Common input to motor units of digit flexors during multi-digit grasping

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ABSTRACT

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 m. 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; Nordstrom et al. 1992).

We found moderate to strong motor unit synchrony between FPL and the index FDP compartment (mean CIS ± S.E.: 0.49 ± 0.03) 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. Santello and Soechting 1998, 2000; Mason et al. 2001; Winges et al. 2003) and object hold (e.g. Johansson and Cole 1994; Burstedt et al. 1999; Reilmann et al. 2001; Baud-Bovy and Soechting 2002; Rearick and Santello, 2002). However, the neural control of grasping, as measured through hand muscle electromyography (EMG), has been inferred primarily through force production tasks (e.g. Bremner et al. 1991a,b,c; Maier and Hepp-Reymond 1995a,b; Mills and Schubert 1995; Valero-Cuevas et al. 1998; Huesler et al. 1998, 2000; Valero-Cuevas 2000; Kilner et al. 2002; Keen and Fuglevand 2004; Reilly et al 2004).

Force production tasks such as exerting force with one digit (e.g. Bremner et al. 1991a,b,c; Valero-Cuevas 2000; Keen and Fuglevand 2004) or two digits (Maier and Hepp-Reymond 1995a,b,c) against a fixed resistance have been very useful in characterizing important features of hand muscle activity coordination. These tasks, however, lack mechanical constraints associated with more natural grasping tasks, e.g. holding an object against gravity, such as the requirement of maintaining equilibrium of forces and moments (Rearick et al. 2003). Furthermore, EMG studies using force production tasks have often required subjects to control force using visual feedback (e.g. Valero-Cuevas 2000). In contrast, natural grasping behavior is characterized by unconstrained modulation of forces that heavily relies on tactile feedback (Edin et al.
Due to these between-task differences, the extent to which the coordination of hand muscle activity elicited during force production tasks might apply to more natural grasping tasks remains to be determined.

One of the neural mechanisms that might contribute to the coordination of forces during grasping is motor unit synchrony (Datta and Stephens 1990; Bremner et al. 1991a,b,c; Datta et al. 1991; Maier and Hepp-Reymond 1995a,b; Huesler et al. 1998, 2000; Reilly and Schieber 2004). A generally accepted view is that short-term synchrony of active motor units is an indirect measure of common synaptic input across motoneurons (Sears and Stagg 1976; Kirkwood and Sears 1978; Nordstrom et al. 1992). If common synaptic input is delivered to motoneuron pools of different hand muscles or compartments of a multi-tendoned muscle such as the flexor digitorum profundus (FDP), it would enhance the coupling of forces exerted by a pair of digits. Indeed, motor unit synchrony has been considered one of the factors responsible for the spill over of forces across non-instructed digits during individuated finger force production (Kilbreath and Gandevia 1994; Zatsiorsky et al. 2000; Reilly and Schieber 2003, 2004). This interpretation has received support by a recent study reporting a negative correlation between the strength of motor unit synchrony across FDP compartments and finger individuation (Reilly and Schieber 2004). The ‘unwanted’ coupling among finger forces reported during individuated finger force production, however, might be desirable for tasks characterized by finger force coupling such as multi-digit grasping. For this task, common input to hand muscle motoneurons might contribute to temporally constrain the production of multiple forces to maintain a stable grasp.
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 m. flexor digitorum profundus (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).

**Materials and Methods**

*Experimental Task*

A total of 8 subjects (4 males and 4 females; mean age 29 years, range 21-37 years) 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 minutes. Before lifting the device, subjects placed the distal finger pad of each digit on its respective force sensor plate (see below). After establishing a firm grip, 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 above 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 minutes to ensure the acquisition of a minimum number of motor unit action potentials, i.e., 900. We gave rest periods of a minimum 5 minutes between trials to ensure that subjects were fully rested before starting a new trial.
Force and electromyographic 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 N and 0.015 N, respectively). The diameter of the sensors for the fingers and the thumb was 17 mm and 25 mm, respectively. For the present study we analysed only forces normal to the sensors. The average normal force measurement error ranged from 0.003 N (± 0.009) to 0.007 N (± 0.003) for the finger sensors and from 0.066 N (±0.108) to 0.143 N (± 0.019) 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 m. flexor digitorum profundus (FDP) and m. flexor pollicis longus (FPL) (Frederick Haer and Co., 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 diameter gold plated silver disc, Model F-E5GH, 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 (a) two digit compartments of FDP or (b) 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 individuated 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 electromyographic (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 to 4 minutes, after which the subject replaced the object on the platform. When single motor units could not be isolated on both channels within 1 minute after onset of object hold, the subject replaced the device on the platform and a rest period was given before repeating the above 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 above until a selective movement of the target finger could be elicited, and the above procedures were repeated. Within a single experimental session we recorded EMG activity from 3-10 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 was acquired synchronously by three 12-bit analog-to-digital 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 analyse 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 analysed by performing Fast Fourier Transform analysis (FFT) and circular statistics as done in previous studies (Santello and Soechting 2000; Rearick et al. 2002). Briefly, we performed FFT on forces exerted during the entire hold period (4 minutes) 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 values 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 non-random or random, respectively (Batschelett 1981; for a detailed description of the analysis see Santello and Soechting, 2000). The mean angle of phase differences was computed only for the non-random phase difference distributions.

**EMG.** EMG data was analysed offline 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, U.K.). 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) interspike intervals (ISI) 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 sub-distributions 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, standard deviation 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 tangential 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 standard deviation 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 (bottom panels, Fig. 4). 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 (top panels, Fig. 4). The peak was defined by the area between the 10\textsuperscript{th} to 90\textsuperscript{th} percentiles of the largest inflection in the cusum within ± 20 ms of the reference unit firing (Schmied et al. 1993; time period within the two 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 pre-synaptic 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 (horizontal lines, bottom row, Fig. 4). 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 at least 900 spikes occurring without large gaps (< 1 sec) 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 above).

CIS computed on hand muscles often ranges from 0 to sometimes slightly over 1.0 (e.g. Semmler and Nordstrom 1998; Keen and Fuglevand 2004; 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 around 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 less than 0.3 are associated with weak motor unit synchrony as no clear peaks in the cross-correlogram can be discerned (i.e., Fig. 2 in Semmler and Nordstrom 1998; our current data, Fig 4A).

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-tests. 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 (a) FPL and FDP compartments and (b) 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). Fig. 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 (Figure 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. Panel C shows a single motor unit discriminated from each EMG record and Panel D shows the interspike interval (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; Santello and Soechting 2000; Rearick and Santello 2002), finger
forces being progressively smaller from the index to the little finger. Mean forces (± standard deviation) produced by each digit were 2.85 (± 1.05), 1.31 (± 0.46), 0.78 (± 0.19), 0.75 (± 0.22) and 0.62 N (± 0.21) for the thumb, index, middle, ring and little fingers, respectively. The horizontal torques exerted by the fingers ranged from –0.12 Nm to 0.09 Nm (index and little fingers, respectively). The average horizontal torques (± SD) were 0.05 (± 0.02), 0.01 (± 0.01), -0.01 (± 0.01) and -0.03 Nm (± 0.02) (index, middle, ring and little fingers, respectively). Net horizontal torques from most trials (94%) were within a ± 0.05 Nm range (average ± SD: 0.02 Nm ± 0.01).

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 0º, i.e., in-phase relationships for all subjects. Almost all distributions (98%) were non-random with mean angles close to 0º (range: –26° to 34°), indicating a consistent tendency for a similar modulation of force fluctuations between pairs of forces. These results are quantitatively 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 Hz ± 1.5.
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.

**INSERT FIGURE 3 AND TABLE 1 APPROXIMATELY HERE**

To allow comparison with previous motor unit studies during force production tasks where firing rate was controlled, we computed the coefficient of variation (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 below). 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). We 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 Hz (± 0.001). 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 was 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 (top traces, Fig. 4) was first computed to define the peak range in the corresponding cross-correlogram (bottom traces, Fig. 4). The peak in the cross-correlogram was quantified within ± 20 ms of the reference motor unit firing using the common input
strength index (CIS; see Methods). Three examples of weak, moderate and strong synchrony are shown in Figure 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 $1,749 \pm 546$. The mean duration of the cross-correlogram peaks was $20.1 \text{ ms} \pm 7.2 \text{ ms}$ (range: 2.9 to 38.6 ms). The center of the peak was within $\pm 10 \text{ ms}$ 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 ($r^2 = 0.008$; $p > 0.05$). 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 ($r^2 = 0.1$). 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 Figure 5, where the vertical dashed line indicates a 0.3 cut-off value separating weak from moderate and strong synchrony (see Methods).

**INSERT FIGURE 5 APPROXIMATELY HERE**

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 column). 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 (a) lower percentages of motor unit with CIS values equal or higher than 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% to 73% of the motor unit pairs in 5 out of 6 FDP compartment pairs (Fig. 5). The strongest synchrony was found in the FPD 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 non-adjacent FDP compartments controlling the index and ring fingers (FDP2 and FDP4; Table 1) was characterized by the weakest synchrony. However, the non-adjacent 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 as are plotted in Fig. 6 as percentage of motor unit pairs exhibiting moderate to strong synchrony as a function of separation between FDP compartments.

**INSERT FIGURE 6 APPROXIMATELY HERE**
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 post-synaptic potentials at the motoneurons resulting from branched axons of common pre-synaptic neurons (Sears and Stagg 1976; Kirkwood and Sears 1978; Nordstrom et al. 1992). 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 common input strength index (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 since 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 below) 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. first dorsal interosseus; Datta and Stephens 1990) as well as to different muscles (across-muscle synchrony; e.g. first and second 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 and Schieber 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 FDP2) - 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. Below 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 above 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 (Schieber 1991, 1995; Schieber et al. 2001; Kilbreath and Gandevia 1994; Kilbreath et al. 2002; Häger-Ross and Schieber 2000; Reilly and Schieber 2003). 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 non-specific 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 (a) define functionally independent FDP compartments based on the selectivity with which motor units could generate forces at individual digits; and (b) 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. While 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 5-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 to 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 to 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 below).

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 to 40 ms and 19 ms, respectively) as well as the percentage of peaks occurring ± 10 ms from time zero (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 vs. non-adjacent 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 Flexor Digitorum Superficialis.

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’; Ellaway and Murthy 1985). The k’ index is computed as the ratio of the mean count per bin within the peak region of the cross-correlogram to the chance counts within that region (Ellaway and Murthy 1985), whereas CIS is normalized by the trial duration (see Methods). Second, Reilly et al. (2004) chose to use k’ because their EMG data was 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 the task used, i.e., object hold against gravity vs. 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 vs. 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,b,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 to 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 vs. FDP might reflect the different roles that these two muscles play in object grasping and manipulation (see below).

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 non-adjacent compartments during isometric force production. As noted above, 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 above 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. Santello et al. 2002; Rearick et al. 2003).

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 individuation. Specifically, the simultaneous discharge of motor units controlling the instructed and non-instructed 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 effect of different levels of across-muscle synchrony strength on the temporal relationship between forces (Santello and Fuglevand in press). It was found that moderate across-muscle motor unit synchrony (CIS = 0.3) was sufficient to reproduce in-phase relationships of normal forces (Santello and Fuglevand, in press), a consistent feature of multi-digit grasping (Santello and Soechting 2000; Rearick and Santello 2002; Rearick et al. 2002, 2003).

The performance of our multi-digit task also requires the control of torques to prevent the object from tilting relative to the vertical. A number of studies have shown that torque control tasks require varying degrees of coupling among normal and tangential forces exerted by radial and ulnar fingers (Shim et al. 2003; see Zatsiorsky and Latash 2004 for review). Therefore it is conceivable that motor unit synchrony across FDP compartments and between FDP and FPL might contribute to modulate the coupling between digit forces also in torque control tasks.
Theoretical and quantitative considerations (Santello and Fuglevand in press) suggest that motor unit synchrony would contribute to the coupling between normal forces. Therefore the present study focused on quantifying motor unit synchrony across finger muscles and muscle compartments. Note, however, that across-muscle/muscle compartments motor unit synchrony is one of several neural mechanisms that would contribute to couple forces exerted during grasping. Force coupling during grasping would also occur as a result of activation of motor units innervating different functional subdivisions of finger flexor muscles, e.g. flexor digitorum profundus (FDP; Kilbreath et al. 2002). Further work is needed to fully characterize the neural mechanisms underlying the fine coordination of forces exerted during grasping.

**Conclusion**

We found moderate to strong motor unit synchrony across compartments of the deep flexors of the fingers (FDP) as well as between FDP compartment of the index finger and an extrinsic thumb flexor muscle, FPL. The weaker strength of common input to FPL and FDP compartments of middle, ring and little fingers might reflect the predominant use of thumb-index finger in object grasping and manipulation. Such difference, however, might not be obligatory as different task requirements might elicit different levels of common input strength. 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


Table Legend

Table 1. Motor unit firing rates, firing rate variability and CIS. 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 mean ± SE.
FIGURE LEGENDS

Figure 1. Grip device. The device used to measure normal forces is shown, frontal and side views.

Figure 2. Normal forces and EMG during object hold. Top traces in panel A are normal forces exerted by the thumb, index, middle, ring and little finger (Tx, Ix, Mx, Rx and Lx, respectively). The bottom traces are EMGs from the thumb muscle (FPL) and the index compartment of FDP (FDP2). The data shown are from a smaller recording period than the entire duration of the object hold trial (~4 minutes). Panel B shows motor units discriminated from each raw EMG trace and their respective firing rates. Panel C shows a single motor unit discriminated from each EMG channel. The number of spikes for the motor units shown in the insets was 2179 and 1927 for FPL and FDP, respectively. Panel D shows the interspike interval distribution (ISI) for the two motor units shown in C. All traces are from the same subject (#4).

Figure 3. Average motor unit firing rates. The plot shows the distribution of mean firing rate computed for each motor unit \(n = 381\) averaged across trials and subjects. For graphical purposes, motor unit firing rates were binned into 1 Hz intervals.

Figure 4. Quantification of motor unit synchrony strength. Bottom traces of panels A, B and C show the cross-correlograms computed on motor unit pairs from FPL vs.
FDP5, FDP2 vs. FDP3, and FDP3 vs. FDP4, respectively (subjects #6, #3 and #6, respectively) characterized by weak, moderate and strong synchrony. The common input strength index (CIS) computed for each cross-correlogram is also shown. Top traces show the cumulative sum (cusum) of the events of each cross-correlogram used to define the peak region. 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 row). The number of events below chance level is denoted by a white area.

**Figure 5. CIS index.** The distribution of the common input strength index is shown for each FPL-FDP compartment combination (1st column on the left) and for each pair of FDP compartments. Vertical line denotes the cut-off CIS value of 0.3 between weak and moderate to strong motor unit synchrony (light and dark bars, respectively). For graphical purposes, CIS values, ranging from 0 to 1, were binned into 0.1 intervals.

**Figure 6. Distributions of common input strength as a function of separation between FDP compartments.** Panel A shows the percentage of motor unit pairs that exhibited moderate to strong synchrony (CIS ≥ 0.3) as a function of separation between FDP compartments (1 indicates adjacency between compartments whereas 3 indicates maximum separation). The digit associated with each muscle compartment is denoted by the letter I, M, R and L (index, middle, ring and little
finger, respectively). Panel B shows the same data shown in panel A pooled across FDP compartments with the same degree of separation.
<table>
<thead>
<tr>
<th>Across muscles</th>
<th>MU pairs</th>
<th>GM firing rate (Hz)</th>
<th>GM CV firing rate (%)</th>
<th>CIS</th>
<th>Peak duration (ms)</th>
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<td>FPL-FDP2</td>
<td>19</td>
<td>11.36 ± 0.29</td>
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<td>0.49 ± 0.03</td>
<td>20.77 ± 3.28</td>
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<td>FPL-FDP3</td>
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<td>10.47 ± 0.16</td>
<td>25.51 ± 1.10</td>
<td>0.26 ± 0.02</td>
<td>21.10 ± 2.56</td>
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<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>
<td>23.11 ± 3.14</td>
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<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>
<td>19.56 ± 3.34</td>
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<td>FDP2-FDP3</td>
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<td>11.00 ± 0.18</td>
<td>23.30 ± 0.64</td>
<td>0.32 ± 0.03</td>
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<td>FDP2-FDP4</td>
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<td>FDP2-FDP5</td>
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<td>FDP3-FDP4</td>
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<td>FDP3-FDP5</td>
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<td>25.66 ± 2.65</td>
<td>0.38 ± 0.06</td>
<td>16.99 ± 2.91</td>
</tr>
</tbody>
</table>

Table 1. Motor unit firing rates, firing rate variability and CIS.
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 mean ± SE.
Figure 1
Figure 2
Figure 3
Figure 4
Figure 5
Figure 6