Task-Dependent Modulation of Multi-Digit Force Coordination Patterns

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Task-dependent modulation of multi-digit force coordination patterns. J Neurophysiol 89: 1317–1326, 2003; 10.1152/jn.00581.2002. When grasping and holding an object with five digits under a variety of task constraints, subjects use well-defined force coordination patterns, i.e., consistent force covariations and in-phase synchronization among all digit pairs. The question arises as to whether these force coordination patterns are default mechanisms for controlling multi-digit force production or whether they are specific to lifting and holding an object. To address this question, we asked subjects to grasp a manipulandum and exert forces with five digits simultaneously so as to match a force template measured from an actual object grasp, lift, and hold task (GLH). Unlike GLH, the force production task (FP) lacked the constraint of having to maintain object stability against gravity. The amplitude of individual finger forces and force covariations were similar for both tasks (with the exception of the little finger, which tended to produce less force in FP). Nonetheless, when multiple grip forces were not required to hold the manipulandum against gravity (FP), there was a significantly lower tendency for forces to be synchronized with higher intertrial variability of phase differences between forces exerted by all digit-pairs. Furthermore, the tendency for force phase differences to cluster at 0° was lower for FP than GLH. These results suggest that some aspects of the control of multi-digit grasping, i.e., force synchronization, are specific to object lift and hold rather than to the production of multi-digit forces. Modeling work suggests that motor unit synchronization might play an important role in the modulation of force synchronization patterns.

INTRODUCTION

It is evident from both experimental data and general observation that humans grasp and manipulate objects with ease and dexterity. The mechanisms that underlie how we grasp, with two (Johansson 1998 for review; Johansson and Cole 1994), three (Baud-Bovy and Soechting 2001, 2002; Flanagan et al. 1999), and five digits (Kinoshita et al. 1995; Radwin et al. 1992; Rearick et al. 2002; Rearick and Santello 2002; Reilmann et al. 2001; Santello and Soechting 2000), has attracted considerable scientific attention. These studies have revealed several important features of force coordination during grasping.

For instance, regardless of the number of digits involved (Flanagan et al. 1999; Santello and Soechting 2000), the object’s weight (Johansson and Cole 1994; Reilmann et al. 2001), and frictional properties (Burstedt et al. 1999; Reilmann et al. 2001), there is a tight coupling of grip and load forces, i.e., normal and tangential to the object, respectively. This pattern persists with virtually no temporal delay between normal and tangential force modulation, even while tilting (pronation and supination) (Johansson et al. 1999) or shaking an object (horizontal and vertical) (Kinoshita et al. 1996). This consistent coupling of normal and tangential forces—which lies as the basis for the concept of the “safety margin,” i.e., the ratio of grip force to load force (Johansson and Cole 1994)—suggests that this relationship is an important control variable for maintaining a stable grasp. Other control strategies underlying the control of multiple force directions (3-digit grasping) have recently been described as well (Baud-Bovy and Soechting 2001, 2002; Flanagan et al. 1999).

How multiple digits systematically parcel forces becomes an important issue when examining the coordination of all digits during grasping. This rests primarily with the notion that the number of possible solutions as to how digits distribute normal forces to match thumb normal force is in effect infinite (Santello and Soechting 2000). However, there appears to be only a minimal number of default-like ways in which force is parcelled out across the digits during both multi-finger force production (Li et al. 1998b; Zatsiorsky et al. 2000) and grasp (Rearick and Santello 2002; Reilmann et al. 2001), even though these patterns can be varied according to task constraints, e.g., the object’s center of mass (Santello and Soechting 2000; Zatsiorsky et al. 2002a,b).

Another important question is how digits coordinate forces moment-to-moment so as to ensure a stable grasp of an object against gravity. Recent evidence suggests that forces exerted by all digit pairs tend to covary and to be synchronized under a variety of task constraints. Specifically, these patterns are consistently found regardless of changes in the object center of mass location (Santello and Soechting 2000), its predictability on a trial-to-trial basis, and hand dominance (Rearick and Santello 2002). These multi-digit force coordination patterns also do not appear to be influenced by aging (Rearick et al. 2002).

Nonetheless, the composite of these findings prompts additional questions. For instance, are these patterns simply default mechanisms underlying force production at the digits or does the recruitment of these patterns take into account the physical
constraints associated with lifting and holding an object? We addressed this question by asking subjects to produce force at the digits in such a way so as to effectively remove the constraints normally associated with grasping and lifting an object, i.e., the object remained stationary on the table. This task was designed to allow a comparison with a grasp, lift, and hold task.

We hypothesized that, if certain interdigit relationships, i.e., high force covariations and synchronization, are phenomena associated with force production per se, then they should be equally present in both tasks. However, if these force relationships are modulated, to some extent, to the constraints associated with maintaining object stability against gravity, then the degree of correlation and in-phase synchronization among digit pairs should be less pronounced during force production.

METHODS

Experimental procedures

We measured normal and tangential grip forces using an apparatus (Fig. 1) consisting of five force-sensing modules (FR1010 force sensors, Futek, Laguna Hills, CA), one for each digit. Within each module, one sensor measured the force tangential to the front face of the module, and the other the force normal to it. Throughout this paper, normal and tangential forces exerted by each digit are denoted by the suffix x and y, respectively. All sensors were calibrated with weights ranging from 0.1 to 2 kg, checked for voltage drift throughout the testing session, and evaluated periodically for accuracy of the calibration. Cross talk between the normal and tangential forces measured by each sensor was eliminated by means of a calibration matrix. The average accuracy of the sensors was ±0.2 and 0.1 N for normal and tangential forces, respectively. The front face of each module consisted of a smooth vertical surface and the modules were fixed to two sidewalls, one for the thumb and one for the fingers. The center-to-center distance between modules was 2 cm, the thumb module being aligned with the module for the middle finger (Fig. 1). Each sensor was sampled at 1 kHz. The weight of the apparatus was 0.795 kg. The width of the manipulandum, i.e., the distance between the front faces of the finger and the thumb modules, was 6.25 cm.

Experimental tasks

Subjects were asked to perform two tasks: 1) grasp, lift, and hold the manipulandum (GLH) and 2) grasp and exert forces on the apparatus without lifting the object (force production, FP). This allowed us to assess force relationships during the development of contact forces as well as the maintenance of static force. For both tasks, we asked subjects to place each digit on individual force sensors before starting the task. Subjects were further instructed not to exert force until informed to do so. Compliance with this requirement was verified on-line during data collection and quantified off-line during data analysis (details of the protocols are given below).

Each subject completed the 10-point Edinburgh Inventory to quantify his or her handedness (Oldfield 1971) on a +100 (maximally right-handed) to −100 (maximally left-handed) laterality quotient scale (LQ). LQs from all right-handed subjects ranged from +65 to +100 (85.0 ± 15.6; mean ± SD). One left-handed subject (LQ, −54) also participated in the experiments. All subjects (n = 9; mean age 27.1 ± 6.0 yr) gave their informed consent and the protocols were approved by the Institutional Review Board of Arizona State University.

GLH task

Subjects grasped and lifted a grip apparatus (Fig. 1) with all digits at a self-selected pace to a height of approximately 5 cm from the table. The manipulandum was held for approximately 3 s and then lowered it to its original location. Subjects were instructed to hold the manipulandum aligned with the vertical during the hold phase. The force exerted by each digit was examined over three time periods: 1) time at which the last digit’s normal force crossed a threshold to onset of object lift (force rise phase; Fig. 2, lines A and B); 2) from onset of object lift to onset of device hold (hold phase; Fig. 2, lines B and C); and 3) from onset to end of device hold (hold phase; Fig. 2, lines C and D). Onset of force rise was defined as the time at which the amplitude of the normal force for the last digit to cross a threshold (approximately 0.1 N). A switch signaled the beginning of the lift phase and the end of the release phase. The end of the lift phase was defined as the time at which the first derivative of the sum of the vertical forces crossed below a threshold (0.001 N/s) and remained below it for 300 ms. A similar criterion was used to define the end of the hold phase.

FP task

For this task subjects were asked to exert forces with all digits on the same manipulandum used in GLH (Fig. 1) but without lifting the device from the table. To allow a comparison between the two tasks, we imposed the constraint that the sum of normal forces exerted by all digits (F_n) had to match the time course and amplitude template of F_n measured from an actual GLH task (see following text for details). The target force range was displayed within ±10% of the average total force measured during the hold phase of the GLH task, this range being equivalent to approximately 2.5 N (±1.4)

A computer monitor, placed approximately 0.6 m in front of the subject, provided on-line feedback of the target force. Five “target” lines, two horizontal and three vertical, provided indices of force control (Fig. 2). The three vertical lines indicated the 1) time at which subjects were required to start producing force at all digits (Fig. 2, line C, right column), 2) time at which the target force had to be reached (Fig. 2, line C, right column), and 3) time at which forces could be released (Fig. 2, line D, right column). For each subject, the duration of the time period between vertical lines A and C (FP) corresponding to the duration of the force ramp phase—was based on the time calculated between the onset of force and onset of the hold phase measured from the GLH task. The horizontal lines (Fig. 2, right) indicated how much total force subjects needed to exert on the grip manipulandum. The duration of the constant force phase, i.e., the time interval between vertical lines C and D, was 3 s.

Subjects were instructed to visually follow the F_n trace that scrolled from left to right (approximately 82 pixels/s) across the bottom portion of the monitor. As the trace reached line A (Fig. 2),
subjects were required to produce force on the grip manipulandum. Force exerted on the sensors was displayed as an upward deflection of the scrolling $F_{\text{tot}}$ trace on the monitor. Importantly, subjects were instructed to produce force at all digits in such a way that the object remained stationary, i.e., the object did not inadvertently slide beyond a square target area (10 × 12 cm). This was verified trial-to-trial by the experimenter. It should be noted that no feedback was given about the forces exerted by individual fingers.

The FP task was divided into two time periods: 1) from the time at which the last digit’s normal force crossed a threshold to onset of constant force phase (ramp phase) and 2) from onset to end of constant force phase (constant force phase). Although a target line was given for when to reach the constant force phase (Fig. 2, line C), we found that subjects tended to reach the $F_{\text{tot}}$ target range either slightly earlier or later than indicated, i.e., on average anywhere between approximately 200 ms before to approximately 100 ms after the second vertical line. We therefore selected data for each trial from the onset of force (Fig. 2, line A) to the time point at which total normal force output reached the midpoint of the $F_{\text{tot}}$ target amplitude, i.e., the onset of the constant force phase. Therefore only the time period congruent with force development was selected as the first time period.

To determine the average $F_{\text{tot}}$ to be used for the FP task, subjects performed the GLH tasks first. For both tasks, subjects were given several practice trials before the actual experiment to familiarize them with the instructions and the tasks. Each subject was required to perform 10 trials for each task with their dominant hand. Rest periods of 2 min were interspersed among the trials to avoid fatigue.

Statistical analysis

In this paper we focused on the coordination of normal forces. For the GLH task, analysis of tangential forces was limited to defining the onset and offset of the hold phase (see above; a comprehensive analysis of tangential and normal forces during 5-digit grasping has recently been provided by Reilmann et al. 2001). For the FP task, tangential forces were analyzed to assess whether subjects were pushing down on the grip apparatus, i.e., producing negative tangential forces, throughout the task.

FORCE AMPLITUDE. One-way ANOVA was performed on data from the hold phase for each experiment to assess the effect of task, GLH versus FP, on the amplitude of force at each digit. In both experiments, we analyzed normal forces in two ways: 1) absolute force and 2) force normalized to thumb normal force. For both tasks, the analysis of absolute force at all digits was performed to assess whether each subject produced forces of similar amplitude, both in terms of the total force exerted by all digits as well as individual finger forces in the GLH and FP tasks.

Since the sum of finger normal forces must equal the magnitude of thumb normal force when no acceleration of the object occurs, i.e., during the hold phase for GLH and all phases for FP tasks, variations in the amplitude of finger normal forces can also be due to variations in thumb normal force. To eliminate the effect of thumb normal force fluctuations, we divided the normal force exerted by the index, middle, ring, and little fingers ($F_{\text{index}}$, $F_{\text{middle}}$, $F_{\text{ring}}$, and $F_{\text{little}}$, respectively) by the thumb normal force ($F_{\text{thumb}}$) for both tasks. We could then examine specifically the relative contribution of each of the four fingers opposite the thumb, i.e., the force sharing pattern.

TEMPORAL EVOLUTION OF FORCE SHARING PATTERNS. To examine the temporal evolution of force sharing patterns, we determined the mean grip force exerted by each digit throughout the entire force-rise, lift, and hold phases (GLH) and the ramp and constant force phases (FP). After time normalizing data sets within each grip phase to compute a mean ± SD of 10 trials, we selected discrete time points for analysis. In the GLH, five points were selected as follows: onset of load forces (onset of positive rise in the sum of tangential force exerted by all digits), onset of lift, and three time points during the hold, i.e., hold onset, midhold, and hold end. For FP, five points were chosen as follows: one-third and two-thirds of total ramp time and three time points during the constant force phase, i.e., onset, midpoint, and end. We determined the rank order of digits based on the amplitude of force they exerted. For both GLH and FP, we performed repeated-measures ANOVA for each digit, with the amplitude of normal force at each of the five time points as the within-subjects factor.

In addition to the evolution of the force sharing pattern, we also evaluated the time derivative of normal forces, i.e., the force rate profile, produced by individual digits during the force-rise and ramp phases for GLH and FP, respectively. Our analysis focused on the time-to-peak force rate and peak force rate. These variables have been shown to be finely controlled during five-digit grasping (Reilmann et al. 2001), i.e., normal forces reach their peak almost simultaneously at all digits before object lift occurs. For our purposes, this analysis was used as an additional measure to assess the extent to which the control
of multi-digit forces underlying five-digit grasping can be compared with our force production task.

INTRA- AND INTERTRIAL VARIABILITY. Intra- and intertrial variability of normal forces exerted by each digit was measured for both tasks. Intratrial variability was calculated as follows. For each trial, the SD and mean amplitude of the normal force during the hold (or constant force) phase were calculated for each digit. Intratrial variability was calculated as the CV, i.e., the SD divided by the force averaged across the time period of interest. The overall intratrial variability was the average CV across the 10 trials. Interttrial variability was calculated by averaging across 10 trials the normal force exerted by each digit throughout the hold (or constant force) phase. We defined intertrial variability to be the CV, i.e., SD of the normal force across 10 trials divided by the mean normal force.

TEMPORAL COVARIATION OF NORMAL FORCES: REGRESSION ANALYSIS AND FOURIER ANALYSIS. Linear regression analysis was performed to assess the extent to which normal forces exerted by pairs of digits covaried at each of the three grasp phases (force-rise, lift, and hold) during the GLH and at each of the two grasp phases (ramp and constant force) during the FP. To further assess force covariation at particular frequencies, we performed a fast Fourier transform analysis (FFT) on the forces exerted during the first approximately 2 s (i.e., 2,048 samples) of the hold and constant force phases, respectively. This analysis was performed for each trial and digit. For each subject, the phase difference between the frequency components was calculated for all pairs of digits and for each trial over frequencies from 0.5 to 17 Hz, i.e., 34 frequencies.

We used circular statistics to compute three parameters for each phase difference distribution: the length of the mean vector (r), the mean angle of the sample (ϕ), and the angular deviation (s) (Batschelett 1981; for more details on this analysis see Rearick et al. 2002; Santello and Soechting 2000). The parameters ϕ and s indicate the mean phase difference of the distribution and the amount of dispersion around ϕ, respectively. Randomness of phase difference distributions was tested using the Rayleigh test, which is based on the amplitude of the parameter r. This parameter was computed on the phase difference distribution associated to each frequency. The value of r ranges from 0 to 1, where 0 indicates that phase differences are evenly distributed and 1 indicates that all data are clustered at one angular value, these two extreme cases being defined as random and nonrandom distributions, respectively. Statistical between-condition differences in the mean angle of phase difference distributions and angular deviations were tested using the Watson-Williams test and the concentration parameter test, respectively (Batschelett 1981). Significant differences were tested by comparing pairs of distributions computed from the same frequency. All circular statistic tests were performed on data from individual subjects as well as data pooled from all subjects. We analyzed individual subjects’ data to assess the existence of idiosyncratic patterns of force synchronization. Data were also pooled from all subjects to allow the analysis of phase difference distributions on a larger sample size (see following text) and to better define patterns of force coordination that were common to all subjects.

For the analysis of individual subjects’ data, all of the above tests were computed on phase difference distributions of 10 values (i.e., 1 value per trial) for each frequency. For each subject, we estimated the number of significant distributions (Rayleigh test) and significant between-condition differences in mean angles and angular deviations. We expressed the number of significant distributions and between-condition differences as a percentage of the total number of distributions and comparisons tested, respectively. These percentages were then averaged across all subjects and are reported as the mean percentage of significant distributions or between-condition differences (±SD) of the total number of distributions or comparisons tested. The SD reflects the between-subjects variability in the percentage of significant phase difference distributions or between-condition differences. For the analysis of data pooled from all subjects, the Rayleigh test was computed on phase difference distributions of 100 values (i.e., 10 trials × 10 subjects) for each frequency. The number of significant distributions is reported as the percentage of the total number of distributions and comparisons tested, respectively.

RESULTS

Figure 2 shows the normal forces exerted by each digit and their sum (Ftot) for one representative subject (MR). It can be noticed that the normal forces exerted by the thumb, index, middle, ring, and little fingers (Tt, It, Mt, Rt, and Lt, respectively) are, in general, comparable between the two tasks and, as required by the protocol, Ftot produced for the FP task was statistically similar to that produced for the GLH task (P > 0.05, one-way ANOVA). Mean force levels during the hold and constant force phases (pooled across subjects) were 13.4 ± 3.1 and 13.5 ± 3.1 N, respectively.

A consistent difference between the two tasks was that subjects tended to develop forces across all digits in a more gradual fashion during the transition from the ramp to the constant force phase in FP than GLH. This was likely due to the constraint of having to decelerate the object in GLH, resulting in larger transient forces toward the end of the object lift than during the hold phase. Low-amplitude tangential forces started to develop at the beginning of the FP ramp (Fig. 2, bottom right A–C), i.e., when subjects started to exert normal forces on the manipulandum. During the FP constant force phase (Fig. 2, bottom right C and D), however, the net tangential force (1.7 ± 0.35 N) remained constant and positive. Hence, subjects did not push the manipulandum against the table, as this would have resulted in a net negative tangential forces.

Figure 3 shows the normal forces and force rates from a single trial for two subjects (MS and TL). We found that the rate at which normal forces were exerted during force development was different between the two tasks. Specifically, in GLH the force rate profile was generally bell-shaped, i.e., single-peaked. In contrast, in FP either subjects produced a single, bell-shaped profile early on in the ramp phase and then gradually reached the target force level (e.g., MS) or they developed multiple force peaks throughout the force rise phase (e.g., TL). Despite these differences, however, the time at which all digits reached peak force rate (vertical markers, bottom traces in each panel) was virtually simultaneous in both conditions. Across all subjects, the time interval from the first to the last digit to reach peak force rate ranged, on average, between 19.5 ± 11.3 and 23.3 ± 19.1 ms for GLH and FP, respectively. Therefore, although subjects used somewhat different strategies to develop force in GLH and FP, they generated forces that were tightly coupled during both tasks, with the force exerted by all digits essentially scaling as a unit both in amplitude and time.

Normal force amplitude and variability

Even though subjects were presented with a force range within which Ftot could have been modulated (see METHODS), they tended to produce a force that consistently fell approximately in the middle of the Ftot range. In fact, after reaching the target force area, total force was maintained at a constant amplitude for most of the static force phase (see Fig. 2, right column, Ftot).
The amplitude of normal forces was analyzed in two ways: 1) absolute amplitude of force exerted by each digit and 2) force exerted by each of the four fingers normalized with respect to thumb normal force (see METHODS). The absolute force amplitude of force across digits ranged from $6.6 \pm 1.6$ to $1.2 \pm 0.4$ N (thumb and little finger, respectively) in GLH and from $6.7 \pm 1.6$ N to $0.7 \pm 0.4$ N (thumb and little finger, respectively) in FP. The little finger was the only digit for which a significant difference ($P < 0.05$) between tasks for both absolute and normalized forces was found. Nevertheless, these differences were small (approximately 0.5 N and 7% of thumb normal force, respectively). This difference might reflect a minor redistribution of normal forces among the digits as a result of not having to balance forces and moments against gravity. When grasping our manipulandum, force produced by the little finger is important to counterbalance torques generated by the index finger, this being particularly evident when the center of mass of an object is located closest to the thumb (Santello and Soechting 2000).

With regard to the force variability, the within- and between-trial CV (see METHODS) was significantly lower ($P < 0.05$) in the FP than in the GLH task in most digits (for the little finger, between-trial CV was similar in GLH and FP). The larger GLH force amplitude variability is likely due to the intrinsic kinematic variability associated with lifting and holding an object against gravity.

Emergence of force sharing pattern across discrete grasping phases

We addressed the question of when force sharing patterns used to hold the object emerge over the course of each trial in both tasks (GLH and FP). Figure 4 shows data pooled across all subjects measured at five discrete time points. It can be noticed that, in both experimental conditions, the force sharing pattern emerged very early in both tasks, i.e., during the force rise (GLH) and ramp (FP) phases, and remained relatively stable throughout the remainder of the trial. Therefore regardless of whether the subject lifted and held the manipulandum or whether they simply produced force at the digits, the over force sharing pattern was selected from the outset of the task.

Covariation of normal forces

As found in two previous studies (Rearick and Santello 2002; Santello and Soechting 2000), normal forces were characterized by strong covariations during the force rise phase in GLH, the correlation coefficient ($r \pm SD$), averaged across all pairs of digits, being $0.99 \pm 0.01$. The same held true for FP, with $r$ values across digit pairs being $0.98 \pm 0.02$. The strength of these covariations across all digit pairs decreased in the hold phase.
phase in both tasks, i.e., 0.63 \pm 0.14 for GLH and 0.27 \pm 0.24 for FP.

The difference in the strength of force covariations between FP and GLH during the constant force phase and hold phase, respectively, might have been attributed to the difference in task constraints. However, one point of contention existed that we wished to explore further. Subjects modulated $F_{\text{tot}}$ over a smaller range during the FP constant force phase (0.8 \pm 0.3 N) than during the GLH hold phase (2.5 \pm 1.4 N). To assess the extent to which this difference might have contributed to the difference in the strength of force covariation, we reexamined the force relationships. This was done by selecting time periods within the GLH hold phase during which the $F_{\text{tot}}$ fluctuated over a range of approximately 0.8 N. This range, computed as the difference between the maximum and minimum $F_{\text{tot}}$ produced during hold phase, was comparable to the $F_{\text{tot}}$ range observed in the FP constant force phase. However, this constraint resulted in selecting new time periods that were shorter in GLH than in FP. To allow between-task comparisons, we selected sets of FP data with similar durations to GLH data. As a result, not all trials could be used for this analysis, i.e., on average 4.6 and 4.1 trials per subject (GLH and FP, respectively). These new data series now exhibited force fluctuations over similar ranges, i.e., approximately 0.8 N, occurring across similar time periods, i.e., 720 \pm 220 and 772 \pm 304 ms (GLH and FP, respectively).

Results of this second analysis showed no difference between GLH and FP in the strength of force covariation within any digit pair, average $r$ values across all digit pairs being 0.41 \pm 18 and 0.38 \pm 20, respectively. This finding indicates that the temporal coupling of forces exerted by pairs of digits occurred in a task-independent fashion.

**Frequency domain analysis**

One of the key questions of the present investigation was to assess whether the tendency for synchronization of normal forces found in previous multi-digit grasping studies (Rearick and Santello 2002; Rearick et al. 2002; Santello and Soechting 2000) would still be found when subjects were asked to produce multi-digit forces without lifting the object. We computed phase differences between normal forces from all pairs of digits on data from individual subjects and frequencies (0.5 to 17 Hz; $n = 34$), as well as data pooled across all subjects. This portion of the data in both conditions contained most of the total power (79 and 74\% for GLH and FP, respectively). Analysis on data from individual subjects revealed that most GLH phase difference distributions were nonrandom (Rayleigh test), significant distributions being found in 73.1 \pm 20\% of all distributions across subjects. In contrast, the number of significant FP phase difference distributions was lower, i.e., 52.7 \pm 20\% of all distributions. Figure 5 shows the phase differences for all digit pairs ($n = 10$) and trials ($n = 10$) pooled together from two representative subjects (DR and TL). A predominant number of GLH phase difference distributions tended to cluster at approximately 0°. Although some small between-subject differences were found across frequencies and pairs of digits, a predominant number of GLH phase difference distributions

![Graph](image_url)

**FIG. 5.** Distributions of phase differences between normal forces exerted by pairs of digits. Phase differences between forces exerted by all digit pairs ($n = 10$) are plotted as 3-D histograms across the range of frequencies from 0.5 to 17 Hz. The data shown are from two subjects (DR and TL) and both experimental conditions (GLH and FP). All trials ($n = 10$) for each digit-pair are displayed. For graphical purposes, phase differences, ranging from $-180^\circ$ to $+180^\circ$, were binned into 5° intervals.
tended to cluster at approximately 0°. In contrast, in FP, there is a more random distribution of phase differences, with much less clustering around approximately 0°. The mean angle was then computed from the significant distributions.

Figure 6 shows means and angular deviations (circles and bars, respectively) computed on the phase differences from one subject (CB) for both tasks. It can be noticed that there are fewer significant mean angles in FP than GLH (missing values in the plot indicate angles from nonsignificant distributions). This finding indicates that the relationships between forces exerted by pairs of digits were characterized by higher intertrial variability in FP than in GLH. Furthermore, oftentimes when a significant mean angle did exist, it did not always vary around approximately 0°. In fact, in some cases significant mean angles could be found anywhere between 0° and 180° (e.g., Ix–Rx, Fig. 6). In contrast, the mean angles in GLH tended to cluster at values of approximately 0° (angular deviation ± 50°), indicating a stronger tendency for normal forces to be synchronized in GLH than FP.

This is further illustrated in Fig. 7, where mean angles from significant phase difference distributions only are plotted as histograms for five subjects. Although there are mean angles in FP that center around 0°, the number of occurrences is much smaller than in GLH. The only exception across all subjects was subject MR, who had a high percentage of significant distributions in both conditions (GLH, 100% and FP, 94%). These findings suggest that the extent to which pairs of normal forces are synchronized is partly task dependent, as this force coordination pattern is not as consistent during static multi-digit force production.

Analysis of data pooled from all subjects confirmed the above observations made on individual subjects, as the number of GLH nonrandom phase difference distributions was larger for GLH than FP, i.e., 100 and 72.9%, respectively. Similarly, in GLH, the mean angles tended to cluster at very small angular values, i.e., approximately 0° (range, −14 to 23.3°) with angular deviation ranging from 28.5 to 70°. In FP, the mean angle of phase differences from several digit pairs (i.e., Tx–Ix, Tx–Mx, Tx–Rx, Ix–Mx, and Mx–Rx) ranged from −21 to 30°, with angular deviation ranging from 36.3 to 70.8°. Yet, at other digit pairs, i.e., Ix–Rx, Tx–Lx, Ix–Lx, Mx–Lx, and Rx–Lx, often phase difference distributions were nonsignificant (52%), and, in extreme cases (i.e., Mx–Lx), most mean angles were approximately 180° out-of-phase. Overall, those digit-pairs containing the little finger were the most influenced by not
lifting and holding the grip apparatus. However, as shown in Fig. 6, the disruption in force synchronization was idiosyncratic to subject and could, as in the case of subject CB, affect many digit pairs to varying degrees.

Reevaluation of phase difference distributions

As with the correlation analysis presented earlier, we were concerned that differences in the extent of force fluctuation between conditions (see previous text) might have also affected force relationships in the frequency domain. To address this issue, we reanalyzed the data over the final 2 s of the hold phase, typically ranging between 3 and 4 s. This represented the time period within which force was more stable across all digits (see Fig. 2), as most of the modulation in digit force occurred during the earliest stages of the hold and constant force phase (GLH and FP, respectively). This time period was selected so as to perform FFT analysis with a similar frequency resolution (0.5 Hz, based on our sampling rate of 1 kHz) as we did in our original assessment. Within this new time period, $F_{\text{tot}}$ modulation occurred to a lesser extent, on average 1.25 ± 0.65 N. This represented a twofold decrease in the amount $F_{\text{tot}}$ fluctuated compared with the entire hold phase of GLH (approximately 2.5 N) and therefore was more comparable with the force fluctuation observed in FP (approximately 0.8 N).

We found that the number of GLH nonrandom phase difference distributions from the last 2 s of the hold phase was the same as that found when evaluating the entire GLH hold phase, i.e., 100% of the distributions were nonrandom (data pooled from all subjects). The mean angles and angular deviations ranged from −22.3 to 19.8° and 36.7 to 70.5°, respectively (original GLH hold phase mean values and angular deviations ranged from −14 to 23.3° and 28.5 to 70°, respectively). Therefore the lower degree of between-digit force synchronization in FP was not due to task differences in the amount of force fluctuation.

Phase distributions: between-condition evaluation

Our findings show that pairs of digits tended to exert normal forces in a synchronous fashion in GLH and less so in FP. Yet the fact that many phase differences distributions were nonrandom and characterized by small mean angle values did not exclude the possibility that systematic mean angle (or angular deviation) differences might have existed between conditions. For instance, just because a phase difference distribution at a given frequency may be significant for two conditions (GLH and FP) does not necessarily imply that the mean angle (or angular deviation) is the same between the conditions. We addressed this issue by performing a Watson-Williams test (see METHODS) on data from individual subjects.

We found significant between-condition differences in mean angle for each subject. These differences were found, on average, in 23 ± 10.9% of the total number of distributions tested. Of these distributions, differences in mean angles varied considerably, ranging anywhere between 12 and 195°. We also used the concentration parameter test to check for significant differences in angular deviations between conditions. We found significant differences for each subject in the total number of distributions tested (35.9 ± 19.6%). Interestingly, these differences were very consistent across digit pairs and subjects, with the angular deviations observed in GLH being, on average, −16.4 ± 4.3° smaller than in FP. Therefore, even though in most cases (>75%) mean angles were statistically similar between conditions, the trial-to-trial variation around those angles was significantly greater in FP.

Overall, in addition to the fact that there were fewer significant mean angles in FP (~23%), often these mean angles were significantly different from those computed at the same frequencies in GLH (23 ± 10.9% of all comparisons). Furthermore, FP mean angles were also more variable from trial to trial, i.e., larger angular deviations (35.9 ± 19.6% of all comparisons). These findings suggest that force synchronization at the digits during multi-digit grasping is party derived from the physical constraints associated with lifting and holding an object and not just with force production at the digits.

DISCUSSION

The present results indicate that the coordination of multi-digit forces is characterized by two main control patterns. The first pattern, i.e., consistent time-invariant force sharing patterns and force covariations, is found whenever multiple contact forces have to be produced simultaneously. In particular, our results indicate that this pattern operates regardless of the task constraints examined here, i.e., independently of whether the coordination of multiple forces is necessary to either hold an object against gravity or to produce ramp and constant forces. In contrast, the second control pattern, i.e., synchronization of normal forces exerted by pairs of digits, seems to be affected by the task functional requirements.

Task-independent force control patterns underlying force production

Before discussing similarities and differences in the control of forces between our two tasks, it is important to briefly review some important features of 5-digit grasping. For whole hand grasping the distribution of normal forces exerted by the fingers is indeterminate. Specifically, many solutions can be used to satisfy the conditions of static equilibrium where the sum of normal forces exerted by all fingers is equal and opposite to thumb normal force. Nevertheless, even though there is no a priori one-to-one relationship between a given force sharing pattern and object properties, i.e., object weight, texture or center of mass location, subjects tend to use force sharing patterns in a consistent fashion from trial to trial (Rearick and Santello 2002; Reilmann et al. 2001; Santello and Soechting 2000; Zatsiorsky et al. 2002a,b).

Another feature that has been consistently reported in the literature on multi-digit grasping is that force sharing patterns are established very early in the task, i.e., before the object is lifted, and maintained throughout object lift and hold (Rearick and Santello 2002; Rearick et al. 2002; Reilmann et al. 2001; Santello and Soechting 2000). The present results extend this observation to our multi-digit force production task (FP), as the overall force sharing pattern was selected (a) at the onset of force production and (b) maintained throughout the task as force amplitude at each digit increased. In fact, the grasp, lift and hold (GLH) force sharing pattern was altered only to a very limited degree (i.e., little finger) when producing forces on the manipulandum.
The early setting of a force sharing pattern has also been suggested by Li et al. (1998b) who reported that all digit forces increase linearly throughout the ramping of forces both in a force production task and grasp, lift and hold (maximal squeeze) task. In addition, these authors reported that peripheral digits, i.e., the index and little fingers, produce higher peak forces during object grasp, lift and hold than during force production, a finding similar to the slightly higher forces we observed in the little finger during GLH. It should be noted, however, that the focus of Li et al.’s (1998b) study was on quantifying force relationships (a) during maximal force output and (b) during ramping but not constant forces. In contrast, our study focused on comparing relationships between sub-maximal forces exerted during object lift and hold versus ramp and constant phases, respectively. In fact, our results show that the major task-dependent difference, i.e., strength and consistency of force synchronization between digit pairs, seems to occur when multi-digit forces are relatively constant, i.e., during object hold and constant force output (see following text).

The present results have revealed other task-independent features of multi-digit force control. Specifically, we found that the normal forces exerted by pairs of digits covaried in the time domain to a similar extent in both tasks. We also found that the peak rate of force production of individual digits during GLH force development and FP ramp phases tended to be synchronized regardless of task differences in the time course of forces (Fig. 3). Although this behavior has been described for 5-digit grasping (Reilmann et al. 2001), the results from our FP task indicate that synchronization of peak force rate is associated with multi-digit force production, rather than being limited to whole hand grasping. Therefore these control mechanisms can be viewed as default-like, as they clearly operate whenever multiple forces are produced simultaneously by all digits regardless of whether the object has to be held against gravity or not.

Both the neural and biomechanical architecture of finger muscles likely play a major role in the simultaneous scaling of normal forces at all digits and their temporal covariation. Several lines of evidence indicate that each hand muscle is represented in a wide area of primary motor cortex that overlaps with cortical areas of other hand muscles. Hence, the control of a given finger movement direction or force is best described by the activation of broadly distributed neural networks rather than well-defined clusters of neurons (Georgopoulos et al. 1999; Poliakov and Schieber 1999). At a more peripheral level, several studies have also described the limited extent to which a given digit can exert force or move independently from other digits (Häger-Ross and Schieber 2000; Zatsiorsky et al. 2000). Here, the architecture of extrinsic flexor and extensor muscles is also likely to be a contributing factor of digit movement and force covariation (Schieber 1991, 1995).

**Task-dependent force control patterns underlying force production**

A closer examination of the temporal coordination of digit forces, i.e., frequency domain analysis, revealed some important differences between the two tasks studied. Specifically, between-digit force synchronization was consistently high when holding the object, but much weaker and less consistent when producing forces without holding the object (Figs. 5–7).

As subjects produced similar average forces during the GLH hold and FP constant force phases, we can rule out force amplitude as a factor responsible for task differences in force synchronization. Nevertheless, total normal force exerted by all fingers fluctuated to a larger extent across the entire GLH hold phase than during the FP constant force phase. To control for this unavoidable difference, we re-analyzed force time series that fluctuated over a force range that was more comparable between the two tasks. The results of this additional analysis revealed the same task differences in the strength and consistency of force synchronization.

We are left to conclude that between-digit force synchronization is not a default mechanism strictly associated with digit force production, as it appears to be dependent - to some extent - on the physical constraints associated with holding an object vertical against gravity. Interestingly, during other lift and hold tasks, force synchronization is still found when forces exerted by individual digits have to be modulated as a function of object center of mass (COM) location (Santello and Soechting 2000), as well as when COM cannot be predicted on a trial-to-trial basis and when grasping with the nondominant hand (Rearick and Santello 2002). Consistent force synchronizations have also been found in elderly subjects and Parkinson’s disease patients, even though these patterns are selectively disrupted at action tremor frequency (6–10 Hz; Rearick et al. 2002).

The consistent and accurate force synchronization between all pairs of digits during object hold might represent a strategy to ensure object stability. This would be attained by constraining the action of all digits to work as a unit, leading to a significant reduction in the risk for object slips. This interpretation is consistent with a more variable and lower tendency for forces to be synchronized during the FP task, where the constraint of ensuring object stability against gravity does not exist. In this case, weaker force synchronization translates into individual digits scaling force on a moment-to-moment basis more independently from each other. Overall, the present results lend support to the notion that force synchronization is a mechanism that maintains an important functional role in multi-digit grasping, i.e., it is a critical feature of force control for balancing an object against gravity, while much less important for force production per se.

**Neural mechanisms underlying the control of multi-digit grasping**

Based on our current understanding of between-digit force synchronization, an open question remains: what is the neural mechanism underlying fingertip force synchronization? We have in the past suggested that motor unit (MU) synchronization might be a mechanism responsible for constraining the temporal relationships between grip forces (Rearick and Santello 2002; Rearick et al., 2002; Santello and Soechting 2000). To support this interpretation, we need to determine whether changes in the strength of MU synchronization can directly affect the extent to which pairs of forces are synchronized. If such a relationship exists, it might account for the present results of variable and task-dependent strength in force synchronization.

For this purpose, we have recently conducted a simulation study (Fuglevand and Santello 2002). A MU model (Fuglevand
et al. 1993) was used to simulate force produced by two muscles using three physiological levels of MU synchrony across the two muscles. In one condition, MUs in the two muscles discharged independently of one another. In the other two conditions, the timing of randomly selected MU discharges in one muscle were adjusted to impose low or high levels of synchrony with motor units in the other muscle (common input strength, CIS = 0.3 or 0.6 extra synchronous events/s; Sears and Stagg 1976). It was found that the number of significant phase difference distributions increased drastically with increasing synchronization strength from 3% for no synchrony to 65% and 76% for low and high synchrony conditions, respectively. Importantly, most of the mean angles of significant distributions clustered at very small phase difference values (approximately 0° to 10°), indicating a strong tendency for forces to be exerted in a synchronous fashion.

These results suggest that a relationship does exist between MU and force synchronization, i.e., increasing strength of MU synchronization leads to stronger force synchronization. Therefore the higher force synchronization found during GLH versus FP could be accounted by stronger - and task-dependent - MU synchronization. Although the MU/force synchronization data are from a simulation study, experimental evidence exists that MU synchronization might be modulated in a task-dependent fashion. Specifically, modulation in the strength of synchronization from intrinsic hand muscles MUs have been reported during isometric finger flexion versus extension (Bremner et al. 1991) as well as power versus precision grip tasks (Huesler et al. 1998). Overall, it appears that MU synchronization might be lowest when the task requires a more independent control of individual digits, i.e., lower during precision than power grip (Huesler et al. 1998).

The results of the simulation study suggest that MU synchronization could play a significant functional role in the coordination of grip forces during grasp, lift and hold. The task-dependency of motor unit synchronization during 5-digit grasping is now being studied in our laboratory to determine the input-output relationship between neural commands and the coordination of grip forces.

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