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Muscle-Pair Specific Distribution and Grip-Type Modulation of Neural Common Input to Extrinsic Digit Flexors

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Abstract

To gain insight into the synergistic control of hand muscles, we have recently quantified the strength of correlated neural activity across motor units from extrinsic digit flexors during a five-digit object-hold task. We found stronger synchrony and coherence across motor units from thumb and index finger flexor muscle compartment than between the thumb flexor and other finger flexor muscle compartments. The present study of two-digit object hold was designed to determine the extent to which such distribution of common input among thumb-finger flexor muscle compartments, revealed by holding an object with five digits, is preserved when varying the functional role of a given digit pair. We recorded normal force exerted by the digits and electrical activity of single motor units from muscle flexor pollicis longus (FPL) and two compartments of the m. flexor digitorum profundus (FDP2 and FDP3; index and middle finger, respectively). Consistent with our previous results from five-digit grasping, synchrony and coherence across motor units from FPL-FDP2 was significantly stronger than in FPL-FDP3 during object hold with two digits [common input strength: 0.49 ± 0.02 and 0.35 ± 0.02 (means $\pm$ SE), respectively; peak coherence: 0.0054 and 0.0038, respectively]. This suggests that the distribution of common neural input is muscle-pair specific regardless of grip type. However, the strength of coherence, but not synchrony, was significantly stronger in two- versus five-digit object hold for both muscle combinations, suggesting the periodicity of common input is sensitive to grip type.

INTRODUCTION

The sophisticated repertoire of hand movements that characterizes tool use and manipulation in humans relies on the ability to flexibly adapt individual or combined actions of the digits to task requirements, i.e., physical characteristics of the object and its intended use. Although many studies have been devoted to determining the interaction between central and peripheral mechanisms underlying dexterity (see Schieber and Santello 2004 for review), the neural mechanisms that underlie coordinated action of the digits are not well understood. We addressed this issue by studying an object-hold task requiring fine coordination of digit forces. We focused on the most basic unit of force control (i.e., single motor units) and the phenomenon of common synaptic input to motor neuron pools of hand muscles as this mechanism might play an important role in the coordination of the digits (Reilly and Schieber 2003; Reilly et al. 2004; Santello and Fuglevand 2004).

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Motor-unit synchrony and coherence, measured in the time and frequency domains, respectively, are two complementary measures used to infer the strength and periodicity of common synaptic input to motor-unit pairs (Hamm et al. 2001; Nordstrom et al. 1992; Semmler et al. 2002). Motor-unit synchrony is considered to be the result of branched presynaptic input to the motor neurons originating from a common source (Farmer et al. 1993; Sears and Stagg 1976; Semmler et al. 2002), whereas coherence is thought to reflect the frequency content of the common synaptic input (Farmer et al. 1993; Halliday 2000; Rosenberg et al. 1998; but see Taylor and Enoka 2004a,b). Significant motor-unit coherence has been observed in the absence of motor-unit synchrony and vice versa (Johnston et al. 2005), suggesting that different mechanisms may underlie these two measures of correlated motor-unit activity (Semmler et al. 2003).

We previously reported a heterogeneous organization of common input across motor neurons supplying muscles and muscle compartments of the extrinsic digit flexors during object hold with five digits (Johnston et al. 2005; Winges and Santello 2004). Specifically, we found greater motor-unit synchrony and coherence across an extrinsic thumb flexor muscle (m. flexor pollicis longus, FPL) and the index finger compartment of the muscle flexor digitorum profundus (FDP2) than across FPL and FDP3, 4 and 5 (middle, ring, and little finger FDP compartments, respectively). This distribution of common input to different muscle pairs can be interpreted in two alternative ways: as specific to the force distribution among digit pairs associated with holding an object with five digits or as specific to each muscle pair. The first interpretation predicts that different distributions of common neural input across hand muscle pairs would be found when holding the object with different grip types. This scenario would be consistent with the results reported by Huesler et al. (1998), on a comparison of two- versus five-digit force production tasks. In contrast, the second interpretation predicts invariant distributions of common neural input to force distributions that would be elicited by different grip types, e.g., grips involving two versus all digits.

To distinguish between these two interpretations, we asked subjects to hold an object using two digits (thumb and either index or middle finger) and measured common neural input to motor neurons supplying extrinsic hand muscle pairs. We used a two-digit grip to elicit a different force distribution among digit pairs relative to that elicited by a five-digit grasp studied previously (Winges and Santello 2004). Specifically, during object hold with two digits, a single digit must counteract thumb forces and torques to prevent object slip, whereas in a five-digit object hold all fingers must be coordinated such that the *sum* of their forces and torques counteract those exerted by the thumb. The strength and periodicity of common neural input during two-digit object hold was compared with that measured during five-digit grasp (Johnston et al. 2005; Winges and Santello 2004).

METHODS

Experimental tasks

A total of 5 healthy subjects (4 males and 1 female; mean age: 32 yr, range: 27–37 yr), with no known neuromuscular disorders or musculoskeletal injuries of the hand, took part in the experiments. Three subjects were right-handed, one subject was ambidextrous (but with a right-hand dominance for object grasping and holding), and one subject was left-handed as defined by the Edinburgh inventory (Oldfield 1971). None of our subjects had a background in manual skill training (e.g., playing a musical instrument). We performed 45 experimental sessions where each subject participated in at least three recording sessions for each grip type. 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 experimental session. Subjects sat in an adjustable dental chair with their right arm semi-pronated and resting on a horizontal platform. We asked subjects to

grasp, lift and hold a grip manipulandum (Fig. 1) vertically for a minimum period of 3 min. The only task requirement was to exert sufficient forces at the fingertips to prevent object slip while maintaining a vertical orientation of the object (see Winges and Santello 2004 for more details). We gave rest periods of ~5 min between trials to ensure that subjects were fully rested before starting a new trial.

For this study, each subject performed an object-hold task with two digits using either thumb and index finger or thumb and middle finger (Fig. 1A). The force and electromyographic (EMG) data collected during this task (35 experimental sessions, 232 motor-unit pairs) was compared with data from a control task, i.e., five-digit object hold (Fig. 1B). Part of the five-digit grip data (2 subjects, 64 motor-unit pairs) was collected for a previous study (Winges and Santello 2004), whereas the remainder of the five-digit data (3 subjects, 159 motor-unit pairs) is unpublished and was collected as control data for the two-digit grip task. Note that each subject was tested on both grip types to allow within-subject statistical comparisons (described in the following text).

Force and EMG recording

For the two-digit grip (Fig. 1A), forces were measured by two Nano17/SI-25-250 force/torque sensors (17 mm diam; ATI Industrial Automation, Apex, NC). For the five-digit grip (Fig. 1B), thumb and finger forces were measured by five force/torque transducers (4 Nano17/SI-25-250 and 1 Nano25/SI-125-03, 25 mm diam, for fingers and thumb, respectively). The vertical positions of the force sensors were adjusted to each subject's hand size to allow a comfortable grip. The mass of the grip device was 125 and 250 g for the two- and five-digit configurations, respectively. Note that when holding the device with five digits, the total grip (normal) force required to prevent object slip is shared among five rather than two digits. Therefore even though the five-digit grip device was twice as heavy as the two-digit grip device, thumb and either index or middle fingers were not required to exert twice the normal force exerted during two-digit object hold. Additional details on the force sensors and recordings have been described previously in Winges and Santello (2004).

Motor-unit action potentials were recorded with tungsten micro-electrodes (Frederick Haer, Bowdoinham, ME; 1–5 μm tip diameter, 5–10 μm uninsulated length, 50-mm shaft length; 250- μm shaft diameter, ~200 k Ω impedance at 1,000 Hz after insertion) inserted into m. flexor digitorum profundus (FDP) and m. flexor pollicis longus (FPL). Weak intramuscular electrical stimulation (50–400 μA , 1-ms duration, 1 Hz; S48 Stimulator, Grass Instruments) was delivered through the same microelectrodes used to record motor-unit activity to verify electrode placement in the target muscle. A detailed description of the motor-unit isolation and recording procedures can be found in Winges and Santello (2004).

Attention demands associated with a given task can affect the strength of common input (Schmied et al. 2000). Therefore consistent with our previous experimental design of five-digit object hold (Winges and Santello 2004), subjects did not receive auditory feedback of discharge rate during the trial to allow physiological variability of motor-unit discharge rate during object hold with two digits. Similarly, no visual feedback of the forces exerted on the device was given to allow a natural distribution and fluctuation of individual digit forces during object hold in response to a more natural constraint, i.e., to prevent object slip against gravity. This is a novel feature of our experimental design as the majority of previous studies examining motor-unit activity of hand muscles required subjects to generate forces against fixed force transducers with thumb and index finger under visual or auditory feedback (e.g., Hockensmith et al. 2005; Huesler et al. 2000).

Normal forces and raw EMG analysis

Force analysis focused on quantifying the amplitude and variability of normal forces exerted by each digit pair for each grip type. Maximal voluntary grip force was measured for each subject in the two-digit grip (thumb-index, thumb-middle) during a separate session to provide a relative measure of the grip force elicited by our grasping task. Subjects were asked to produce maximal grips during three 5-s trials separated by rest periods of 3 min. The maximum two-digit grip force performed by a subject for each digit pair was used to normalize forces exerted by thumb-index and thumb-middle during two- and five-digit grasping.

A typical record of EMG and forces exerted during a two-digit grasp with the thumb and middle finger is shown in Fig. 2A. Single motor units were identified off-line from the raw data and discriminated for each EMG channel (Fig. 2, B and C) using commercial and custom designed software (Spike2 v5.09, Cambridge Electronic Design, Cambridge, UK). For each discriminated motor unit, the instantaneous discharge rate was computed as the inverse interspike interval (ISI). To assess whether there were any systematic increases or decreases in the discharge rate within each trial, we performed least-square regression analysis on the instantaneous discharge rate of each motor unit. We then subtracted the slope of the regression line from the data to remove any trend (Laidlaw et al. 2000). We found that the mean difference between the de-trended and raw motor-unit discharge rates was very small (0.009 ± 0.003 Hz), the maximum difference being 0.019 Hz. The mean and SD of the motor-unit discharge rate were computed on the de-trended data from each trial and used to compute the coefficient of variation (CV) of motor-unit discharge rate. We then computed the geometric mean (GM) of the discharge rate and the GM of the CV of discharge rate for each motor-unit pair (Nordstrom et al. 1992) to quantify the within-trial variability of discharge rate.

Motor-unit synchrony analysis

Custom software was used to quantify motor-unit synchronization. Reference and test channels were defined 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. 2D, bottom). A cumulative sum (CUSUM) (Ellaway 1978) was computed to determine the existence of a peak in the cross-correlogram indicating synchronous discharge of the two motor units (Fig. 2D, top). The peak was defined by the area between the 10th and 90th percentiles of the largest inflection in the CUSUM (time period within the 2 dotted vertical lines in Fig. 2D) (Keen and Fuglevand 2004; Schmied et al. 1993) within ± 20 ms of the reference unit discharging. If a peak could not be defined within this region, a narrowed region of 11 ms centered at *time 0* was used for the assessment of the strength of motor-unit synchrony for that motor-unit pair (Semmler et al. 1997). To assess possible differences in the patterns of common input, we also 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 rate of synchronous discharges for a motor-unit pair above chance level. Chance level (horizontal line, Fig. 2D, bottom) 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. 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 including a motor unit for the computation of the CIS was tonic discharge defined as ≥ 900 spikes occurring without large gaps (< 1 s) between spikes. We rejected a significant amount of trials ($\sim 20\%$) due to insufficient number of events (< 900 spikes within a trial) or when activity from other motor units prevented a reliable discrimination.

Motor-unit coherence analysis

For the purposes of coherence analysis only, the motor-unit data were down-sampled to 200 pulses per second (pps) by binning the data into 5-ms segments and assigning a value of 1 if that segment contained a discharge and a 0 if it did not (Semmler et al. 2003). The mean of each 1-s segment of data were calculated and subtracted from that segment of data to remove any artifact resulting from the rectangular waveform (due to the data set consisting of only 1's and 0's) (Warner 1998). We then computed the coherence between individual motor-unit pairs to determine their linear dependence in the frequency domain (Fig. 2E).

Coherence Magnitude—We computed coherence between motor-unit pairs for each trial using the cross-spectrum and auto-spectra of each motor-unit spike train. These measures were estimated from 1.28 s of nonoverlapping segments of data (i.e., 256 point windows) (Semmler et al. 2003), resulting in a bin resolution of 0.78 Hz. The 95% confidence level above zero coherence was computed using the test provided by Rosenberg et al. (1989). If the estimated coherence at a particular frequency exceeds the confidence level, the hypothesis of noncorrelated activity at that frequency is rejected (see Johnston et al. 2005 for more details on coherence analysis).

Maximum coherence was determined by finding the largest coherence magnitude within the frequency range of interest (see following text) and then subtracting the coherence magnitude at the 95% significance level. The resulting maximum coherence value represents the largest coherence magnitude above significance level within a given frequency range. If the largest coherence magnitude within a given frequency range did not reach significance, the maximum coherence was assigned a value of 0. Most of the significant coherence from ~1 to 50 Hz (88%) was found in the 1- to 20-Hz frequency range in our data. Therefore we computed maximum coherence within two frequency ranges: 1–10 and 10–20 Hz (the actual ranges given the frequency bin resolution of 0.78 were: 0.78–9.38, 10.16–19.53 Hz, respectively).

Pooled Coherence—We also computed pooled coherence (see Amjad et al. 1997 for details) to determine the strength of coherence across entire data sets, i.e., across all trials and subjects within digit pairs and grip types. Pooled coherence can be considered a weighted average of individual coherence estimates. To assess possible differences in the strength of coherence as a function of digit pair and grip type, pooled coherence was computed separately for all motor-unit pairs from FPL-FDP2 and FPL-FDP3 during the two- and five-digit grasps (i.e., 4 pooled coherences).

Statistical analysis

Motor-Unit Behavior and Synchrony—As differences in CIS may result from differences in motor-unit behavior (e.g., discharge rate variability) (Nordstrom et al. 1992), we performed linear regression analysis to assess the extent to which GM of motor-unit discharge rate or GM of the CV of discharge rate affected the amplitude of the CIS index or maximum coherence within 1- to 10- and 10- to 20-Hz frequency ranges. We performed multivariate ANOVA (2×2) with repeated measures with muscle pair (FPL-FDP2 vs. FPL-FDP3) and grip type (2 vs. 5 digits) as independent variables. The dependent variables were: CIS index magnitude, GM of motor-unit discharge rate, GM of the CV of motor-unit discharge rate and the width of the cross-correlogram peaks, and sum of normal forces (see *Digit forces*). To explore the main effects and interactions, we performed post hoc tests with Bonferroni correction. With regard to fourth variable in the preceding text, note that motor-unit pairs for which a peak in the cross-correlogram could not be defined (see preceding text) were excluded from the statistical comparison of peak widths.

Pooled Coherence—The “difference of coherence test” (Amjad et al. 1997; Rosenberg et al. 1989) was performed to determine the frequencies at which significant differences occurred between the pooled coherences of the motor-unit pairs from each muscle pair and grip type (Amjad et al. 1997; Johnston et al. 2005). This test of difference was computed between the two- and five-digit grasps separately for FPL-FDP2 and FPL-FDP3 to assess differences between grip types for each muscle pair and between FPL-FDP2 and FPL-FDP3 separately for both two- and five-digit grasps to assess differences between muscle pairs for each grip type. Because the coherence magnitude of the two- was greater than that of the five-digit grip, and the coherence magnitude of FPL-FDP2 was greater than that of FPL-FDP3, the test of difference was computed as two- minus five-digit grasps and FPL-FDP2 minus FPL-FDP3. This resulted in all positive differences (see Fig. 4, panels in last row and column).

Digit Forces—We used the sum of forces exerted by two digits instead of the force of individual digits because our measures of common input are based on correlating activity of motor units across muscles of two digits. We also performed regression analysis between the sum of the forces produced by the two digits and either CIS or maximum coherence to establish whether across-trials differences in force exerted by the two digit pairs were associated with systematic differences in our measures of common input.

Relation Between Motor-Unit Synchrony and Maximum Coherence—We performed linear regression analysis to assess the extent to which the CIS correlated with maximum coherence within 1- to 10- and 10- to 20-Hz frequency ranges. Note that this analysis was performed on pairs of CIS and coherence values computed on individual, rather than averaged, trials. Linear regression analysis was computed separately for motor-unit pairs from each muscle pair during each of the two grip types. A significance level of $P \leq 0.05$ was used for all statistical analyses. All data are reported as mean $\pm$ SE.

RESULTS

As found for five-digit object hold, analysis of motor-unit activity during object hold with two digits revealed moderate to strong synchrony and significant coherence in both the FPLFDP2 (thumb-index finger) and FPL-FDP3 (thumb-middle finger) muscle pairs. The average motor-unit synchrony and pooled coherence were significantly stronger from FPL-FDP2 than from FPL-FDP3 in both grip types. This difference was not associated with differences in motor-unit behavior or forces across the two muscle pairs. No significant difference in the strength of motor-unit synchrony was found between the two grip types. However, coherence was significantly stronger in two- than in five-digit object hold in both muscle pairs.

Normal forces during object hold

The net horizontal torque was computed to quantify the extent of object tilt around the long axis of the forearm during the five-digit grip. As the thumb and finger sensors were collinear for the two-digit grip, the extent of misalignment of the device relative to the vertical was quantified as the mismatch between thumb and finger (index or middle finger) normal forces. Both measures were very close to zero (net horizontal torque: 0.08 ± 0.02 Nm; difference in normal forces: -0.03 ± 0.02 N and -0.01 ± 0.03 N for thumb-index and thumb-middle finger, respectively), indicating that the subjects held the object close to vertical in both grip conditions.

During the five-digit object hold, the proportion of force exerted by each digit relative to the total normal force corresponded to 43.8, 17.6, 13.7, 12.6, and 12.3% (thumb, index, middle, ring, and little finger, respectively). The index finger exerted slightly larger ($+0.23$ N) normal force than middle finger (on average, 1.07 vs. 0.84 N). This was also found for the two-digit

object hold, the index finger exerting larger (+0.36 N) normal force than the middle finger (on average, 1.52 vs. 1.17 N). The average of the sum of normal force exerted by the thumb-index and thumb-middle digit pairs were 3.59 ± 0.71 and 3.66 ± 0.49 N, respectively, for the five-digit grasp, and 3.02 ± 0.41 and 2.32 ± 0.24 N, respectively, for the two-digit grasp. There were no main effects of muscle pair or grip type on the sum of normal forces ($P > 0.05$). Note that during object hold with either grip type, the sum of thumb-index or thumb-middle finger forces were <5% of maximal voluntary grip force (range: 1.25–4.69%). Therefore as our object-hold task elicited small forces in both grip types and digit pairs, the motor units sampled in this study ($n = 589$) were presumably restricted to small, low-threshold motor units.

Motor-unit discharge rate and variability

A total of 589 motor units were discriminated from EMG records of FPL, FDP2, and FDP3, yielding 457 motor-unit pairs for analysis of synchrony and coherence. For each subject, we discriminated a minimum of 15 motor-unit pairs for each muscle pair and grip type, the mean number of motor-unit pairs per subject being 26 ± 3 and 21 ± 4 for FPL-FDP2 (2- and 5-digit grip, respectively), and 20 ± 2 and 23 ± 2 for FPL-FDP3 (2- and 5-digit grip, respectively). The range of motor-unit discharge rates was broad and similar to that reported by our previous study, i.e., 7–16 pps (Winges and Santello 2004). Table 1 shows the GM of discharge rates computed from motor-unit pairs (see Methods). Our post hoc analysis revealed that the GM of discharge rate for five-digit grip was significantly higher than that from two-digit grip [$F(1,4) = 4.48$; $P < 0.05$]; however, this difference was <0.4 pps (see Table 1). There was no significant effect of muscle pair on the GM of discharge rate. There was also no significant effect of either muscle pair or grip type on the GM of the CV of motor-unit discharge rate. This measure ranged from ~20 to ~24% (Table 1) and is comparable to that reported by our previous study (~21 to ~28%) (Winges and Santello 2004).

Motor-unit synchrony during object hold

The mean number of events used to generate the cross-correlograms of each motor-unit pair (e.g., Fig. 2D, bottom) was $1,969 \pm 27$. The center of the cross-correlogram peak was within ± 10 ms of the reference motor unit in 77% of the cross-correlograms. The widths of the cross-correlogram peaks ranged from 1.30 to 37.43 ms (mean values are shown in Table 1) with 7.9% having a peak <10 ms wide. There was no significant difference in the width of the cross-correlogram peaks between grip types. However, there was a main effect of muscle pair on the peak widths [$F(1,4) = 275.83$; $P < 0.001$] with FPL-FDP3 exhibiting greater peak widths than FPL-FDP2 (average difference <1.5 ms). There were no interactions between grip type and muscle pair.

Figure 3 shows the distributions of CIS values for each muscle pair from two- and five-digit object hold (A and B, respectively). The mean CIS values for each muscle pair and grip type are shown in Fig. 3C. The mean of the distributions of CIS values from FPL-FDP3 was 0.35 ± 0.02 and 0.38 ± 0.2 when subjects held the device with two- and five-digits, respectively (Table 1). In contrast, the distributions of CIS values from FPL-FDP2 were centered at larger values (mean values: 0.49 ± 0.02 and 0.45 ± 0.02 for 2 and 5 digits, respectively; Table 1).

The difference in the strength of CIS between FPL-FDP2 and FPL-FDP3 was clearer in two- than five-digit object hold (Fig. 3C). In the two-digit grip, all subjects exhibited higher mean CIS values for FPL-FDP2 than FPL-FDP3. In the five-digit grip, mean CIS values for the majority of subjects (3/5) followed the same pattern. In one subject (5); however, higher mean CIS values were found for FPL-FDP3 than FPL-FDP2, whereas in another subject (1) the CIS values from both muscle pairs were very similar. Post hoc analysis confirmed a main effect of muscle pair, with CIS values from FPL-FDP2 being significantly larger than FPL-FDP3 [$F(1,4) = 9.78$; $P \leq 0.05$; Fig. 3, A and B; Table 1]. However, grip type had no significant effect

on the strength of motor-unit synchrony, and there was no significant interaction between grip type and muscle pair.

Strength of pooled coherence

Figure 4 shows the pooled coherence computed from motor units belonging to FPL-FDP2 and FPL-FDP3 during the two- and five-digit grasps (Fig. 4, A-D). For each digit pair and grip type, the magnitudes of pooled coherence were significant over a broad range of frequencies, i.e., ~1–20 Hz, and decreased with increasing frequency. Test of difference (see Methods) revealed significantly stronger coherence, particularly at low frequencies, in the two- as opposed to the five-digit grasp (last row of Fig. 4). Specifically, both FPL-FDP2 and FPL-FDP3 exhibited stronger coherence during the two-digit grasp (0.0054 at 6 Hz and 0.0038 at 7 Hz, respectively, compared with 0.0026 at 8 Hz and 0.0025 at 10 Hz, respectively, in the 5-digit grasp). Furthermore, FPL-FDP2 generally exhibited stronger coherence than did FPL-FDP3 over a broad range of frequencies (~1–20 Hz), however, this was particularly clear in the 10- to 20-Hz frequency range (last column of Fig. 4).

Common input as a function of force and motor-unit discharge characteristics

To assess the extent to which the stronger synchrony and coherence exhibited by FPL-FDP2 versus FPL-FDP3 might have resulted from differences in digit forces or motor-unit discharge characteristics, we performed linear regression analysis (see Methods).

Force—There was no significant relation between the sum of the normal forces produced by the thumb and index finger and the magnitude of CIS values computed from FPL-FDP2 in either grip type. The same result was found for CIS computed from FPL-FDP3 versus the sum of thumb and middle finger force for the five-digit grip. For the two-digit grip, there was a significant negative linear correlation between CIS and the sum of the thumb-middle finger force. However, this correlation was very weak ($r^2 = 0.07$; $P < 0.05$). Significant but very weak positive and negative relations were also found between the sum of the normal forces exerted by thumb-index ($r^2 = 0.07$; $P < 0.05$) and thumb-middle ($r^2 = 0.05$; $P < 0.05$), respectively, and maximum coherence in the 10- to 20-Hz range during the two-digit grip.

Motor-Unit Discharge Characteristics—A significant, but weak, positive linear relation was found between GM of discharge rate and the magnitude of CIS values computed on FPL-FDP3 in the five-digit grip ($n = 117$; $r^2 = 0.095$; $P < 0.001$) and FPL-FDP2 in the two-digit grip ($n = 132$; $r^2 = 0.101$; $P = 0.001$). Although a significant positive linear correlation was found between CIS and the GM of the CV of motor-unit discharge rate for FPL-FDP3 in the five-digit grip, the strength of this correlation was very weak ($r^2 = 0.05$; $P < 0.01$). There was a weak, but significant effect of GM of discharge rate on the 10- to 20-Hz coherence magnitude for the FPL-FDP3 ($P < 0.05$, $r^2 = 0.05$ and 0.04, 2- and 5-digit grip, respectively). A similar weak relation was observed between the GM of the CV of motor-unit discharge rate and 10- to 20-Hz coherence magnitude for FPL-FDP3 during the two-digit grip ($r^2 = 0.04$; $P < 0.05$).

In summary, the stronger synchrony and pooled coherence exhibited by FPL-FDP2 versus FPL-FDP3 could not be accounted for by slight differences in motor-unit discharge characteristics or force between the two muscle pairs in either grip type.

Correlation between motor-unit synchrony and maximum coherence

The relation between the strength of motor-unit synchrony and coherence was assessed by linear regression analysis on CIS values and maximum coherence within 1- to 10- and 10- to 20-Hz frequency ranges across the motor-unit pairs in FPL-FDP2 and FPL-FDP3 during each grip type. We found significant linear correlations in each digit pair during both grip types for

both frequency ranges of interest ($P < 0.001$); however, these relations were generally weak (r^2 range: 0.07–0.30; mean r^2 : 0.19).

DISCUSSION

One of the main findings of the present study is that thumb and index finger flexors exhibited a higher degree of correlated neural activity than thumb and middle finger flexors regardless of grip type used for object hold. Another important finding is that the strength of motor-unit synchrony was not affected by grip type for either FPL-FDP2 or FPL-FDP3. However, coherence revealed significant differences for grip type in both muscle pairs. The implications of these results in relation to neural control of the hand are discussed in the following text.

Common neural input to extrinsic flexors of the digits during object hold

The motor units innervating long flexors of the thumb-index finger and thumb-middle finger were characterized by moderate to strong synchrony and significant coherence regardless of the number of digits used for object hold (Figs. 3 and 4). Common neural input to motor neurons supplying hand muscles may be delivered directly through the divergence of corticospinal axons contacting motor neuron pools innervating different muscles (Lemon 1993) or indirectly through one or more interposed neurons (Semmler et al. 2004). In the present study of extrinsic hand muscles, most of the peaks of the cross-correlograms computed from concurrently active motor units were broad, suggesting that common input was primarily delivered through synchronized presynaptic inputs. Frequency-domain analysis revealed broad coherence peaks (Fig. 4,A–D), thus suggesting a prevalence of nonperiodic neural input across a wide frequency range, i.e., ~ 1 –20 Hz (Halliday 2000). The weak correlations between CIS and coherence values suggest the existence of two independent mechanisms (Johnston et al. 2005; Semmler et al. 2003) through which common input was delivered to motor unit pairs of the hand muscles studied. This interpretation is further supported by the influence of grip type on the strength of coherence but not on that of synchrony (see following text).

Heterogeneous organization of common input to hand muscles

One of the novel findings of the present study is that the tendency for significantly stronger synchrony and coherence exhibited by FPL-FDP2 relative to other thumb-finger muscle compartments of FDP during five-digit object hold (Johnston et al. 2005; Winges and Santello 2004) was preserved when subjects used a two-digit grip (Figs. 3 and 4). We found that small differences in motor-unit discharge characteristics between FPL-FDP2 and FPL-FDP3 or in the total force exerted by thumb and index finger versus thumb and middle finger could not account for the higher CIS and coherence exhibited by FPL-FDP2 relative to FPL-FDP3. Therefore it appears that the general organization of common neural input across motor units of thumb, index, and middle finger flexors is preserved regardless of differences in force coordination patterns elicited by different grip types.

Muscle-pair differences in the strength of motor-unit synchrony have also been reported by a recent study by Hockensmith et al. (2005). These authors found stronger synchrony across motor units from FPL-FDP2 compared with FPL-FDP3 during a force production task that mimicked two-digit grasping (Hockensmith et al. 2005). Note that these force production tasks do not have the same mechanical requirements as object hold against gravity, such as the constraint of accurately matching thumb and index fingertip forces to prevent object slip or tilt. Therefore the stronger common input exhibited by thumb and index finger flexor muscles or compartments found by both studies suggests that the muscle pair-specific distribution of common neural input might be independent of task requirements. Further comparison between our results and those by Hockensmith et al. (2005), however, is limited by the fact these authors did not measure coherence or examine the extent to which the differences in common input

strength between muscle pairs was invariant with respect to the number of fingers used to generate force together with the thumb.

Common neural input and hand muscle synergies

During static hold of an object with thumb and one finger, hand muscle activity has to be modulated such that normal force exerted by the finger matches normal force exerted by the thumb as to prevent object slip (Forssberg et al. 1991). However, in a grip where more than one finger is used in conjunction with the thumb (e.g., 5-digit object hold), it is the *sum* of normal forces exerted by all fingers that has to match thumb normal force (Santello and Soechting 2000). Hence, as long as equilibrium between thumb and *all* finger normal forces is achieved, a given finger is not constrained to exert a specific force. An additional difference between the two grip types used in this study is that in a five-digit grip, a given finger force has to be coordinated not only with respect to the thumb force but also with respect to other finger forces. Hence the activity of a given hand muscle has to be finely modulated not only to produce a given force at one digit, but it also needs to be finely *coordinated* with the activity of other hand muscles inserting onto different digits. Specifically, the force generated by hand muscles inserting into a given finger has to be modulated such that when combined with forces generated by hand muscles inserting into the remaining fingers, the total finger force matches the force generated by thumb muscles.

A mechanism that could potentially be involved in modulating the coordination of hand muscle activity is common neural input. The coupling of neural activity of a motor-unit pair resulting from branched presynaptic inputs and/or synchronized inputs to motor neurons innervating *different* muscles (across-muscle motor-unit synchrony or coherence) can be considered as the fundamental unit of a muscle synergy. Specifically, near synchronous discharge of motor-unit pairs from synergistic muscles would constrain the temporal relations among the forces they exert, this behavior being particularly relevant to inter-digit coordination during object grasping (Santello and Fuglevand 2004).

It has been suggested that modulation of strength of common neural input across motor units of different muscles would lead to different degree of movement and force coupling across digits (Reilly and Schieber 2003; Santello and Fuglevand 2004; Santello and Soechting 2000). As discussed in the preceding text, a change in the number of fingers that has to be used in conjunction with the thumb would elicit a change in the distribution of forces across the digits, hence a possible change in the organization of common neural input to hand muscles. Indeed, Huesler et al. (1998) reported that force production tasks performed using different grip types (power vs. precision grips) were characterized by different magnitudes of motor-unit synchrony.

We found that across-muscle motor-unit coherence, but not synchrony, was significantly affected by grip type, coherence being stronger for two- than five-digit object hold. This effect, however, did not result in a re-organization of the *relative* distribution of common neural input across different muscle pairs, i.e., FPL-FDP2 were still characterized by stronger coherence than FPL-FDP3. Both findings suggest that a muscle-pair specific distribution of common neural input co-exists with the capability of modulating it to grip type. The functional consequences of modulating motor-unit coherence remain to be investigated, and therefore we are unable to interpret the behavioral significance of such modulation as a function of grip type. However, the selective effect of grip type on across-muscle coherence but not on synchrony provides further support to the notions that these two measures of correlated neural input reflect different mechanisms of neural coupling (Johnston et al. 2005; Semmler et al. 2003) and suggests that coherence might be more sensitive to task characteristics than synchrony. The higher sensitivity of coherence as a measure of common input might be partly due to its ability to detect correlation in motor-unit activity at low frequencies outside of the

central peak region of the cross-correlogram that is quantified by time domain measures such as the CIS, i.e., ± 20 ms relative to the discharges of the reference unit (see Methods). In fact, the differences between grip types only occur in the 1- to 10-Hz frequency range.

Last, caution should be observed in interpreting time and frequency domain measures of common neural input as they are indirect measures of neural connectivity patterns. Nevertheless, one may speculate that the higher degree of neural coupling across motor nuclei of thumb and index finger muscles might reflect neural adaptations to the higher degree with which these two digits are consistently used for dexterous manipulation, i.e., the thumb and index fingers—unlike other thumb-finger pairs—are involved in most if not all hand-object interactions ranging from precision to power grips.

Conclusion

Consistent with our previous results from five-digit object hold, the average strength of motor-unit synchrony and coherence across motor units from FPL and FDP2 was significantly larger than those from FPL and FDP3 when object hold was performed with two digits. This organization of common neural input might reflect the higher degree of involvement and functional importance of the thumb and index finger relative to other thumb-finger combinations for manipulative actions. Within such muscle-pair specific distribution of common neural input, we also found that the coupling of motor-unit activity in the frequency domain was stronger in two- versus five-digit grasping. These findings suggest that a certain degree of flexibility in modulating coupling of motor-unit activity is maintained within an invariant, muscle-specific distribution of common input to hand muscle motor nuclei.

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FIG 1. Grip device. The devices used to measure normal forces of 2- and 5-digit grasp (control task) are shown (A and B, respectively). Figures are not to scale.

FIG 2.

Normal forces, electromyographic (EMG), motor-unit synchrony, and coherence during object hold. *A*: normal forces exerted by the thumb and middle finger (Tx and Mx, respectively) and EMGs from the thumb muscle (FPL) and the middle finger compartment of FDP (FDP3) during a 2-digit object hold (*subject 3*). The data shown are from a smaller recording period than the entire 4-min duration of the object-hold trial. *B*: motor units discriminated from each raw EMG trace and their respective instantaneous discharge rates. *C*: the action potential of a single motor unit discriminated from each EMG channel. The number of spikes for the motor units shown was 1,400 and 1,743 for FPL and FDP3, respectively. *D*: cumulative sum (CUSUM) of the events of the cross-correlogram and the cross-correlogram (*top* and *bottom* trace, respectively) for the same 2 motor units. Vertical solid lines denote the ± 20 ms time period relative to 0. Vertical dotted lines indicate 10 and 90% of the CUSUM value within ± 20 ms used to define the width of the cross-correlogram peak above chance level (horizontal line, *bottom* trace). The number of events below chance level is calculated from the corresponding gray area. *E*: coherence estimate for this pair of motor units. The values on the y axis are the magnitudes of the coherence across the frequency range of interest (x axis; bin width = 0.78 Hz). Horizontal dotted line indicates the 95% confidence limit above which the magnitude of the coherence is defined as statistically significant.

FIG 3.

Common input strength (CIS) index. *A* and *B*: CIS distributions for FPL-FDP2 (—) and FPL-FDP3 (---) in the 2- and 5-digit grips, respectively, computed on all motor-unit pairs from all subjects. For graphical purposes, CIS data were binned into 0.1 intervals. Gaps in the distributions indicate no motor-unit pairs with that CIS value. *C*: mean $\pm$ SE of CIS values computed across subjects for each grip type and muscle pair (*, $P < 0.05$; main effect of muscle pair on CIS, ANOVA with repeated measures).

FIG 4.

Pooled coherence and test of difference. Pooled coherence of all motor-unit pairs from FPL-FDP2 and FPL-FDP3 during 2-digit grasp (A and B, respectively) and 5-digit grasp (C and D, respectively). The values on the y axis are the magnitude of the pooled coherence across the frequency range of interest (x axis; bin width = 0.78 Hz). Horizontal dashed line indicates the 95% confidence limit above which the magnitude of the pooled coherence is statistically significant. *Right:* test of difference between the transformed coherence functions of FPL-FDP2 and FPL-FDP3 during the 2- and 5-digit grips, (*top* and *bottom*, respectively). *Bottom:* the test of difference between the transformed coherence functions of the two- and five-digit grips, for both FPL-FDP2 and FPL-FDP3 (*left* and *right*, respectively). Values falling outside the 95% confidence interval (horizontal dotted lines) indicate a significant difference between the two transformed coherence functions at that frequency.

TABLE 1

Motor-unit discharge rates, discharge rate variability, and CIS

	Motor-Unit Pairs	GM Discharge Rate, pps	GM CV Discharge Rate, %	CIS (Extra Synchrony), spikes/s	Peak Width, ms
2-digit	FPL-FDP2 FPL-FDP3	132	10.83 ± 0.12	21.49 ± 1.60	0.49 ± 0.02
		102	10.65 ± 0.10	20.70 ± 0.85	0.35 ± 0.02
5-digit	FPL-FDP2 FPL-FDP3	106	11.33 ± 0.11	23.67 ± 1.05	0.45 ± 0.02
		117	10.93 ± 0.10	22.42 ± 0.68	0.38 ± 0.02

Values are means ± SE. For each grip, the number of motor-unit pairs from flexor pollicis longus (FPL)-first flexor digitorum profundus (FDP2) and FPL-FDP3 used for analysis is given together with the geometric mean (GM) of motor-unit discharge rate and the GM of coefficient of variation (CV) of motor-unit discharge rate, the common input strength index (CIS) and the width of the cross-correlogram peak.