Common Input to Motor Units of Digit Flexors During Multi-Digit Grasping

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Winges, Sara A. and Marco Santello. Common input to motor units of digit flexors during multi-digit grasping. J Neurophysiol 92: 3210–3220, 2004. First published July 7, 2004; doi:10.1152/jn.00516.2004. The control of whole hand grasping relies on complex coordination of multiple forces. While many studies have characterized the coordination of finger forces and torques, the control of hand muscle activity underlying multi-digit grasping has not been studied to the same extent. Motor-unit synchrony across finger muscles or muscle compartments might be one of the factors underlying the limited individuation of finger forces. Such “unwanted” coupling among finger forces, however, might be desirable when a high level of force coupling is required to prevent object slip during grasping. The goal of this study was to quantify the strength of synchrony between single motor units from extrinsic hand muscles as subjects held a device with a five-digit grasp. During the hold phase, we recorded the normal force exerted by each digit and the electrical activity of single motor units from each of the four divisions of the muscle flexor digitorum profundus (FDP) and one thumb flexor muscle, m. flexor pollicis longus (FPL). The strength of motor-unit synchrony was quantified by the common input strength index (CIS). We found moderate to strong motor-unit synchrony between FPL and the index FDP compartment [CIS: 0.49 ± 0.03 (SE)] and across most FDP compartments (0.34 ± 0.02). Weak synchrony, however, was found between FPL and the middle, ring, and little finger FDP compartments (0.25 ± 0.01). This difference might reflect the larger force contribution of the thumb-index finger pair relative to other thumb-finger combinations in five-digit grasping.

INTRODUCTION

Grasping requires an exquisite coordination of finger motion and forces. Due to the complex biomechanical and neural architecture of the hand, several complementary approaches have been used to improve our understanding of how the hand is controlled. The coordination of finger motion and forces has been studied directly using behavioral tasks such as reach-to-grasp (e.g., Mason et al. 2001; Santello and Soechting 1998, 2000; Winges et al. 2003) and object hold (e.g., Baud-Bovy and Soechting 2002; Burstedt et al. 1999; Johansson and Cole 1994; Rearick and Santello 2002; Reilmann et al. 2001). However, the neural control of grasping, as measured through hand muscle electromyography (EMG) has been inferred primarily through force-production tasks (e.g., Bremer et al. 1991a–c; Huesler et al. 1998, 2000; Keen and Fuglevand 2004; Kilner et al. 2002; Maier and Hepp-Reymond 1995a,b; Mills and Schubert 1995; Reilly et al. 2004; Valero-Cuevas 2000; Valero-Cuevas et al. 1998; but see Brochier et al. 2004 and Weiss and Flanders 2004 for recent investigations of hand shaping and hand muscle EMG).

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This study was designed to characterize the organization of common input to extrinsic hand muscles during a natural five-digit grasping task. As normal forces exerted by all digit pairs are coupled to ensure a stable grasp (e.g., Rearick et al. 2003), we expected that our task would elicit a uniform strength of common input across muscles and muscle compartments controlling each pair of digits. We quantified the strength of common input received by motor units from each of the four divisions of the muscle FDP and one thumb flexor muscle, m. flexor pollicis longus (FPL). We found moderate to strong motor-unit synchrony across FDP compartments and between FDP compartments and FPL. Contrary to our expectation, however, we found that across-muscle synchrony was significantly stronger for FPL and the FDP index finger compartment than for FPL and any other finger FDP compartment. The strength of motor-unit synchrony across FDP compartments was generally more uniform. Furthermore, our data revealed a distribution of synchrony strength across FDP compartments that is different from that reported during static force production (Reilly et al. 2004). Preliminary accounts of these results have been published as abstract (Winges et al. 2003).

METHODS

Experimental task

A total of eight subjects (4 males and 4 females; mean age: 29 yr, range: 21–37 yr) took part in the experiments. The experimental procedures were approved by the Institutional Review Board at Arizona State University and were in accordance with the declaration of Helsinki. All subjects gave their informed consent prior to each recording session. Subjects sat in an adjustable dental chair with their right arm resting on a flat platform. The subject’s elbow remained on the platform surface during the hold phase to prevent fatigue of the arm and shoulder muscles. We asked subjects to grasp, lift, and hold a grip manipulandum (weight: 0.250 kg; Fig. 1) upright for a minimum period of 3 min. Before lifting the device, subjects placed the distal finger pad of each digit on its respective force sensor plate (see following text). After establishing a firm grasp, subjects were asked to lift the device at a height of ~5 cm from the support surface. After object lift, the experimenter placed a soft support (a rolled towel) under the forearm and proximal to the ulnar styloid to prevent fatigue of the elbow flexor muscles. Hence the only task requirement was to exert sufficient forces at the fingertips to prevent object slip while maintaining the object aligned with the vertical. We did not measure the orientation of the object during object hold, hence the alignment with the vertical was approximate. Before starting data recording, the subject aligned the object with the vertical based on visual estimation of the device orientation and verbal feedback provided by the experimenter. This orientation was maintained throughout the experiment.

Note that the preceding forearm support did not relieve extrinsic digit flexor (and extensor) muscles of the need to generate a radial moment at the wrist while holding the object. Hence, we expect the neural control of digit flexors assessed by our task to be similar to that required to hold an object when elbow muscles are also active to support the forearm. The statistical analysis of motor-unit activity required a minimum recording session of 3 min to ensure the acquisition of a minimum number of motor unit action potentials, i.e., 900. We gave rest periods of a minimum 5 min between trials to ensure that subjects were fully rested before starting a new trial.

Force and EMG recording

Forces exerted by the fingers and the thumb were measured by five force/torque transducers (4 Nano17/SI-25-250 and 1 Nano25/SI-125-03, respectively; ATI Industrial Automation, Apex, NC; nominal resolution: 0.0015 and 0.015 N, respectively). The diameter of the sensors for the fingers and the thumb was 17 and 25 mm, respectively. For the present study, we analyzed only forces normal to the sensors. The average normal force measurement error ranged from 0.003 ± 0.009 to 0.007 ± 0.003 (SE) N for the finger sensors and from 0.066 ± 0.108 to 0.143 ± 0.019 N for the thumb sensor. The vertical position of each sensor (Fig. 1) was adjusted to each subject’s hand size to allow a comfortable grip.

Motor-unit potentials were recorded with tungsten microelectrodes inserted into FDP and FPL (Frederick Haer, Bowdoinham, ME; 1- to 5-μm tip diameter, 5- to 10-μm uninsulated length, 50-mm shaft length; 250-μm shaft diameter, ~200 kΩ impedance at 1.000 Hz after insertion). One surface electrode (10-mm-diam gold-plated silver disc, Model F-ESGH, Grass Instruments; West Warwick, RI) was placed on the radial styloid to serve as a reference electrode for each intramuscular electrode. On the day of the experiment, the coordinates of the insertion sites were estimated based on anatomical location (Agur et al. 1991), a map of hand muscles devised from previous intramuscular EMG recordings (courtesy of Dr. A. Fuglevand, University of Arizona) and palpation during flexion of the digit associated with the target muscle or muscle compartment. Two microelectrodes were inserted to record the activity of separate motor units in either two digit compartments of FDP or one digit compartment of FDP and FPL. Once both electrodes were in place, we verified microelectrode placement using weak electrical stimulation (50–400 μA, 1-ms duration, 1 Hz; S48 Stimulator, Grass Instruments). The depth and/or angle of insertion of the microelectrode were adjusted until an individual movement of the target digit was achieved. Isolated movement of the distal phalange indicated that the microelectrode was in the desired target muscle or muscle compartment. Verification of electrode placement through electrical stimulation was essential to distinguish motor units belonging to FDP from those belonging to m. flexor digitorum superficialis (FDS) inserting on the middle phalange, as both of them are active during finger flexion. After this procedure, subjects performed isometric contractions at each digit to confirm that the microelectrode detected only the electrical activity of the target muscle or muscle compartment. Electrodes were then connected to differential amplifiers and the intramuscular EMG signals were amplified (×1,000), band-pass filtered (0.3–3 kHz; Grass Instruments), and displayed on oscilloscopes.

After the position of each microelectrode was verified, the subject grasped, lifted, and held the manipulandum vertically above the platform surface. The output of both electrodes was monitored on oscilloscopes while the subject held the grip device. The trigger level of the oscilloscopes was adjusted to determine the extent to which a single motor unit could be reliably discriminated from other motor
units firing in the background. We also used an audio monitor of the motor unit firing to further assess the quality of the EMG signal before starting the recording. The orientation and/or the depth of penetration of each microelectrode were slightly adjusted until the activity of a single motor unit could be detected. Data recording lasted for 3–4 min after which the subject replaced the object on the platform. When single motor units could not be isolated on both channels within 1 min after onset of object hold, the subject replaced the device on the platform, and a rest period was given before repeating the preceding procedures. Before recording a new trial, the needle electrodes were slightly repositioned until a new motor unit could be detected in at least one channel. Subjects were then asked to exert tension with each digit to verify that the needle electrode was still detecting EMG activity from the target muscle. For some compartments of FDP (i.e., FDP3 and FDP4), the repositioning of the needle electrode occasionally did cause the detection of muscle activity from compartments other than the one studied. In these cases, we used electrical stimulation as described in the preceding text until a selective movement of the target finger could be elicited, and the preceding procedures were repeated. Within a single experimental session, we recorded EMG activity from 3 to 10 pairs of motor units from either FPL and one compartment of FDP (FDP2, -3, -4, or -5 acting on the index, middle, ring, and little finger, respectively) or two different FDP compartments.

Experimental constraints such as maintaining a constant motor-unit firing rate or force amplitude are often imposed when studying motor-unit behavior. Both constraints are generally used to facilitate the analysis of single motor-unit action potentials. These constraints, however, might also interfere with a natural modulation of muscle activity and forces. Therefore to allow physiological variability of motor-unit firing rate during object hold, subjects did not receive auditory feedback of firing rate during the trial. Similarly, no visual feedback of the forces exerted on the device was given to allow a natural distribution and fluctuation of individual fingertip forces during object hold.

**Data acquisition and analysis**

EMG and force data were acquired synchronously by three 12-bit A/D converter boards (National Instruments, Austin, TX). One 16-channel board (E-Series DAQ 6023E) was used to acquire the EMG data with a sampling frequency of 20 kHz. Another 16-channel board and a 64-channel board (E-Series DAQ 6701) were used to acquire the force data at a sampling frequency of 1 kHz. Custom software (LabVIEW 6.1, National Instruments) was used to acquire, display, and store EMG and force data.

**NORMAL FORCES.** Custom software written in MATLAB (version 6.5, The MathWorks, Natick, MA) was used to analyze force data. In this study, our main analysis focused on normal forces exerted by each digit and their temporal relationships. We also computed the horizontal torques exerted by each digit as these are important in preventing the object from tilting around the long axis of the forearm. Horizontal torques were computed as the product of normal forces and the vertical distance between the center of each finger sensor and the center of the thumb sensor. Positive and negative values denote counterclockwise and clockwise torques, respectively.

The temporal relationships between forces exerted by pairs of digits were analyzed by performing fast Fourier transform analysis (FFT) and circular statistics as done in previous studies (Rearick et al. 2002; Santello and Soechting 2000). Briefly, we performed FFT on forces exerted during the entire hold period (4 min) and computed the phase response by calculating the arctangent of the ratio of the imaginary and real components of the Fourier transform. The phase difference between pairs of forces is indicative of the temporal relationship between forces at a particular frequency. For comparison with previous grasping studies, phase differences were calculated over frequencies from 0.5 to 17 Hz in 0.5-Hz frequency increments (n = 34). For each frequency, a distribution of 10 phase differences was generated, i.e., one phase difference value per trial.

For each frequency, we used circular statistics (Rayleigh test) to assess whether phase differences tended to cluster at a particular angular value or to be distributed uniformly across ±180° range of phase differences, i.e., whether the phase difference distributions were nonrandom or random, respectively (Batschelet 1981; for a detailed description of the analysis, see Santello and Soechting 2000). The mean angle of phase differences was computed only for the nonrandom phase difference distributions.

EMG. EMG data were analyzed off-line using commercial and custom-designed software. Individual motor units were discriminated from each channel using an algorithm that developed templates based on amplitude and temporal characteristics of the action potential (Spike2, Cambridge Electronic Design, Cambridge, UK). The template matching resulted in the identification of at least one motor unit per channel. The quality of the automatic discrimination was visually inspected for each trial before performing further data processing. Motor-unit discharges characterized by very short (<20 ms) intervals between action potentials (ISIs) were classified as false-positive errors and eliminated from analysis. The motor-unit discrimination was reliable as demonstrated by the very low incidence of false-positive errors, i.e., less than ~1% of ISIs per trial. In tasks where subjects are asked to maintain a constant motor-unit firing rate, it is also possible to define false-negative discrimination errors (Nordstrom et al. 1992). These errors can be visualized as banding of intervals at multiples of the target firing rate and result from chance superimposition with action potentials of other motor units. In our task, however, we did not require subjects to maintain a constant motor-unit firing rate. As a result, most of our ISI distributions lacked well-defined ISI subdistributions at multiples of the mean firing rate (~10 Hz, i.e., ISIs centered within ~50 and ~150 ms; Fig. 2D). ISI sub-distributions centered at longer ISIs are more likely to reflect the natural (unconstrained) variability of motor-unit firing rate during object hold. Therefore we used the entire ISI distribution (after elimination of false-positive discrimination errors) to compute mean, SD, and coefficient of variation of motor-unit discharge rate.

The within-trial variability of firing rate (Table 1) was comparable to the coefficient of variation of firing rate reported by other studies using visual or auditory feedback (e.g., Kilbreath et al. 2002). As the extent to which normal and temporal forces fluctuate during static object hold is fairly small, the quality of most of our EMG recordings (~70%) was sufficiently good to allow reliable discrimination of single units (Fig. 2C). We did, however, reject a significant amount of trials (~30%) due to insufficient number of events (<900 spikes within a trial) or when other units started firing and prevented a reliable discrimination of single motor units.

Motor-unit discharge rate was subsequently computed on the discriminated units. To assess whether there were any average increases or decreases in the discharge rate within each trial, we performed least-square regression analysis on each motor unit. We then subtracted the slope of the regression line from the data to remove any trend (Laidlaw et al. 2000). The mean and SD of the mean motor-unit discharge rate were computed on the detrended data from each trial. These values were then used to compute the coefficient of variation (CV) to quantify the within-trial variability of discharge rate.

Custom software developed by Dr. A. Fuglevand was used to quantify motor-unit synchronization. A reference and test channel were defined (arbitrary) and a cross correlogram (1-ms bin, 201 bins) between the two motor units was computed for ±100 ms from the discharge of the reference unit (Fig. 4, bottom). A cumulative sum (cusum) (Ellaway 1978) was computed to determine the existence of a peak in the cross correlogram indicating synchronous firing of the two motor units (Fig. 4, top). The peak was defined by the area between the 10th to 90th percentiles of the largest inflection in the
cusum within ±20 ms of the reference unit firing (Schmied et al. 1993) (time period within the 2 dotted vertical lines in Fig. 4). If a peak could not be defined within this region, a narrowed region of ±6 ms from the firing of the reference unit was used for the assessment of the strength of motor-unit synchrony for that motor-unit pair.

The duration of the cross-correlogram peak has been used to further interpret the mechanisms leading to motor-unit synchrony. Narrow cross-correlogram peaks resulting from motor units discharging within a few milliseconds of each other (short-term synchronization) would arise from shared inputs from branched axons of single last-order neurons (Kirkwood 1979). Broader cross-correlogram peaks would reflect synchrony of separate presynaptic inputs to the motoneurons. To assess possible differences in the patterns of common input, we computed the width of the cross-correlogram peak for each motor-unit pair.

We used the common input strength index (CIS) (Nordstrom et al. 1992) to quantify the strength of motor-unit synchrony. The value of the CIS index represents the number of synchronous discharges for a motor-unit pair above chance level. Chance level is defined as the mean number of counts (spikes) per bin occurring in time bins from 100 to 40 ms and from 40 to 100 ms (Fig. 4, bottom row, horizontal lines). The CIS was computed as the ratio of the total counts in the peak of the cross correlogram defined by the cusum minus the counts due to chance normalized by trial duration. The criterion for using a pair of motor units for the computation of the CIS was tonic discharge defined as 900 spikes occurring without large

### TABLE 1. Motor-unit firing rates, firing rate variability, and CIS

<table>
<thead>
<tr>
<th>MU Pairs</th>
<th>GM Firing Rate, Hz</th>
<th>GM CV Firing Rate, %</th>
<th>CIS</th>
<th>Peak Duration, MS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Across muscles</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FPL-FDP2</td>
<td>19</td>
<td>11.36 ± 0.29</td>
<td>28.22 ± 2.50</td>
<td>0.49 ± 0.03</td>
</tr>
<tr>
<td>FPL-FDP3</td>
<td>51</td>
<td>10.47 ± 0.16</td>
<td>25.51 ± 1.10</td>
<td>0.26 ± 0.02</td>
</tr>
<tr>
<td>FPL-FDP4</td>
<td>14</td>
<td>11.12 ± 0.25</td>
<td>25.22 ± 1.92</td>
<td>0.25 ± 0.03</td>
</tr>
<tr>
<td>FPL-FDP5</td>
<td>31</td>
<td>10.21 ± 0.22</td>
<td>27.17 ± 0.81</td>
<td>0.23 ± 0.03</td>
</tr>
<tr>
<td>Across FDP compartments</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FDP2-FDP3</td>
<td>31</td>
<td>11.00 ± 0.18</td>
<td>23.30 ± 0.64</td>
<td>0.32 ± 0.03</td>
</tr>
<tr>
<td>FDP2-FDP4</td>
<td>32</td>
<td>10.68 ± 0.15</td>
<td>23.10 ± 0.72</td>
<td>0.20 ± 0.03</td>
</tr>
<tr>
<td>FDP2-FDP5</td>
<td>16</td>
<td>11.74 ± 0.30</td>
<td>21.66 ± 1.36</td>
<td>0.39 ± 0.06</td>
</tr>
<tr>
<td>FDP3-FDP4</td>
<td>47</td>
<td>10.72 ± 0.25</td>
<td>27.08 ± 1.47</td>
<td>0.37 ± 0.03</td>
</tr>
<tr>
<td>FDP3-FDP5</td>
<td>15</td>
<td>11.39 ± 0.30</td>
<td>25.03 ± 1.76</td>
<td>0.48 ± 0.05</td>
</tr>
<tr>
<td>FDP4-FDP5</td>
<td>21</td>
<td>11.14 ± 0.22</td>
<td>25.66 ± 2.65</td>
<td>0.38 ± 0.06</td>
</tr>
</tbody>
</table>

For each muscle/muscle compartment pair, the number of motor-unit (MU) pairs included in the analysis is given along with the geometric mean (GM) of firing rate and coefficient of variation (CV), the common input strength index (CIS), and the duration of the cross-correlogram peak. All values are means ± SE.
gaps (<1 s) between spikes. The CIS was preferred over other synchrony measures due to its lower sensitivity to across-trials differences in discharge rate (Nordstrom et al. 1992). This was an important factor for our study since motor unit discharge rate was not constrained (see preceding text).

CIS computed on hand muscles often ranges from 0 to sometimes slightly over 1.0 (e.g., Keen and Fuglevand 2004; Semmler and Nordstrom 1998; our current data) (Fig. 5) although higher values (i.e., CIS >2) have also been reported from studies of maximal and sub-maximal isometric forces (e.g., Kamen and Roy 2000). On average, units within the same hand muscle or muscle compartment usually have CIS values ~0.4–0.5. Therefore a CIS value of 0.6 would indicate relatively strong synchrony, whereas 0.3 would be a moderate but still significant level. CIS values <0.3 are associated with weak motor-unit synchrony as no clear peaks in the cross-correlogram can be discerned (Fig. 4A) (i.e., Fig. 2 in Semmler and Nordstrom 1998; our current data).

We performed linear regression analysis to assess the extent to which motor-unit firing rate and the coefficient of variation of firing rate affected the amplitude of the CIS index. For this analysis, we computed the geometric mean of the firing rate and of the coefficient of variation of firing rate for each motor-unit pair (Nordstrom et al. 1992). One-way ANOVA was used to test for main effect of muscle/muscle compartment combination on the duration of the cross-correlogram peaks and CIS values. We also tested whether the degree of separation between FDP compartments had a significant effect on the strength of motor-unit synchrony. When a main effect was found post hoc comparisons were performed using t-test. A significance level of \( P < 0.05 \) was used for all comparisons.

RESULTS

Analysis of motor-unit activity during object hold revealed moderate to strong motor-unit synchrony between FPL and FDP compartments and across FDP compartments. For the across-muscle analysis, we found that the strength of synchrony was particularly strong between motor units from FPL and the index finger compartment of FDP. In contrast, motor units from FPL and the remaining finger compartments of FDP exhibited weak synchrony. For the across-FDP compartment analysis, we found moderate to strong motor-unit synchrony across all but one pair of FDP compartments, i.e., FDP2 and FDP4.

Motor-unit activity and grip forces during object hold

Intramuscular EMG was recorded from either two different muscles (FPL-FDP) or two different compartments of the FDP (see METHODS). Figure 2A shows a typical record of forces exerted by all digits and EMG from a thumb muscle (FPL) and the index compartment of the FDP (FDP2) during object hold. The forces measured were normal to the surface of the sensor for each digit (Fig. 1). Although the object was held static, small fluctuations in individual fingertip forces occurred during the hold.

Single motor units were identified from the raw data and discriminated within each channel (Fig. 2B; see METHODS). In some recordings, more than one motor unit could be detected and discriminated from a single channel. As the force exerted by each digit was relatively constant, the firing rate of each motor unit was fairly stable throughout the entire trial as demonstrated by the sample section of recording shown in Fig. 2B. C shows a single motor unit discriminated from each EMG record, and D shows the ISI distribution for each motor unit.

We were able to reliably record single motor-unit activity from the target muscle (FPL) and each FDP muscle compartment. The little finger compartment of FDP (FDP5) was the most difficult to record from due to its smaller size relative to other FDP compartments. Often the motor units from this FDP compartment would fire tonically at the beginning of the trial and then stop firing or they would fire intermittently. This irregular firing rate behavior was probably due to the smaller force contribution relative to the total force required to hold the object. Due to the low yield of motor units after two or more recording sessions, two subjects were excluded from our group. A total of 381 motor units were discriminated from raw EMG records of FPL and the four compartments of FDP, yielding 277 motor unit pairs for analysis of synchrony.

Although the device was light, the distribution of thumb and finger normal forces was similar to those reported by previous studies on multi-digit grasping with heavier objects (i.e., >1 kg) (Rearick and Santello 2002; Santello and Soechting 2000), finger forces being progressively smaller from the index to the little finger. Mean forces produced by each digit were 2.85 ± 1.05, 1.31 ± 0.46, 0.78 ± 0.19, 0.75 ± 0.22, and 0.62 ± 0.21 (SD) N for the thumb, index, middle, ring, and little fingers, respectively. The horizontal torques exerted by the fingers ranged from −0.12 to 0.09 Nm (index and little fingers, respectively). The average horizontal torques were 0.05 ± 0.02, 0.01 ± 0.01, −0.01 ± 0.01, and −0.03 ± 0.02 (SD) Nm (index, middle, ring, and little fingers, respectively). Net horizontal torques from most trials (94%) were within ±0.05 Nm range (0.02 ± 0.01 Nm).

For a complete description of the grasp behavior, we also quantified the temporal relationships of normal forces as phase differences between normal forces (see METHODS). Phase differences tended to cluster at values close to 0°, i.e., in-phase relationships for all subjects. Almost all distributions (98%) were nonrandom with mean angles close to 0° (range: −26–34°), indicating a consistent tendency for a similar modulation of force fluctuations between pairs of forces. These results are qualitatively similar to those reported by studies of multi-digit grasping requiring significantly larger fingertip forces (e.g., Rearick and Santello 2002).

Motor-unit synchrony during object hold

To allow physiological fluctuations in motor unit firing rate during object hold, we did not provide auditory or visual feedback of this variable (see METHODS). As a result, motor units fired at a fairly broad range of rates. Figure 3 shows the distribution of mean firing rate of the entire motor unit pool from FPL and all FDP digit compartments. Mean firing rates ranged from ~7 to 16 Hz with a mean of 11.3 ± 1.5 Hz. Motor units across muscles and across FDP compartments were characterized by similar geometric means of firing rate (Table 1) ranging from 10.2 to 11.8 Hz.

To allow comparison with previous motor-unit studies during force production tasks where firing rate was controlled, we computed the CV of firing rate. Within-trial firing rate variability was computed also to assess the extent to which it might have affected the strength of common input (see following text). Before computing the CV of firing rate, we detrended the data to eliminate possible drifts in motor-unit discharge rate that might have occurred during the trial (see METHODS).
found no consistent drift in motor-unit firing rate, the difference between raw and detrended data averaged across all motor unit pairs being 0.01 ± 0.001 Hz. The geometric mean of the CV of firing rate ranged from ~21 to ~28% (FDP2–FDP5 and FPL–DFP2, respectively; Table 1). The CV of firing rate from our data were comparable to the CV of firing rate reported by other studies using visual or auditory feedback (e.g., Kilbreath et al. 2002). The range of geometric means of coefficient of variations, computed from Table 1 in Kilbreath et al. (2002), ranged from ~20 to 22% (FDP2–3 and FDP3–5, respectively).

To determine the strength of synchrony for each motor-unit pair, a cumulative sum (Fig. 4, top) was first computed to define the peak range in the corresponding cross-correlogram (Fig. 4, bottom). The peak in the cross-correlogram was quantified within ±20 ms of the reference motor-unit firing using the CIS (see METHODS). Three examples of weak, moderate, and strong synchrony are shown in Fig. 4. With increasing strength of motor-unit synchrony, the slope of the cusum becomes increasingly steeper at ~0 ms as a clearer peak emerges in the cross-correlogram.

The mean number of events used to generate the cross-correlograms across all pairs of motor units was 1,749 ± 546. The mean duration of the cross-correlogram peaks was 20.1 ± 7.2 ms (range: 2.9–38.6 ms). The center of the peak was within ±10 ms of the reference motor unit in 69% of all cross-correlograms. Table 1 shows the mean CIS values and duration of the cross-correlogram peaks from each pair of muscles/muscle compartments. A significant main effect of muscle/muscle pair combination was found on the strength of motor-unit synchrony (P < 0.05) but not on the duration of the cross-correlogram peak. Regression analysis computed on all motor-unit pairs (n = 277) showed that there was no significant linear correlation between the geometric mean of CV of motor-unit firing rate and the amplitude of the CIS index (r² = 0.008; P > 0.05). Although a significant positive linear correlation was found between CIS and the geometric mean of motor-unit firing rate (P < 0.01), the strength of this correlation was weak (r² = 0.1). Hence, differences in the strength of common input among the muscle/muscle compartment combinations (Table 1) did not result from differences in firing rate across motor units or their within-trial variability of firing rate.

The distributions of CIS values are shown in Fig. 5, where the vertical dashed line indicates a 0.3 cutoff value separating weak from moderate and strong synchrony (see METHODS).

With regard to synchrony across muscles (FPL vs. FDP), we found moderate to strong motor-unit synchrony (Table 1) in most motor-unit pairs (18/19; 95%) from FPL and the index finger compartment of FDP (i.e., FDP2; Fig. 5, left). In contrast, it was less likely to find moderate to strong synchrony in motor units from FPL and FDP3, -4, and -5, as indicated by lower percentages of motor unit with CIS values ≥0.3 (Fig. 5) and smaller CIS values (Table 1). Motor-unit synchrony from FPL–FDP2 was also significantly stronger than that measured from FDP compartments of index-middle, index-ring, and middle-ring finger combinations (Table 1; FDP2–FDP3 and FDP2–FDP4, P < 0.01; FDP3–FDP4, P < 0.05).

The strength of motor-unit synchrony across FDP digit compartments was more homogeneous than that measured from FPL and FDP compartments (Table 1). We found moderate to strong synchrony in 50–73% of the motor unit pairs in
five of six FDP compartment pairs (Fig. 5). The strongest synchrony was found in the FDP compartment pairs involving the little finger, i.e., FDP2-FDP5, FDP3-FDP5, and FDP4-FDP5 (Table 1) and in the middle-ring finger combination (FDP3-FDP4), with CIS from individual sessions occasionally reaching values of 0.7–0.9 (Fig. 5). Motor units from the index and ring finger FDP compartments (FDP2-FDP4) were characterized by the weakest synchrony across all muscle/muscle compartments combinations (Table 1; \( P < 0.05 \); Fig. 5). Motor units from middle-ring, middle-little, and ring-little finger FDP compartments were also characterized by a significantly stronger synchrony than motor units from FPL and FDP3, -4, and -5 \( (P < 0.05) \). Motor unit pairs from FDP2-3 and FDP2-5 had larger CIS values than FPL-FDP2 \( (P < 0.05) \).

Motor-unit synchrony as a function of separation between FDP compartments

The strength of synchrony found in adjacent FDP compartments (e.g., index and middle finger FDP compartments; FDP2 and FDP3, Table 1) was similar to that found in FDP compartments with the maximum degree of separation (i.e., FDP2 and FDP5; Table 1). One pair of nonadjacent FDP compartments controlling the index and ring fingers (FDP2 and FDP4; Table 1) was characterized by the weakest synchrony. However, the nonadjacent middle and little finger FDP compartments (FDP3 and FDP5; Table 1) exhibited stronger synchrony than adjacent FDP compartments. Hence, no clear trend in the strength of motor-unit synchrony was found with increasing separation between FDP compartments.

To further illustrate the distribution of common input strength across FDP compartment pairs, the data presented in Table 1 are plotted in Fig. 6 as percentage of motor-unit pairs exhibiting moderate to strong synchrony as a function of separation between FDP compartments.

The degree of separation between FDP compartments did not correlate with the relative number of synchronized motor-unit pairs. No significant effect of degree of separation between FDP compartments \( (P > 0.05) \) was found on the strength of
motor-unit synchrony or the percentage of motor units exhibiting moderate to strong synchrony.

**DISCUSSION**

This study revealed that multi-digit grasping is characterized by moderate to strong motor-unit synchrony across extrinsic thumb and finger flexors, i.e., FPL-FDP, and across most digit compartments of the FDP. The strength of motor-unit synchrony, however, was not uniform across all motor-unit pairs, in particular for motor units from FPL and FDP compartments. This indicates that the organization of common input to hand muscles might be digit pair-specific. The digit-pair specificity of motor-unit synchrony might reflect the role that given digit pairs play in coordinating forces and torques during object hold.

**Motor-unit synchrony**

Holding an object against gravity requires a fine temporal coordination of normal forces to prevent object slip (Santello and Soechting 2000). One of the neural mechanisms that might contribute to constrain the production of multiple forces among digits is motor-unit synchrony. Motor-unit synchrony is defined as greater than chance tendency for simultaneously active motor units to discharge within a few milliseconds from each other (e.g., Nordstrom et al. 1992). Motor-unit synchrony has been attributed to excitatory or inhibitory postsynaptic potentials at the motoneurons resulting from branched axons of common presynaptic neurons (Kirkwood and Sears 1978; Nordstrom et al. 1992; Sears and Stagg 1976). The strength of motor-unit synchrony depends on the number of shared inputs as well as on activation pattern of last-order neurons. It is recognized, however, that the strength of motor-unit synchrony results from a complex interaction among other factors such as background excitation and inhibition and motoneurons intrinsic properties (Taylor and Enoka 2004).

The strength of motor-unit synchrony was quantified by CIS (Nordstrom et al. 1992). Although several synchrony measures have been used by other motor-unit studies, the CIS was chosen because it is an unbiased estimate of common neural input due to its lower sensitivity to across-trials differences in motor-unit discharge rate (Nordstrom et al. 1992). This was an important factor because we did not use constraints or feedback of motor-unit firing rate during object hold (see METHODS). As a result, our motor-unit population was characterized by a fairly wide range of firing rates (Fig. 3). Nevertheless, the differences in the strength of common input (i.e., CIS values) found across muscle/muscle compartment pairs (see following text) were not accounted for by motor unit firing rate or its within-trial variability.

Synchrony may occur between motor units belonging to the same muscle (within-muscle synchrony; e.g., 1st dorsal interosseus) (Datta and Stephens 1990) as well as to different muscles (across-muscle synchrony; e.g., 1st and 2nd dorsal interossei) (Bremner et al. 1991c). Synchrony has also been measured between motor units that belong to different compartments of the same muscle [across-muscle compartment synchrony; e.g., extensor digitorum communis (Keen and Fuglevand 2004), FDP (Reilly et al. 2004)]. Within-muscle motor-unit synchrony has been attributed to common neural input to motoneurons within a pool that innervate a single muscle. Across-muscle or muscle-compartment synchrony is the result of common input to multiple motoneuron pools or sub-pools that produce movement at different digits (Keen and Fuglevand 2004).

The present study focused on across-muscle and across-muscle-compartment synchrony as this might serve a functional role in the control of multiple forces. Specifically, synchronous discharge of motor units belonging to different hand muscles (e.g., FPL and FDP)—or muscle compartments acting on different digits (e.g., FDP2 and FDP5)—would enhance the temporal coupling of forces exerted by these muscles during object hold. In the following text, we discuss the functional significance of our results in relation to previous studies of motor-unit synchrony of hand muscles.

**Methodological considerations**

Previous studies examining motor-unit synchrony of hand muscles are somewhat limited in their application to more natural multi-digit grasping tasks due to experimental constraints and/or the use of tasks that only partially reflect natural grasping, i.e., producing forces under visual and/or auditory feedback of motor-unit firing rate or force (see Introduction). The current study tried to overcome the limitations of previous research by examining a natural multi-digit grasping task performed without the preceding laboratory constraints. We also made a particular effort to record from a large number of motor units to obtain a representative motor-unit sample.

We chose to quantify motor-unit synchrony on two important hand muscles for multi-digit grasping, FPL and FDP. These are the only muscles responsible for flexion of the distal phalange of the thumb and fingers, respectively. As FDP gives rise to four tendons inserting on each digit, many studies have examined the extent to which FDP can be considered as four separate neuromuscular compartments and their role in the production of individuated finger movements (Häger-Ross and Schieber 2000; Kilbreath and Gandevia 1994; Kilbreath et al. 2002; Reilly and Schieber 2003; Schieber 1991, 1995; Schieber et al. 2001). A recent multi-unit EMG study suggests that human FDP contains core regions that are selectively active during individuated finger movements as well as regions whose activity is nonspecific to the movement of any given digit (Reilly and Schieber 2003).

To address our research question, we defined functional compartments of FDP by selecting FDP regions that were responsible for the production of individuated finger movement as verified by muscle electrical stimulation and examination of EMG cross-talk (see METHODS). This criterion allowed us to define functionally independent FDP compartments based on the selectivity with which motor units could generate forces at individual digits and assess the extent to which these FDP compartments might receive common input during a task requiring the simultaneous action of multiple digits.

**Organization of common input to FDP compartments and FPL**

We found that common input to motor units from FPL and FDP compartments was not uniformly distributed. Whereas strong synchrony was consistently found between motor units...
from FPL and the index finger compartment of FDP, weak synchrony was found between FPL and the FDP compartments of middle, ring, and little fingers (Table 1; Fig. 5). This difference might reflect differences in the connectivity patterns of common input to FPL and FDP compartments arising from the greater extent to which thumb and index finger are involved in object grasping and manipulation regardless of the type of grip used, i.e., precision and power grip. Therefore it is conceivable that FPL and FDP2 would consistently exhibit a stronger motor-unit synchrony than the other FPL-FDP compartment regardless of the type of grasp used. In a five-digit grasp, however, the index finger also exerts the largest force among all the fingers, and therefore it might play a prominent role in the maintenance of a stable grasp compared with the other fingers. Hence it is also possible that the strongest synchrony exhibited by FPL and FDP2 relative to other thumb-finger combinations might be dependent on the relatively larger force contribution of the index finger in multi-digit grasping. The implication of this second interpretation is that the strength of motor-unit synchrony would not be specific to a given digit pair as a stronger motor-unit synchrony might be elicited when a digit pair becomes functionally more important. The task used in the present study cannot distinguish between these two interpretations. Ongoing work in our laboratory is addressing the issue of task dependency of motor-unit synchrony elicited by different types of grasp.

**Organization of common input to FDP compartments**

The distribution of common input to motor units across FDP compartments was more homogeneous than that observed between FPL and FDP compartments as indicated by similar strength of synchrony and cross-correlogram peak duration (Table 1). The strength of synchrony was moderate to strong in all but one FDP compartment pair, i.e., index and ring finger FDP compartments. The extent to which moderate to strong synchrony was found across the remaining FDP compartments (50–73% of motor unit pairs; Fig. 6B) strongly suggests that common input is a consistent feature of neural drive to hand muscles during simultaneous production of finger forces (the functional consequences of common input are discussed in the following text).

Our results are in general agreement with a recent study of motor-unit synchrony across FDP compartments during isometric force production (Reilly et al. 2004). Their range and average duration of significant cross-correlogram peaks (3–40 and 19 ms, respectively) as well as the percentage of peaks occurring ±10 ms from time 0 (85%) are in quantitative agreement with our results. However, an important difference was found in the distribution of synchrony strength across FDP compartment pairs. Specifically, the present results show that the strength of motor-unit synchrony is similar when measured from motor-unit pairs belonging to adjacent versus nonadjacent FDP compartments (Fig. 6A). Furthermore, the degree of separation between FDP compartments did not correlate with the strength of motor-unit synchrony (Fig. 6B). In contrast, Reilly et al. (2004) reported that FDP compartments that are further apart (e.g., index and little fingers) were characterized by weaker synchrony than adjacent compartments (e.g., index and middle fingers). Bremner et al. (1991b) also reported stronger synchrony for adjacent compartments of extrinsic finger flexors but did not report whether the muscle studied was FDP or FDS.

A direct comparison between our study and Reilly et al.’s (2004) study cannot be made for the following reasons. First, Reilly et al. (2004) used a different index to quantify the strength of motor-unit synchrony (i.e., k’). Second, Reilly et al. (2004) chose to use k’ because their EMG data were characterized by phasic, rather than tonic, motor-unit discharge. It is possible that this difference in the EMG firing pattern might have further contributed to the difference between our results and those reported by Reilly et al. (2004). A third difference between our study and those by Reilly et al. (2004) and Bremner et al. (1991c) is that the term used, i.e., object hold against gravity versus isometric force production. The differences between these two tasks are not merely biomechanical as the attention demands required to perform them are also very different, i.e., trying to prevent object slip versus maintaining a constant motor unit firing rate using auditory or visual feedback. Hence, an additional factor that might account for the discrepancy between our results and those reported by Reilly et al. (2004) could be attention demands, as these have been shown to play an important role in modulating the strength of common input (Schmied et al. 2000).

In summary, our results support recent observations of motor-unit synchrony occurring across FDP compartments during force production and extend them to the control of multi-digit grasping. Nevertheless, the distribution of common input to FDP compartment pairs we observed appears to be different from that observed during force-production tasks (Bremner et al. 1991c; Reilly et al. 2004). Methodological differences prevent us from establishing the extent to which differences in the distribution of common input to FDP compartments might have resulted from differences in the task studied.

**Common input to finger flexor and extensor muscles**

Several studies of finger force-production tasks have revealed a tendency for motor-unit synchrony to be stronger within muscle than across muscles (Bremner et al. 1991a–c; Huesler et al. 2000) or across muscle compartments for m. extensor digitorum communis (EDC) (Keen and Fuglevand 2004). This indicates that common inputs are stronger to motoneurons acting on the same digit than those common inputs that diverge to motoneurons acting on different digits. Human FDP, however, appears to be characterized by a different organization of common inputs to motor-unit pools as compared with EDC as the strength of synchrony between motor units belonging to the same compartment is similar to that found between adjacent compartments (Reilly et al. 2004). These differences in the organization of common input within and across compartments of EDC versus FDP might reflect the different roles that these two muscles play in object grasping and manipulation (see following text).

As done by Reilly et al. (2004) and the present study, Keen and Fuglevand (2004) also addressed the question of whether
the distribution of common input strength varies as a function of adjacency between muscle compartments of EDC. These authors reported that EDC is characterized by stronger motor-unit synchrony between adjacent than nonadjacent compartments during isometric force production. As noted in the preceding text, however, we did not find such trend in FDP. Although Keen and Fuglevand (2004) used a force-production task to assess across-compartment motor-unit synchrony (see preceding comments), the strength of motor-unit synchrony was quantified using CIS. This allows us to interpret their results as indicative of a different organization in common inputs to compartments of finger extensors as opposed to the one that was revealed by our study. Functional coupling of motion of the digits is primarily required when flexing—as opposed to extending—the digits during object grasping and manipulation. A uniform degree of motor-unit synchrony across all flexor compartments might contribute to the consistent coupling of finger motion and forces, a recurrent feature of multi-digit grasping tasks (e.g., Rearick et al. 2003; Santello et al. 2002).

**Functional role of across-muscle motor-unit synchrony**

Our results indicate that motor-unit synchrony occurs both across muscles and across compartments of FDP when all digits are engaged in grasping. As noted by Reilly et al. (2004), motor-unit synchrony is likely to be one of the factors that may limit finger force indivisibility. Specifically, the simultaneous discharge of motor units controlling the instructed and noninstructed digit would couple the forces these digits exert. At the same time, however, behaviors such as multi-digit grasping might benefit from such a constraint. Hence, an important question is whether the motor-unit synchrony serves a functional role during grasping by constraining the exertion of multiple forces. The current data cannot answer this question. However, a recent simulation study was conducted to quantify the extent to which motor-unit synchrony may be modulated to grasping task constraints is not well understood, yet, but appears to be a promising avenue for further investigation.

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**References**


