Coordination between digit forces and positions: interactions between anticipatory and feedback control

Qiushi Fu and Marco Santello
School of Biological and Health Systems Engineering, Arizona State University, Tempe, Arizona

Submitted 23 October 2013; accepted in final form 2 January 2014

Fu Q, Santello M. Coordination between digit forces and positions: interactions between anticipatory and feedback control. J Neurophysiol 111: 1519–1528, 2014. First published January 8, 2014; doi:10.1152/jn.00754.2013.—Humans adjust digit forces to compensate for trial-to-trial variability in digit placement during object manipulation, but the underlying control mechanisms remain to be determined. We hypothesized that such digit position/force coordination was achieved by both visually guided feed-forward planning and haptic-based feedback control. The question arises about the time course of the interaction between these two mechanisms. This was tested with a task in which subjects generated torque (± 70 N·mm) on a virtual object to control a cursor moving to target positions to catch a falling ball, using a virtual reality environment and haptic devices. The width of the virtual object was varied between large (L) and small (S). These object widths result in significantly different horizontal digit relative positions and require different digit forces to exert the same task torque. After training, subjects were tested with random sequences of L and S widths with or without visual information about object width. We found that visual cues allowed subjects to plan manipulation forces before contact. In contrast, when visual cues were not available to predict digit positions, subjects implemented a “default” digit force plan that was corrected after digit contact to eventually accomplish the task. The time course of digit forces revealed that force development was delayed in the absence of visual cues. Specifically, the appropriate digit force adjustments were made 250–300 ms after initial object contact. This result supports our hypothesis and further reveals that haptic feedback alone is sufficient to implement digit force-position coordination.

If information acquired through vision is congruent with actual object properties, digit forces could be developed in a feed-forward fashion, usually featuring a “bell-shaped” force rate profile (Johansson and Westling 1984). However, when visual information before object contact is unavailable or inaccurate, the feed-forward planning was shown to be based on sensorimotor memory, although it may not be appropriate for executing the intended manipulation. For instance, subjects cannot correctly anticipate digit forces when low ambient illumination prevents visual discrimination of surface friction (Cole et al. 1999). Similarly, subjects cannot anticipate the direction of the torque necessary to lift an object vertically when mass distribution is changed on a trial-to-trial basis by the addition of a hidden mass at the bottom of the object (Lukos et al. 2013). In both cases, shortly after contact, digit forces in the current trial are similar to the digit forces exerted in the preceding trial. It has been proposed that the CNS detects the mismatch between the actual and predicted sensory consequences during an ongoing manipulation and compensates for the mismatch by changing the force scaling after acquiring feedback from tactile afferents. This feedback-driven mechanism has been extensively studied and explained within the “sensorimotor control point” framework, which proposes that the CNS compares actual vs. expected sensory inputs at behaviorally important events throughout the manipulation task (for review see Johansson and Flanagan 2009). The common sensory events are usually transient mechanical events, such as digit contact, micro-slips, and object lift onset (Johansson and Westling 1987).

In our recent studies using manipulation tasks that do not constrain digit placement, we have shown that subjects could scale their digit forces to variable digit relative positions (Fu et al. 2010, 2011). The trial-to-trial variability in digit relative positions could be attributed to natural end-point variability caused by motor planning or execution noise during reach and/or by active digit planning to meet given grasp optimality criteria. The first scenario requires the CNS to adjust digit forces after contact if a mismatch occurred between actual and planned digit positions, whereas the second scenario implies that the CNS could have planned both digit positions and forces together as a unit before contact. However, these studies could not distinguish between these two control mechanisms. The present study was designed to address this question by using a virtual reality setup that could induce predictable and unpredictable changes of digit horizontal relative position, i.e., grip aperture after contact, both of which required significant adjustments of digit forces. We hypothesized that J) subjects would be able to plan digit forces correctly based on visual information about contact locations on the object when avail-

DEXTEROUS MANIPULATION is a motor task that involves physical interactions between digits and objects through contact sites. In the past three decades, most studies have focused on how the central nervous system (CNS) controls digit forces using constrained grasps, i.e., tasks that do not allow choice of digit placement. It has been shown that digit forces can be planned before actual contact based on visual information about the object’s properties and/or “sensorimotor memory” built through preceding manipulations. For instance, vision of the object before movement initiation can be used to extract information such as object identity and weight (Gordon et al. 1993), mass distribution (Fu and Santello 2012), material (Buckingham et al. 2009), texture (Cole and Rotella 2002), and contact surface geometry (Jenmalm and Johansson 1997; Jenmalm et al. 2000), all of which could influence the anticipatory scaling of digit forces.

Address for reprint requests and other correspondence: M. Santello, School of Biological and Health Systems Engineering, 501 East Tyler Mall, ECG Bldg., Suite 334, Arizona State Univ., Tempe, AZ 85287-9709 (e-mail: marco.santello@asu.edu).
able before contact, and 2) when visual feedback about contacts was not available, subjects would plan digit forces based on the sensorimotor memory built from the previous trial and make force adjustments quickly after contact as a result of sensing a mismatch between actual and expected digit positions.

MATERIALS AND METHODS

Subjects

Twelve healthy self-reported right-handed subjects (18–34 yr of age, 7 women) participated in this study. All participants were naive to the purpose of the study and gave informed written consent according to the Declaration of Helsinki. The protocols were approved by the Office of Research Integrity and Assurance at Arizona State University.

Apparatus

Two haptic devices (Phantom premium 1.5; Geomagic) were attached to the tip of the thumb and index finger (Fig. 1A) through custom-made interfaces. These interfaces were designed to fit the shape of the finger pad and were fixed to the fingertips through Velcro strips wrapped on the nail side. Each interface was connected to the arm of the haptic device through a tri-axix gimbal joint, allowing each digit to move and rotate in three dimensions each. The three-dimensional positions of the tips of the thumb and index finger were recorded through internal encoders (position resolution: 0.03 mm) for the computation of the forces that were applied to the fingers. The rendering of the virtual reality (VR) environment was achieved using the CHAI3d library (Conti et al. 2005). The two fingertips were modeled as two spheres of 9-mm radius whose centers corresponded to the endpoints of the two devices, i.e., the center of the real fingertips. The contact between the fingertips and virtual objects in the VR environment are based on a stick-slide contact point model that could generate compelling haptic properties such as shape, stiffness, and friction (Conti et al. 2005). The stiffness of the graspable surface was set at 0.5 N/mm (feels like rubber). The virtual environment was rendered on a computer monitor located in front of the subject. Because of the strict spatial and temporal task constraints, subjects were asked to focus on the monitor to ensure successful task performance. The hand was out of the field of the view throughout each trial (horizontal distance between subjects’ eyes and monitor: ≈70 cm, horizontal distance between subjects’ hand and monitor: ≈35 cm; vertical distance between subjects’ eyes and hand: ≈45 cm). Subjects were asked to perform a series of tasks in the VR (see Experimental Task for details). Movement of their digits was always constrained within a virtual plane parallel to the subjects’ frontal plane located ≈35 cm from the subjects. All manipulation tasks were constrained in this plane. Constraint forces were applied to the fingertips when they moved outside of the plane to ensure that object manipulation would not occur beyond or outside of the vertical plane. These constraint forces were provided by a bi-directional virtual spring-damper (spring constant: K = 0.25 N/mm; damping constant: C = 0.01 Ns/mm). Before the experiment started, subjects were instructed to avoid moving their digits forward or backward during all tasks to avoid feeling the constraint force provided by the virtual wall. Offline analyses indicated that subjects successfully complied with this requirement by eliciting a very small constrain force (≈0.25 N on each digit).

Experimental Task

All VR tasks involved grasping and manipulating a virtual box that, in turn, controlled a cursor (c; Fig. 1B) that was moved laterally to catch a downward-moving target ball (d; Fig. 1B). Clockwise and counterclockwise rotations of the box moved the cursor to the right or left, respectively. Note that the box could be translated, but the translations were not mapped to the cursor, and therefore had no effects on its lateral motion. The box width (w; Fig. 1B) could be changed according to the task condition. Despite the variable width of
the virtual box, resistive external forces and torque were applied to the box according to the same equation:

\[
\begin{bmatrix}
    f_x \\
    f_y \\
    \tau
\end{bmatrix} =
\begin{bmatrix}
    0.1 & 0 & 0 \\
    0.1 & 0 & 0 \\
    0 & 0.1 & 0
\end{bmatrix}
\begin{bmatrix}
    x_B \\
    y_B \\
    \theta_B
\end{bmatrix} +
\begin{bmatrix}
    0.1 & 0 & 0 \\
    0 & 0.1 & 0 \\
    0 & 0 & 1
\end{bmatrix}
\begin{bmatrix}
    \dot{x}_B \\
    \dot{y}_B \\
    \dot{\theta}_B
\end{bmatrix}.
\]

The vector \((x_B, y_B, \theta_B)^T\) denotes the position and orientation of the virtual box, and the vector \((f_x, f_y, \tau)^T\) denotes the resistive forces and torques generated on the box. The entries of the vector \((f_x, f_y, \tau)^T\) were computed as a spring-damper system connected to the center of the box \((O, \text{Fig. } 1C)\) with the equilibrium point at \((x_B, y_B, \theta_B)^T = (0, 0, 0)^T\). These resistive forces required subjects to produce a torque to rotate the box, hence to move the cursor. The box had its own inertia, but it was very small (equivalent to 10-g mass) and negligible compared with the resistive forces. Therefore, the horizontal position of the cursor on the screen was linearly related to the control torque subjects generated on the box.

There were three possible target ball drop locations: left, center, or right, which required subjects to exert a torque \((T_{\text{task}})\) of 70, 0, or −70 N·mm, respectively. The precision requirements for \(T_{\text{task}}\) associated with the definition of successful trial were torques within ±7 N·mm of \(T_{\text{task}}\) (±10% of \(T_{\text{task}}\)). Note that although the torque was zero for the center target, subjects still needed to grasp the box and maintain the cursor at zero position while waiting for the ball to drop. There were also three possible box widths \((w)\): small (S, 57 mm), medium (M, 71 mm), and large (L, 85 mm). The box height was kept constant (57 mm). Note that different box widths elicit different digit horizontal relative positions, i.e., grip widths.

Subjects were asked to manipulate the boxes with different widths to control the cursor to catch the ball dropping to the left or right of the box’s start position. Because the magnitude of the torque required for catching the ball was always the same, subjects needed to exert larger forces to manipulate the small box and smaller forces to manipulate the large box (Fig. 1C). Specifically, let the thumb and finger contact location be \(P_T\) and \(P_F\), respectively, and the position of the center of the box be \(O\). The moment arm of the thumb and index finger forces \((F_T \text{ and } F_I)\) can be written as the distance between the finger positions and object center: \(d_T = P_T - O\), and \(d_I = P_I - O\). We define the effective digit forces \(F_{Te}\) and \(F_{Ie}\) as the thumb and index finger force components, respectively, projected to the vectors perpendicular to the corresponding moment arms (effective forces that generate torque in clockwise direction are positive; Fig. 1C). These effective digit forces act on the moment arm contributing to the generation of cursor control torque \((T_{\text{con}})\) as described in the following equation:

\[
T_{\text{con}} = F_{Te}d_T + F_{Ie}d_I.
\]

The digit forces and positions, as well as the box position, were recorded from the haptic device at 500 Hz.

To initiate a trial, subjects were asked to first move their digits into fixed start positions. The start positions were rendered as two spheres (12-mm radius) located at a horizontal distance of 110 mm from each other. When both digits reached the start positions, the target ball appeared and started to fall from the top of the screen, and the box was rendered haptically between the two virtual digits. The visual rendering of the box, cursor, and digits may have selectively occluded depending on the experimental conditions (see below for details). The appearance of the falling ball was also the GO signal indicating subjects could start to grasp and manipulate the box regardless of the visual condition (Fig. 1D). The target ball always moved downward at a constant velocity of 12 cm/s and reached the horizontal line (Fig. 1B) along which the cursor moves in 1.5 s. Therefore, subjects had to grasp the box and move the cursor to the desired location within 1.5 s to catch the ball. Successful catches were rewarded by an auditory cue. A score system was designed to motivate and engage subjects based on the absolute errors they made \((|T_{\text{err}}| = |T_{\text{task}} - T_{\text{con}}|)\) at the end of each trial, i.e., when the target ball hit the horizontal line (Fig. 1B). Specifically, successful catches \((|T_{\text{err}}| < 7 \text{ N-mm})\) gave subjects 10 points, and success on consecutive trials was awarded with bonus points (1 point for each consecutive successful trial), whereas barely missing the target \((7 < |T_{\text{err}}| < 14 \text{ N-mm})\) gave 5 points, and no points were given for \(|T_{\text{err}}| > 14 \text{ N-mm}\). After each trial, subjects were asked to release the box. Once released, the box was not rendered until the beginning of the following trial.

**Experimental Procedure**

**Practice sessions.** Subjects were first introduced to the tasks by being asked to freely explore the VR to become familiar with the experimental setup. To avoid subjects exerting too much force beyond the capability of the haptic device, we also let subjects squeeze the virtual object until it broke (>6 N) and asked them not to use such high forces during the experiment. After familiarization, a practice session was designed to teach subjects the basic rules of the tasks (Fig. 1E; see Supplemental Video 1). (Supplemental data for this article is available online at the Journal of Neurophysiology website.) Subjects were presented with the medium-width box, and R and L targets were randomly interspersed with full visual feedback of the cursor, box, and digits. These practice sessions were used until subjects were able to successfully perform 10 consecutive catches. The first and second practice sessions lasted ~3 min each. Subjects were given a 2-min rest before starting the training session.

**Training session.** The training session consisted of 8 blocks of 20 trials each (Fig. 1E; see Supplemental Video 2). Subjects used the same box width (L or S) within each block and switched to the other box width after completing each block. Subjects were counterbalanced to start with either the L or S box width. Visual rendering of the cursor position was removed during each trial, and subjects were given visual feedback of the cursor position only at the end of the trial to allow them to assess their performance, i.e., how far they were from the target. Visual feedback of the box width and digit tip locations was always available during each trial. The target positions were always in the center for the first 3 trials and then switched pseudorandomly between right and left (Fig. 1E). We used the center target location as a “washout” task, and subjects were not required to learn this condition. The rationale for this approach was that washout trials have been shown to reduce interference and improve learning in novel dual contexts (Krakauer et al. 2005). The last two blocks (blocks 7 and 8) were used to determine baseline performance. A 2-min rest was given after the training session.

**Test session.** The first test session (test A) consisted of 4 blocks of 20 trials each (Fig. 1E; see Supplemental Video 2). The target ball location was the same (left or right) within each block but alternated across blocks. Subjects were counterbalanced to start with either the left or right target. Visual condition was the same as for the previous training session. The goal of this session was to test whether subjects could use visual information about the box width, which indirectly provides information about the relative digit positions, to plan digit forces accordingly. The box width was always medium for the first 3 trials but then switched pseudorandomly between large and small across trials (Fig. 1E). The sequence of box widths was designed to present subjects with four instances of each of the following trial pair conditions within each block: large-small, large-large, small-small, and small-large (LS, LL, SS, and SL, respectively; the rationale is explained in Statistical Analysis). A 2-min rest was given after subjects finished this test session.

The second test session (test B) also consisted of 4 blocks of 20 trials each (Fig. 1E). These trials were similar to the first test session except that visual rendering of the box was removed throughout the entire duration of the session and visual rendering of the digit tips was removed as soon as they moved out of the starting areas. Subjects were told that they could still grasp the box after the target ball start.
to fall, although the box and digits were visually occluded. This session was designed to test whether subjects could use only haptic information about box width acquired at and after contact to modulate digit forces as a function of box width.

It should be emphasized that in test A, subjects would have been able to plan digit forces before making contact with the box because of the visual object width cue, which allowed for visually based predictive control. In contrast, although subjects in test B could have still planned their digit forces based on sensorimotor memory of previous manipulations, they might have had to make corrections to their motor plan after contact when the actual box width did not coincide with the width they had planned for.

**Statistical Analysis**

The recorded digit forces and positions were filtered using low-pass Butterworth filter with a cutoff frequency of 30 Hz. We assessed learning of the manipulation task by computing the mean absolute torque error, \( T_{err} \), that each subject made within each training block (excluding the first 3 washout trials). One-way repeated-measures ANOVA (8 levels; number of training blocks) and planned contrast between adjacent blocks were used to quantify block-by-block learning of \( T_{con} \). Since the magnitude of \( T_{task} \) was constant, we also evaluated subjects’ ability to respond to different box widths by computing the total effective force, \( F_{eff} \) (Eq. 3).

It should be pointed out that vertical digit placement on the box was not constrained, and therefore the relative digit vertical positions could have varied across trials as noted in our earlier work (Fu et al. 2010). However, the digit vertical positions have a much smaller influence on the moment arm length \( d_T \) and \( d_I \) because the moment arm is mainly determined by the width of the box \( w \). This was verified by offline analysis showing that although subjects did modulate digits’ vertical position, the magnitude of modulation was ten times smaller than the width-dependent changes in horizontal digit positions (~6 mm; see RESULTS). Therefore, we could approximate the compensatory torque production equation as

\[
T_{con} = F_{TEd} + F_{IEd}
\]

where \( d \) is the average moment arm length: \( d = (d_T + d_I)/2 \). In turn, \( F_{eff} \) can be expressed as \( F_{eff} = |F_{TE} + F_{IE}| \). In principle, to control the cursor for successful ball catching, the subjects should produce a large \( F_{eff} \) for the small box width (i.e., shorter moment arm) and a small \( F_{eff} \) for the large box width (i.e., longer moment arm). Note that the modulation of \( F_{eff} \) represents the digit force modulation relevant to the completion of the task and combines force modulation of both digits.

It has been shown that without visual feedback for anticipating object properties, the CNS tends to use sensorimotor memory of the manipulation forces acquired during the previous trial (Cole et al. 1999; Jenmalm and Johansson 1997; Loh et al. 2010; Lukos et al. 2013). Therefore, the test trials can be separated into four categories according to the box width used in preceding trial for the analysis of \( F_{eff} \) in response to the box width presented on the current trial: LL, LS, SS, and SL. This trial grouping and design allowed us to examine the effects of sensorimotor memory of the previous trial and visual cues in the current trial.

We computed the mean \( F_{eff} \) using trials from the last two blocks in test A and test B, i.e., eight trials for each trial pair for each subject. To examine the \( F_{eff} \) subjects used at the end of each trial, i.e., when the target ball arrived at the horizontal line, we performed three-way repeated-measures ANOVA using vision conditions (2 levels: test A and test B), preceding trial box width (2 levels: small and large), and current trial box width (2 levels: small and large) as within-subject factors. In addition, we performed two-way repeated-measures ANOVA (2 levels for vision conditions: test A and test B; 4 levels for trial conditions: LL, LS, SS, and SL) using \( F_{eff} \) measured at multiple time points ranging from 100 to 600 ms after the initial contact between the digits and the box (see RESULTS for details). The initial contact was determined as the time at which one of the fingers first made contact with the box (digit force > 0.1 N; Fig. 2, A and B). Post hoc paired \( t \)-test were performed when appropriate using Bonferroni corrections.

**RESULTS**

**Learning of Manipulation Tasks**

Subjects made small performance errors when they started the training blocks because these trials were preceded by a practice session in which they performed the task with complete visual feedback of box width and cursor position. Therefore, subjects already had implicit knowledge about how to successfully perform the task. Nevertheless, subjects still needed to learn to perform the task by scaling digit forces to two box widths (L and S) they had not interacted with during the practice sessions. Subjects’ performance significantly improved across eight training blocks. Specifically, the within-block mean torque error \( |T_{err}| \) significantly decreased from 17.43 ± 1.67 N-mm (mean ± SE) in block 1 to 12.59 ± 1.33 N-mm in block 8 \( [F(7,27) = 4.325, P < 0.001] \). We also found that after an initial improvement in performance after the first two blocks, performance reached a plateau. Planned contrasts between each block and the average of the following training blocks revealed significant differences only between the first block and the other seven for both mean torque error \( [F(1,11) = 10.23, P = 0.008] \) and torque variability \( [F(1,11) = 10.06, P = 0.009] \). It should be pointed out that the timing and spatial requirements of our task are quite challenging, because subjects could not reach a “perfect” task performance, i.e., staying within the 10% error margin. However, they were able to comply with the 20% error margin for most trials. Most importantly, subjects learned to perform the task by using significantly different effective force \( (F_{eff}) \) in response to the

**Fig. 2. Single-trial performance and experimental variables. A and B show the time courses of the experimental variables: magnitude of thumb and index finger forces \((F_T \text{ and } F_I, \text{ respectively})\), magnitude of the effective thumb and index finger forces \((F_{TE} \text{ and } F_{IE}, \text{ respectively})\), and the distance between the thumb and index fingertip position and the object’s center \((d_T \text{ and } d_I, \text{ respectively})\). C shows the time course of the cursor control torque and object rotation \((T_{con} \text{ and } \theta_B, \text{ respectively})\). T_{task} torque subjects are required to exert to complete a task. Data are from 1 representative trial from the training block with the large object width.**
large and small box widths. This was quantified by computing mean $F_{\text{eff}}$ from the last two training blocks (blocks 7 and 8, one with large box width and the other with small box width). Subjects used significantly different $F_{\text{eff}}$ digit forces when manipulating the two boxes ($2.22 \pm 0.04$ and $1.77 \pm 0.04$ N for the small and large box, respectively; 2-tailed paired t-test, $t = 8.95, P < 0.001$; Fig. 3).

**Digit Forces Control With and Without Visual Feedback of Box Width**

We examined whether subjects could adjust their digit forces to the actual box width. In test A, subjects could use visual feedback about object width to predict the digit position and forces, but not in test B. Since we did not constrain subjects' digit vertical positions, we first tested whether making object width unpredictable on a trial-to-trial basis would change the vertical relative positions of the digits. We found that the modulation of digit vertical relative position was small ($5.7 \pm 1.1$ and $4.9 \pm 0.8$ mm for test A and test B, respectively, averaged across trial conditions) compared with the changes in digit horizontal positions induced by different object widths. Statistical analysis revealed no significant difference in the digit vertical relative positions between test A and test B ($t$-test, $P > 0.05$) for any of the trial conditions (i.e., LL, LS, SS, and SL). Furthermore, we examined $d_T$ and $d_I$ at initial contact of each digit (Fig. 2C). Three-way repeated-measures ANOVA revealed only a significant effect of current trial [$F_{\text{effect}}(1,11) = 8.716, P < 0.001$, and $F_{\text{effect}}(1,11) = 10.144, P < 0.001$, for $d_T$ and $d_I$, respectively]. This suggests that removing vision of object width only affected the predictability of the digit relative positions at contact, i.e., fingertips closer or farther apart for small and large object widths, respectively, but did not lead subjects to use digit positions that differed from those used when they could see object width.

More importantly, we found that despite the difference in the predictability of digit positioning between test A and test B, subjects performed similarly in both tests (Fig. 3). This was confirmed by three-way ANOVA showing no effect of experimental condition on $F_{\text{eff}}$ ($P > 0.05$). In addition, subjects were able to modulate digit forces to the current box width, but digit forces were also affected by the box width experienced in the previous trial. Statistically significant main effects of both current and preceding box width were found [$F_{\text{effect}}(1,11) = 38.80, P < 0.001$, and $F_{\text{effect}}(1,11) = 13.57, P = 0.004$, respectively]. We then used the paired $t$-test to examine $F_{\text{eff}}$ subjects exerted in tests A and B with respect to those used in the last two blocks of training. No statistical difference was found between the training S trials and test S trials regardless of the preceding box size in the tests (the same result was found for L trials). Last, we compared the within-block $\overline{F_{\text{eff}}}$ from the last two blocks from training, test A, and test B and found no significant difference between these three conditions. These results indicate that although the preceding box size may have slightly biased digit forces in the current trial, the resulting force production was similar to that found during the training (Fig. 3) and did not negatively affect task performance.

**Differential Development of Effective Force**

The above results indicate that subjects responded to the box width by exerting digit forces that matched the box width to generate the required torque regardless of whether they had visual feedback about box width for predictive digit force control. This raises the question about the sensorimotor mechanisms that subjects used to adjust digit forces when actual and expected box width did not match. To address this question, we examined the time course of $F_{\text{eff}}$ by computing the ensemble average of effective force traces for each subject and each trial pair condition ($n = 8$ for each test) and made two observations. First, in both test A and test B, the force profiles showed one or two small “bumps” that each lasted about 40 ms after the first contact (Fig. 4A). These initial bumps are digit contact impact forces caused by a lack of a deceleration phase before object contact in our VR setup (average peak digit velocity: $98.6 \pm 8.5$ mm/s; average contact digit velocity: $69.3 \pm 7.7$ mm/s; no effect of vision condition, $P > 0.05$), as well as contact time differences between thumb and index finger ($56.8 \pm 6.3$ and $55.2 \pm 7.6$ ms for test A and test B, respectively; no effect of vision condition, $P > 0.05$). Second, lack of vision in test B delayed force development in all trial conditions relative to test A, although both subject groups eventually attained the appropriate forces required to perform the manipulation task (Fig. 4A). These two features were consistent across all subjects as shown by the ensemble average force profiles for each trial pair combination (Fig. 4B). To avoid the initial impact force and to account for the contact time difference between thumb and index finger, for statistical analysis we chose 100 ms after first contact as the first time point.

We found that $F_{\text{eff}}$ in test A was significantly higher than in test B at 100 and 200 ms postcontact [significant effect of vision condition: $F_{\text{effect}}(1,11) = 5.09, P = 0.045$, and $F_{\text{effect}}(1,11) = 25.55, P < 0.001$, respectively; Fig. 4C]. At 300 ms after initial object contact, we found a statistically significant interaction between vision condition and trial condition [$F_{\text{effect}}(3,9) = 4.27, P = 0.039$]. Post hoc comparisons revealed that within each trial condition, subjects produced significantly greater $F_{\text{eff}}$ in test A than in test B ($P < 0.05$). At 400 ms after initial contact, a significant interaction between vision condition and trial condition was found [$F_{\text{effect}}(3,9) = 5.91, P = 0.016$]. Post hoc
comparisons revealed no difference between test A and test B for LL. However, subjects still produced significantly smaller $F_{\text{eff}}$ in the other three cases ($P < 0.05$). At 500 ms after initial contact, the same statistically significant interaction was again found [$F_{(3,9)} = 4.71$, $P = 0.037$]. Post hoc comparisons revealed that subjects still produced significantly smaller $F_{\text{eff}}$ in test B for the LS condition ($P < 0.05$). No difference was found in the other three trial conditions. At 600 ms after contact, the magnitude of $F_{\text{eff}}$ was close to that exerted at the end of trials showing similar box-size-dependent force modulation [effect of box width conditions; $F_{(3,9)} = 14.62$, $P < 0.001$], and no significant effect of vision condition was found.

To summarize, we found that subjects took longer to develop digit forces to produce the required torque when they could not predict the actual digit relative positions (test B) but eventually attained the same box width-dependent force modulation. To further quantify this difference, we compared the force rate profiles from LL, LS, SL, and SS conditions in tests A and B using cross-correlation analysis. For each subject and each trial pair condition, we first computed the ensemble average of effective force rate traces ($n = 8$ for each test; Fig. 5A).

We then computed cross-correlation between ensemble averages of $F_{\text{eff}}$ rates from tests A and B for each trial pair condition within the 100- to 600-ms interval postcontact. The time shift at which the highest correlation is found denotes the temporal difference in force development between the two experimental conditions. We found that for all trial conditions, force development started later for test B than for test A (Fig. 5B). Two-way repeated-measures ANOVA using current trial box width (2 levels: small and large) and box width change (2 levels: same or different box widths in current and previous trial) revealed that the small box width caused a significantly longer delay than the large width in test B [$F_{(1,11)} = 8.68$, $P = 0.013$], but there was no effect of box width change [$F_{(1,11)} = 2.35$, $P = 0.154$]. These delays could be further demonstrated by taking the ensemble average of $F_{\text{eff}}$ rate traces from all subjects (Fig. 5C). These data confirmed the results from cross-correlation analysis by showing a temporal difference between test B and test A of 100–200 ms in all trial pair combinations.

Last, we qualitatively examined how subjects responded to each trial condition within each test. We visually examined the ensemble averages (100–600 ms postcontact) of all subjects for visual examination because the individual force rate profile can be quite noisy. For test A, the width of the box can be seen before object contact, thus allowing anticipation of digit forces appropriate for the digit horizontal separations. This is shown by the early divergence (~100 ms postcontact) of the force rate profiles depending on the box width in the current trial regardless of the width used in the previous trial (Fig. 6A). Specifically, if the current box width for test A was small, subjects tended to use a force rate profile characterized by a larger peak. In contrast, for test B, the divergence of the force rates occurred much later (~300 ms postcontact) than in test A for all cases (Fig. 6B). Specifically, it appears that subjects used a “default” rate of $F_{\text{eff}}$ development regardless of the box sizes in the current and previous trial, but made subsequent adjustments according to the actual object width they experienced haptically. This is consistent with the overall delay between test A and test B revealed by cross-correlation analysis. This result further suggests that when subjects could not predict the
upcoming box width, they did not start to exert the digit forces that were appropriate for the previous trial.

**DISCUSSION**

We used a virtual reality setup to investigate the ability of human subjects to modulate digit forces to compensate for predictable and unpredictable changes in the digit position induced by a change in object width. We found that after learning a novel manipulation task with different box widths, subjects could successfully modulate digit forces to accomplish the manipulation goal despite trial-to-trial changes in box width regardless of whether they had visual feedback about object width and digit positions before contact. However, our findings only partially supported our hypothesis of a hybrid anticipatory and feedback control mechanism being implemented when subjects could not predict object width change.

**Fig. 5. Effective force development.** A shows the ensemble averages of $F_{\text{eff}}$ rates from the LS trial condition (subject LZ). B shows the temporal difference between test B and test A in force development computed from cross-correlation analysis (see text for details). Black dashed line and gray solid line denote test A (visual + haptic feedback) and test B (haptic feedback only), respectively. Data are mean values averaged across all subjects, and vertical lines denote SE. C shows the ensemble average of $F_{\text{eff}}$ rates from all subjects and trial pair conditions.

**Fig. 6. Effective force rates across trial pair conditions.** A and B compare the ensemble average of $F_{\text{eff}}$ rates from all subjects across different trial pair conditions for tests A and B, respectively.
Specifically, although subjects did make force corrections after contact by using haptic feedback of the actual digit relative positions, they did not anticipate digit forces according to the box width experienced in the previous trial, but rather adopted a default initial force strategy. Therefore, regardless of whether current trial and previous trial were characterized by the same box width, subjects always had to verify the actual digit positions (i.e., box width) after contact to adjust to the appropriate digit forces. This phenomenon caused an ~150-ms delay in force development relative to the condition where subjects could predict forces based on visual feedback of object width before contact.

Methodological Considerations

It should be pointed out that modulation of digit forces to digit positions is only functionally relevant when the task involves torque production. For instance, when lifting and balancing a cup of water or rotating the lid of a jar, the hand needs to either maintain zero torque or generate sufficient torque in a given direction, respectively. During the execution of such tasks, multiple digits are in contact with the object at different locations, and relative distances between the contact points of the fingertips act as mechanical “moment arms.” If digit forces were not modulated according to the digits’ relative positions, the resulting torque might not be appropriate to perform the task. In our previous work, digit positions were quantified as the vertical distance between the centers of pressure of two digits (Fu et al. 2010) because the object width remained invariant across trials. However, subjects increased vertical relative digit position, and this essentially increased grip aperture, thus altering the effective moment arm and optimizing digit forces necessary to accomplish the task (i.e., smaller grip forces). It should be noted that in that study, trial-to-trial differences in digit placement occurred spontaneously. In contrast, digit placement in our novel VR task in the current study was induced in a systematic fashion to quantify the extent to which subjects could modulate digit forces accordingly. Specifically, our task conditions required subjects to scale digit forces to the digits’ horizontal distance (i.e., grip aperture) to attain the control torque since the object width changed significantly across trials. Nevertheless, digit force/position coordination plays a crucial role in both VR and real-object balancing tasks. It is important to understand how such coordination is achieved because the phenomenon of digit position-force coordination is likely to underlie a wide range of everyday manipulation tasks that do not constrain digit placement (Fu et al. 2010).

Another difference between our VR task and real-object manipulation tasks is the digit contact events. We observed that force development in our experiment was always characterized by an initial impact force with a peak of ~0.25 N during the first 50 ms, or sometimes two impact force peaks during the first 100 ms if two digits landed on the object asynchronously (Fig. 4A). The initial impact force was likely caused by lack of deceleration before digit contact and the fact that the simulated object surface could not have the same stiffness as rigid physical object surfaces. These initial impact forces were not found, at least not to this extent, when subjects made contact with real objects with their finger pads (Säfström and Edin 2008). This could be due to the fact that there was no “reaching” phase in our design; the subjects simply had to close their digits toward the object located between them. Additionally, and unlike other grasping studies, our design had a 1.5-s time constraint for task completion that might have led subjects to close their digits without decelerating them, thus causing relatively large initial impact forces. It has been demonstrated that subjects can predict the time of contact and release the motor plan of digit forces at the expected contact time (Säfström and Edin 2008). For our study, it is likely that subjects started to develop digit forces at the predicted time when both digits had made stable contacts.

Anticipatory Digit Force Scaling to Object Properties

It has been shown that the CNS can anticipate the digit forces required for object manipulation by using visual information about object properties. This anticipatory control was demonstrated with the use of tasks that require lifting or transporting an object that often can be grasped at small grasp surfaces. These tasks have no explicit task goals, and the only requirement is to maintain grasp stability (i.e., no finger slip at local contact sites) that is achieved by keeping the grip force larger than a certain magnitude (i.e., safety margin) to sustain frictional load forces. In these scenarios, subjects could scale the grip force in an anticipatory fashion appropriately to the load forces induced by different object weights (Johansson and Westling 1984), local surface shape (Jenmalm and Johansson 1997), friction coefficient (Cole et al. 1999), object weight distribution (Salimi et al. 2003), or even movement-induced perturbations (Flanagan and Tresilian 1994). However, when the properties of the upcoming object or task are unpredictable, often induced by removal of visual feedback, subjects tend to scale digit forces according to the object properties experienced in the previous trial (Cole et al. 1999; Jenmalm et al. 2006; Lukos et al. 2013). These observations have led to the proposition that the CNS builds and stores “sensorimotor memories” of digit forces after only a few object lifts. Recently, the ability to use sensorimotor memory to scale finger forces also has been found in tasks that did not constrain digit placement and had a more explicit task-level goal, i.e., the object had to be lifted and balanced. It was found that if object weight distribution (therefore the task torque) could not be predicted, sensorimotor memory of the previous object weight distribution was used to coordinate digit forces and positions (Lukos et al. 2013).

In the current study, we found that when visual feedback about object width was available from the beginning of the trial, appropriate force scaling to the relative digit position could be implemented as soon as ~100 ms after initial contact (Fig. 6A). This indicates that visual cues allowed subjects to start exerting forces appropriate for the digit positions soon after attaining a stable grasp. In contrast, when object width could not be predicted through vision of object width, subjects could have used sensorimotor memory of the forces used in the previous trial to develop digit forces after contact. Previous studies have shown that subjects could build up sensorimotor memories with only one or two trials when object properties were presented through random trial sequences (Cole et al. 1999; Jenmalm et al. 2006; Lukos et al. 2013). However, we did not find evidence for such an effect of sensorimotor memory on force development in our task. This could be
explained by the fact that our task had very high precision requirement. Specifically, subjects would miss the target if they made an error larger than 10% of the required torque. Given the actual digit forces were less than 4 N, the range of force errors they could have made was quite small. Because subjects had only 1.5 s to accomplish the task goal and there was a score system to motivate them in being accurate, it is likely subjects might have chosen a more conservative default strategy for the initial development of the digit forces, thus bypassing the tendency to use the same forces experienced in the previous trial. Additionally, it has been shown that the ability of sensorimotor memory to drive the force production in an unpredictable trial sequence may depend on the number of repetitions in the same trial condition (Witney et al. 2001). It is possible that subjects could have relied on sensorimotor memory in our task if the unpredictable changes of box width had occurred less often, thus allowing sensorimotor memory of this precision task to build up. Nevertheless, such a default strategy still points to a feed-forward force control strategy deployed shortly after initial digit contact. Furthermore, the initial default force development phase might be used to acquire somatosensory feedback of the object width for later corrections.

**Execution of Dexterous Manipulation: Digit Contact Event and Force Corrections**

Despite the aforementioned differences in the anticipatory control found between our task and manipulation tasks involving physical objects, the present study demonstrates that the CNS can use somatosensory information about the actual digit relative positions to adjust digit forces after contact. It has been shown that if the prediction of anticipatory control matches actual object property, e.g., mass (Jenmalm et al. 2006), planned force development does not need to be changed. In contrast, if a mismatch occurs, feedback mechanisms will respond to change ongoing force development. It has been proposed that tactile afferent signals elicited by initial object contact are powerful enough to detect several local features of the contact sites, such as friction and shape, thus leading to observable force rate changes as early as 100 ms postcontact (Cole et al. 1999; Jenmalm and Johansson 1997). For our task, we found similar feedback mechanisms, although they implemented through sensing a mismatch between planned and actual digit positions. Specifically, when analyzing force development 100 ms postcontact, subjects exhibited ~100- to 200-ms latency in initiating force development for all trial pair conditions relative to the full vision condition (test A; Figs. 4 and 5). This indicates that when the object width was unpredictable, subjects always verified the actual digit positions before starting the development and appropriate scaling of digit force to the perceived box width. This “check” should occur during the initial contact event, and two potential sources of information can be envisioned. First, box width could be sensed by the timing of digit contacts. Because the subjects’ digits always started to move from the same starting area, and assuming a stereotypical digit closure velocity, it took longer (~200 ms) to make contact with the small box than with the large one. Such a contact event (mechanical vibration and pressure change) could be encoded in the tactile afferent signals conveying precise timing information (Johansson and Birznieks 2004). The second source of feedback could result from integrating tactile and proprioceptive signals associated with changes in fingertip distance when contacting a small vs. large object (Santello and Soechting 1997; Shibata et al. 2013). It should be pointed out that the earlier force differentiation as a function of object width found for the vision condition does not rule out the possibility that the vision group also might have used haptic feedback to adjust digit forces. Nevertheless, this finding underscores the significant role of visual feedback for anticipatory scaling of digit forces as a function of digit position.

**Neural Mechanisms**

Several studies have characterized the neural circuitry involved in feed-forward planning and feedback-driven adjustments of digit forces during manipulation tasks. Premotor areas are believed to be involved in predictive planning of digit force and shaping. It has been shown that virtual lesions induced by transcranial magnetic stimulation (TMS) to premotor ventral cortex (PMv) during reaching disrupt peak grip force scaling based on previous lifts (Dafotakis et al. 2008) as well as consistent positioning of the digits (Davare et al. 2006). TMS-induced inhibition of premotor dorsal cortex (PMd) was found to negatively affect grip force scaling based on learned visual cues (Chouinard et al. 2005). Primary motor cortex (M1) and cerebellum were also found to influence predictive force scaling and are thought to store internal representations of digit forces experienced during previous lifts (Chouinard et al. 2005; Loh et al. 2010; Nowak et al. 2004). In our study, visual feedback about object size could be responsible for the fast development of digit forces through predictive visuomotor transformations (test A). When visual information was not available (test B), it is possible that the sensorimotor system established an intermediate initial force plan influenced by the stochastic nature of the preceding object width trial sequence (Verstynen and Sabes 2011).

Anterior intraparietal area (AIP) has been shown to play an important role in online force adjustment during grasping. TMS-induced virtual lesion in AIP 170–120 ms before contact can disrupt digit force scaling in an object lifting task (Davare et al. 2007). This disruption was likely due to AIP involvement with reactive control in response to the detection of mismatches in goal-dependent grasps and manipulations (Dafotakis et al. 2008; Tunik et al. 2005). Furthermore, it has been shown that AIP might facilitate online grasp control through the M1-PMv-AIP circuit (Buch et al. 2010). In addition, event-related functional MRI during lifting of heavy and light objects presented through unpredictable sequences also revealed the involvement of inferior parietal cortex in detecting mismatches between predicted and actual object weight (Jenmalm et al. 2006). The same study also indicated that primary sensorimotor cortex is involved in making adjustments to digit forces when the actual object weight is unpredictably changed from heavy to light, thus requiring pulsatile increase of digit forces between contact and object lift onset. In our study, it is possible that AIP was involved in monitoring the sensory consequence of digit landing on object sites that did not match the expected digit positions (including contact event and grip aperture) and that it triggered corrective digit force responses. However, further work is needed to establish whether this mismatch between expected vs. actual digit positions triggers retrieval of learned mappings between digit positions and forces, or recombination of digit forces as a function of perceived (actual) digit positions.
Conclusions

In the present study, we have shown that subjects can scale their digit forces to the horizontal digit placement using both vision-based anticipatory control (test A) and somatosensory-based feed-forward control (test B) in a manipulation task with high precision requirements. Although minor discrepancies exist between our VR task and manipulation tasks performed with physical objects, we argue that the CNS could have used similar mechanisms to control digit forces in unconstrained real-object manipulation tasks as shown by subjects’ ability to modulate digit forces to variable digit positions resulting from trial-to-trial variability when grasping the same object (Fu et al. 2010, 2011). Our results extend the sensorimotor control point framework by showing for the first time that the sensorimotor system monitors not only local surface properties (e.g., friction and curvature) and the time course of mechanical events (e.g., contact and lift onset) but also digit relative positions when this information is functionally relevant for successful task performance (i.e., to modulate digit forces). Such digit force modulation could be accomplished by both visually based feed-forward planning and postcontact feedback control using nonvisual information.

ACKNOWLEDGMENTS

We thank Dr. Pranav Parikh for comments on an earlier version of the manuscript.

REFERENCES

Buckingham G, Cant JS, Goodale MA. Living in a material world: how visual cues to material properties affect the way that we lift objects and perceive their weight. J Neurophysiol 102: 3111–3118, 2009.