the onset of the rather rapid increase in torque load in a manner resembling the preparatory grip force increase that appear about 150 ms prior to a self-generated transient load force increase. Such preparatory grip actions, employed to prevent slippage, occur when subjects drop a weight from one hand into a receptacle held by the other hand (Johansson and Westling 1988b) and when subjects move hand-held objects to collide with another object (Turrell et al. 1999). Subjects scale these preparatory grip forces to the frictional conditions of the grasp and to the peak in load force at impact, which is influenced by the overall dynamics of the task (Johansson and Westling 1988b). Similarly in the present task, subjects targeted the increase in the grip force for the requirements imposed by the final torque load under the prevailing surface curvature. Thus the grip force controller predicted the destabilizing effects of the torque load well before it developed. Deviations from a linear relationship between grip force and fingertip load may also occur in self-paced tasks not involving transient load increases. In particular, the grip force does not follow the fluctuations in torque that subjects generate to produce smooth angular movements during rapid object rotations (Goodwin et al. 1998; see also Johansson et al. 1999). In such tasks, the changes in grip force tend to be more smoothly coordinated to kinematics aspects of the task than to the changes in torque. Deviations from a stable linear relationship between grip force and load also occur during self-generated linear load forces. Compared with holding an object motionless, subjects generally employ higher grip-to-load force ratios in tasks involving inertial forces. This occurs when objects are moved along the grip axis (Werremeyer and Cole 1997) and during oscillatory movements tangential to grasped surfaces, the depth of the modulation of the grip force with load changes is reduced with increasing frequencies (see Blakemore et al. 1998; Flanagan and Tresilian 1994; Flanagan and Wing 1995). Thus rather than offering a precise moment-to-moment prediction of fingertip load, the control of the grip force is influenced by a variety of intrinsic task factors, including type of task, its phase and speed of execution. This may have implications for using grip force to probe the capacity of the CNS to predict various classes of loads and thus to probe both the nature of various internal models proposed in motor control and their functional relationships (cf. Kawato 1999).

Although we instructed the subjects to keep the object level, there was a small, hardly visible, dip in object elevation during the lifting. To avoid this dip, the subjects should have applied a twist before object motion that produced a torque that exactly matched the torque required for a level liftoff. This would have required exact estimates of object mass and mass distribution and of the rotational yield with the prevailing surface curvature. These and related precision demands probably exceed the capacity of the sensorimotor system, or it may not be worth the CNS’s effort to make the required predictions for a marginal improvement of the outcome.

Use of sensory information in the adaptation of fingertip actions to changes in surface curvature

A central role of sensory information in the control of dexterous manipulation is to allow swift and efficient adaptation of the motor output to critical physical properties of the target objects. The present results demonstrate that sensory
information related to objects’ curvature not only controlled the grip force but also the action by which subjects counteracted the effects of rotational yield of the grasp, i.e., the twist of the grasp around the grip axis. Without vision and digital sensibility, subjects generated a coordinated motor output apt to the task but that failed to predict the consequences of the prevailing curvature regarding rotational friction and yield of the grasp. In agreement with principles established in previous studies concerning adaptation to other object properties (Johansson 1996, 1998), adaptation to surface curvature took place by parametric adjustments of the motor commands, supported by memory mechanisms for predictive control.

**USE OF VISUAL CUES.** When subjects had full vision available, the motor output expressed the prevailing surface curvature from the beginning of the grip force attack even though the curvature changed unpredictably between trials. Thus well before somatosensory information was available, subjects used visual information to identify the target object in terms of grip force requirements. This type of control has been described as anticipatory parameter control based on internal memory representations pertaining to critical properties of the environmental objects acquired during previous manipulatory experience (Johansson 1998; Johansson and Cole 1992). The use of vision for activation of such internal models for retrieval of relevant motor command parameters has been demonstrated regarding other object features, including aspects of object shape (Jenmalm and Johansson 1997), prediction of object weight based on object size (Gordon et al. 1991; see also Flanagan and Beltzner 2000), and identification of common objects regarding force requirements in lifting tasks (Gordon et al. 1993). However, available data suggest that vision is of little importance for anticipatory adjustments of the force output to frictional conditions (Edin et al. 1992); tactile sensibility seems to be the principal modality in frictional adaptation (Johansson and Westling 1987).

That digital anesthesia caused no severe impairments of the adaptation of the grip force to curvature when subject had vision available underlines the proficiency of visual cues for the retrieval of motor output parameters. Furthermore vision of the curvature was critical; the adaptation of the grip force was delayed when the anesthetized subjects were prevented from seeing the surface curvature but could see the rest of the object. In this experimental condition, subjects apparently used visual cues pertaining to the initial movement of the object (dip in object elevation) for adapting the grip force. However, vision of the contact surface did not help to scale the twist during digital anesthesia. In contrast to the grip force, the twist was delayed similarly regardless of whether the subject saw the surface curvature or only the rest of the object. Only visual cues obtained after the object begun to move appeared useful to scale the twist in the absence of digital afferent input. This differential use of vision may have a bearing to the two-stream model of human visual processing, with a “ventral stream” for object and form vision that projects to the inferior temporal region, and a “dorsal stream” for spatial and motion vision that projects to the parietal region (Goodale and Milner 1992; Mishkin and Ungerleider 1982; Ungerleider and Haxby 1994). Thus the adaptation of the twist (grip kinematics) may have relied on dorsal stream processes, whereas the ventral stream may have been involved in object form identification used for anticipatory parameter control of grip force. Although it has repeatedly been emphasized that the dorsal stream mediates the control of skilled manual actions, Milner and coworkers have demonstrated that also the ventral stream is of importance for dexterous manipulation (Carey et al. 1996). Many different memory functions are certainly involved in the control of manipulation (Johansson and Cole 1992). That vision of the surface curvature efficiently addressed memory representations for anticipatory control of grip forces but not for control of the twist of the grasp suggests that different memory systems were engaged in the control of these components. Indeed, the two visual streams appear to correlate to different memory domains in the prefrontal cortex, one supporting spatial working memory and the other working memory for object recognition (Ungerleider et al. 1998; Wilson et al. 1993). However, the “two-stream” model of visual processing is simplistic and is subject to increasingly frequent challenges (e.g., Faillenot et al. 1997; Rao et al. 1997; Sereno and Maunsell 1998).

**USE OF DIGITAL AFFERENT INFORMATION.** With blindfolded subjects, in agreement with the anticipatory parameter control policy, the grip force initially developed according to the force requirements of the previous trial. Likewise after a change in curvature, digital afferent information about the new curvature influenced the grip force and the twist of the grasp about 0.1–0.2 s after contact. This adaptation was associated with a change of the internal models pertaining to the object properties because the grip force in the subsequent trial initially developed according to the requirement imposed by this “new” curvature. Thus the use of somatosensory information in selecting or updating the relevant internal models followed the discrete-event, sensor-driven control policy previously described for manipulation concerning adaptation to friction of the grasp, object shape, mass, and mass distribution (see Johansson 1996, 1998; Johansson and Cole 1992; Johansson et al. 1999). According to this policy, recognition of a mismatch between the actual somatosensory input and a predicted somatosensory input generated by the active sensorimotor program (in conjunction with the efferent signals) is critical to accomplish the relevant model changes. This scheme has indeed elements in common with aspects of recent schemes that have attempted to organize concepts of sensorimotor integration (e.g., Kawato 1999; Merfeld et al. 1993; Miall and Wolpert 1996; Prochazka 1993; Wolpert 1997).

Tactile afferents that innervate the fingertip most probably provided the significant information about surface curvature when the subjects were blindfolded (see Goodwin et al. 1995, 1997; LaMotte and Srinivasan 1987; LaMotte et al. 1998). Importantly, subjects did not rely on tactile feedback pertaining to rotational slips and misalignment of object orientation because the motor output expressed the prevailing curvature before a substantial torque was applied. Instead subjects appeared to use tactile information for feedforward control. Accordingly at some processing level, tactile and visual information pertaining to object shape may merge and support similar feedforward control regimes. Indeed there are brain areas engaged in control of manipulation in which information derived from somatosensory and visual sources seem to converge at the level of individual neurons (see Fadiga et al. 2000; Sakata et al. 1995; Taira et al. 1990). Furthermore it has been proposed that vision and tactile sensibility are based on neural mechanisms...
organized in similar ways and that there may be tactile analogs to the functions of the visual dorsal and ventral steams (Hsiao 1998).

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