Short-Term Synchronization Between Motor Units in Different Functional Subdivisions of the Human Flexor Digitorum Profundus Muscle

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Abstract: Short-term synchronization between motor units in different functional subdivisions of the human flexor digitorum profundus muscle. J Neurophysiol 92: 734–742, 2004. First published March 31, 2004; 10.1152/jn.00027.2004. The ability to independently move the digits is limited by peripheral as well as central factors. A central limitation to independent finger movements might arise from the inability of the human nervous system to activate motor units (MUs) that exert force on one finger without also activating MUs that exert force on adjacent fingers. Short-term synchronization between MU pairs is thought to be the result of the two motoneurons receiving common input from last-order neuronal projections. The human flexor digitorum profundus (FDP) muscle contains four subdivisions, one for each of the fingers. We hypothesized that the distribution of MU synchrony within and between subdivisions of FDP might parallel the ability to selectively activate different functional subdivisions within FDP, and the ability to flex one digit independently of another. We found that the degree of MU synchrony indeed was not uniform among the different functional subdivisions of FDP; MUs acting on ulnar digits (d5, d4) were more synchronized than MUs acting on radial digits (d2, d3). Furthermore, synchrony was observed between MU pairs where each unit acted on a different digit and was highest when both units of a pair acted on the least-independent digits (d4, d5). This indicates that the CNS does not exert completely independent control over the different functional subdivisions of FDP. The strength of synchrony appears related to the inability to produce completely independent forces or movements with the digits. These observations reflect widespread divergence of last-order inputs within the FDP motoneuron pool, thus may cause MUs acting on other fingers to be co-activated with MUs acting on the intended finger.

INTRODUCTION

Positioning of the fingers during grasping and object manipulation requires the coordinated activity of many different muscles (Maier and Hepp-Reymond 1995a,b). The final location of the fingertips, however, is determined by the position of the distal interphalangeal joint. Flexor digitorum profundus (FDP) is the only muscle that attaches to the distal phalanx (Wood Jones 1949), and it therefore plays a unique and important role in grasping and object manipulation. The four-tendoned FDP is commonly assumed to achieve independent mechanical actions at the four fingertips by selective activation of a separate compartment within the muscle serving each finger. Recent electromyographic evidence suggests, however, that FDP is not completely functionally compartmentalized but instead contains core regions that are selectively active during flexion of only one finger, and other less-selective regions that are active during the flexion of more than one finger (Kilbreath and Gandevia 1994; Reilly and Schieber 2003). This incomplete functional subdivision probably contributes to the inability of humans to produce completely independent finger movements (Häger-Ross and Schieber 2000) or finger forces (Li et al. 1998; Reilly and Hammond 2000; Zatsiorsky et al. 2000).

Factors contributing to the incomplete functional subdivision of FDP could be peripheral and/or central in origin. In the periphery, for example, FDP might contain subpopulations of motor units (MUs) that exert tension on more than one finger. This could occur if some MUs contain subsets of muscle fibers that insert on tendons serving adjacent fingers or if they contain muscle fibers that act on a tendon to one finger that is biomechanically coupled to a tendon serving another finger. Motor-unit-triggered averaging (MUTA) of finger forces suggests that multidigit MUs might indeed be present in the human multi-tendoned muscles FDP (Kilbreath et al. 2002; Reilly and Schieber 2002) and extensor digitorum communis (Keen and Fuglevand 2004b).

One central limitation to independent finger movements might arise from the inability of the human nervous system to activate MUs that exert force on one finger without also activating MUs that exert force on adjacent fingers. FDP MUs first recruited at low threshold during flexion of a given fingertip, for example, also are recruited during flexion of adjacent fingertips at slightly higher force (Kilbreath and Gandevia 1994). Incomplete specificity of the excitatory command within the FDP motoneuron pool, thus may cause MUs acting on other fingers to be co-activated with MUs acting on the intended finger.

A second central limitation can be inferred from observations that MUs in the same, and even in anatomically distinct, hand muscles do not discharge completely independently. Instead, many pairs of MUs show a tendency to discharge synchronously (within a few milliseconds) more frequently than can be explained by chance alone (Datta and Stephens 1990). This short-term synchronization between MU pairs is thought to be the result of the two motoneurons receiving common input from the same branched last-order neuronal projections (Kirkwood 1979; Sears and Stagg 1976). Short-term synchronization has been reported for FDP MUs (Garland and Miles 1997; Huesler et al. 2000), indicating that FDP motoneurons do receive common last-order inputs. MUTAs that reveal forces on more than one digit time-locked to the
discharge of one MU could also arise from short-term synchronization between single-digit MUs acting on different fingers (Taylor et al. 2002). Whether MU synchrony varies for MU pairs within and between functional subdivisions of FDP remains unknown, however. The extent of within- and between-subdivision synchrony reflects the ability of the CNS to independently control the various functional subdivisions of FDP. We hypothesized that the distribution of MU synchrony within FDP might parallel the ability to selectively activate different functional subdivisions within FDP and the ability to flex one digit independently of another.

We therefore examined the strength and distribution of short-term synchronization between MUs in the same and different functional subdivisions of FDP. We recorded concurrently active single MUs from up to four bipolar fine-wire electrodes placed throughout the radio-ulnar extent of the muscle belly as subjects performed weak isometric flexion of the digits. Cross-correlation histograms were used to estimate the strength of synchrony between each pair of discriminable MUs. The strength of MU synchrony was not uniform across the muscle. Pairs of MUs in the same subdivision or in adjacent subdivisions showed more synchrony than pairs in nonadjacent subdivisions. MU synchrony was higher for pairs located within the digit 5 or digit 4 subdivisions, than within the digit 2 or digit 3 subdivisions. These findings have implications for the independence of CNS control of digit flexion. Part of this material was presented previously in abstract form (Reilly et al. 2003).

METHODS

Subjects

Eight right-handed subjects (5 female and 3 male; mean age, 36 yr; range, 23–47 yr), including two of the authors (M. A. Nordström and M. H. Schieber), participated in one to eight separate recording sessions. The majority of the data were recorded from three subjects in whom repeated experiments were performed to sample from as many combinations of muscle locations as possible. Subjects gave written informed consent according to the Declaration of Helsinki, and the protocol was approved by The Research Subjects Review Board of the University of Rochester Medical Center. None of the participants had any history of trauma, degenerative, or neurological disease affecting the upper limbs. Four of the present 12 recording sessions also provided MU electromyographic (EMG) data reported previously (Reilly et al. 2003).

MU recordings

MU action potentials were recorded from two or four bipolar fine-wire electrodes placed in the left FDP while participants produced isometric force at the distal phalanges of the five digits. A detailed description of the techniques for making and inserting electrodes into FDP has been published previously (Reilly and Schieber 2003). Briefly, the intramuscular electrodes were made from two Teflon-insulated stainless steel wires (unsualled single-wire diameter: 40 μm) threaded through the lumen of a disposable needle (approximate diameter of electrode: 100 μm). Approximately 5 mm of the wire-tips was bent back over the bevel of the needle to make a small hook. Each sterilized electrode was inserted percutaneously from the medial aspect of the forearm at a proximodistal level roughly one-third of the distance from the olecranon to the wrist crease. The digit 5 portion of FDP is located in the most ulnar aspect of the muscle, whereas the digit 2 portion is located most radially. Therefore we inserted electrodes to different radio-ulnar depths to sample regions of the muscle acting on different fingers. In some sessions, we also inserted more than one electrode to the same radio-ulnar depth to record MU pairs from within the same subdivision. Once the electrode was in the appropriate subdivision of FDP, identified by having the subject flex each fingertip in turn, the needle was removed leaving only the flexible wires in place. Placement of the recording tips in FDP was confirmed by having the subject flex each digit or the wrist in turn against resistance provided by the examiner. The appearance of EMG activity during flexion at an interphalangeal joint greater than that of EMG activity around the time of discharge of any proximal interphalangeal joint, at the thumb, or at the wrist indicated appropriate placement in FDP, and not in flexor digitorum superficialis, flexor pollicis longus, flexor carpi ulnaris, or flexor carpi radialis. During task performance (described in the following text), EMG activity was amplified (5,000–20,000), band-pass filtered (0.3–3 kHz), and then sampled at 17 kHz per channel by a micro1401 interface (CED, Cambridge, UK) hosted by a PC-compatible computer.

Experimental setup and behavioral task

After insertion of the electrodes, participants placed their left hand in an apparatus that measured the flexion and extension force at the distal phalanx of each digit. The distal phalanx of each digit was placed in a plastic ring and held in place by a small plastic thumb-screw pressed gently but firmly against the fingernail. Each plastic ring was attached to a load cell that measured flexion and extension forces (see Fig. 2 of Reilly and Schieber 2003). The position of the ring was adjusted for each digit such that the shape of the hand was similar to that used to grasp a medium-sized spherical object. The seated subjects placed their forearm horizontally on a table with their elbow flexed to ~130°, the forearm in neutral pronation/supination, and the wrist extended ~45°. A vacuum cast stabilized the forearm and elbow. EMG activity from one electrode was amplified and played through a speaker so the subject could hear all active MUs detected by that electrode. Subjects were instructed to choose one of these MUs (the target MU) and attempt to make it fire as slowly as possible, at a rate just sufficient to maintain tonic discharge. While the experimenters monitored the other EMG channels on an oscilloscope, the subject was instructed to selectively increase or decrease flexion forces in the digits so that discriminable MU potentials were tonically active in multiple channels. Thus for each experimental run the subjects may have been flexing a single digit or maintaining small flexion forces in two or more digits.

Tonic discharge of a target MU was recorded for 5–15 (mean 8) minutes. After this, subjects used auditory feedback to recruit a different MU from the same electrode. We recorded any other MUs that could be tonically activated and recruited concurrently with a discriminable MU in at least one other electrode. This process was continued for each electrode until no novel pairs of concurrently active MUs could be identified from the various electrode combinations. Subjects were allowed to rest as necessary between trials. A single recording session lasted 1–5 h.

MU action potential waveforms were discriminated off-line using a computer-based software template-matching algorithm (Spike2; CED). Waveform shape was used to identify action potentials belonging to a particular MU, and the inter-spike intervals (ISIs) for each template were examined to ensure discrimination accuracy. Action potentials with abnormally short ISIs that were clearly the result of discrimination error were manually corrected or rejected (cf. Nordstrom et al. 1992). The ISI mean and SD of the retained action potentials then were calculated using the Spike2 software.

Care was taken to ensure that action potentials from the same MU were not present in multiple intramuscular EMG channels as this could contaminate the cross-correlation due to discrimination errors from waveform superimposition around the time of discharge of the common unit. In some cases such cross-talk was not detected in the
Assessment of short-term synchrony

The strength of short-term synchronization between concurrently active pairs of MUs recorded from different electrodes was quantified by first constructing a cross-correlation histogram (bin-width, 1 ms) for a period of ±100 ms around the discharge time of the reference MU (randomly chosen from the pair of MUs). Histograms with a mean bin count <4 were not analyzed further. The position and duration of any synchronous peak within the cross-correlogram was determined visually from the cumulative sum (CUSUM) of the cross-correlogram (Ellaway 1978). Figure 1 shows an example of a cross-correlogram and its corresponding cusum for two FDP MUs that showed short-term synchronization; an increased incidence of near-coincident discharge is evident as the elevated counts in the bins around time 0. The points of inflection of the CUSUM were used to define the boundaries of the peak and non-peak regions of the cross-correlogram. The significance of any synchrony peak in the cross-correlogram was assessed using the technique described by Wiegner and Wierzbicka (1987).

The strength of short-term synchrony between each pair of MUs was quantified from the cross-correlogram using the index $k'$ (Ellaway and Murthy 1985), which is the ratio of the mean bin count in the peak region of the cross-correlogram ($X/N$ from Fig. 1) to the mean bin count expected due to chance alone ($M$ from Fig. 1). This synchronization index is, therefore, sensitive to the duration of the peak. We were interested in quantifying the strength of synchrony for all MU pairs, whether or not a significant peak was present. Therefore if no significant synchrony peak was apparent in the CUSUM, a standard window of 11 ms width centered at time 0 was used to assess the strength of synchrony for that pair (Semmler and Nordstrom 1998; Semmler et al. 1997, 2000).

Although other indices, such as the common input strength (CIS), normalize for the firing rate of the MUs, we chose $k'$ for the present study for three reasons. First, $k'$ is relatively insensitive to spikes missed due to waveform superimposition. Second, like many other synchronization indices, $k'$ is influenced by the firing rate of the MU pair (Nordstrom et al. 1992), but MU firing rates did not vary systematically for the different subdivisions of FDP in the present study (see RESULTS). Finally, rather than a single continuous period of concurrent discharge of the two MUs in a pair, our recordings often contained multiple periods of concurrent tonic discharge of a pair of MUs interspersed with periods in which one or other unit did not discharge tonically or could not be discriminated reliably due to superimpositions. Given the large number of MU pairs examined here ($n = 488$), and the duration of the recording sessions ($\leq 5$ h), manually determining the total duration of concurrent discharge for each MU pair to normalize for firing rate, which is required to calculate other indices like the CIS (Nordstrom et al. 1992), would have been prohibitively time consuming.

Classifying position of the electrode within the muscle

Investigating whether the strength of MU synchronization was dependent on the location of the MUs within different functional subdivisions of FDP required a means of assigning each MU to a particular subdivision. The exact location of the electrode tips within the muscle belly (e.g., index finger region vs. middle finger region of FDP) could not be confirmed by direct visualization, and pilot studies of intramuscular electrical stimulation through these electrodes typically failed to evoke detectable twitches. We therefore classified the functional location of each MU using the parent EMG activity

![Figure 1](image-url)

**FIG. 1.** A cross-correlogram (bottom) from a pair of motor units recorded from flexor digitorum profundus (FDP) and its corresponding cusum (top). The position and duration of the synchronous peak was judged from the points of inflection of the cusum. The strength of motor-unit (MU) synchrony between the 2 units was quantified using $k'$, which was calculated as the ratio of the mean bin count in the peak region ($X/N$) to the mean bin count outside the peak region ($M$), $k' = X/N \times M$. 

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recorded from the electrode while subjects performed a task in which they produced isometric, individuated flexion forces of each of the four fingers in turn. Our assignment of each MU to a given functional subdivision thus was independent of any assumptions about the physical location of the electrode within the muscle. The task used for this functional assessment has been described previously in detail (Reilly and Schieber 2003). Briefly, subjects produced isometric flexion forces of each finger alone and concurrent changes in the EMG activity were recorded at an electrode. The mean change in EMG associated with flexion of a particular finger was denoted as ΔEMG, and separate ΔEMG values were calculated for each of the four instructed flexion forces (flexion of the index (2f), middle (3f), ring (4f), and little (5f) fingers). Figure 2 shows the EMG activity recorded at a single electrode during five trials of each of the four instructed flexion forces (bottom), and the top trace shows the average rectified EMG from all 10 trials. Instead of classifying the position of the electrode by choosing which digit was associated with the largest EMG from all 10 trials of that instructed force, two dots under raw EMG from each individual trial indicate task events: onset (for details, see Reilly and Schieber 2003).

### RESULTS

We analyzed cross-correlograms from 488 pairs of tonically firing MUs recorded via 47 electrodes in 12 recording sessions. The mean firing rates of the individual MUs ranged from 7.8 to 15.6 Hz, with an average of 11.9 ± 0.06 Hz. The mean k value for all MU pairs was 1.23 ± 0.01. Statistically significant peaks were present in 201 of the 488 (41%) cross-correlograms. Mean k value for MU pairs with a significant synchrony peak in the cross-correlogram was 1.38 ± 0.01. The mean firing rate for MU pairs with significant synchrony was 11.9 ± 0.09 Hz, which was not significantly different from the mean firing rate of MU pairs with nonsignificant peaks 11.9 ± 0.07 Hz. The duration of the significant peaks ranged from 3 to 40 ms with an average of 19 ± 0.6 ms, and the center of 85% of these peaks was within ± 10 ms of time 0. Table 1 shows the total number of MU pairs in each subdivision combination, as well as the number of pairs with significant k values.

Figure 3 shows four example cross-correlograms and their corresponding cusums. Figure 3A shows an example constructed from the spike trains of two MUs both recorded from the digit 2 subdivision of FDP while the subject maintained a weak isometric contraction of multiple digits. The central peak in the histogram represents an increased probability of discharge from MU 1 about the time of occurrence of each discharge from MU 2. These two MUs were in the same functional subdivision of FDP (separation = 0). Some pairs of MUs located in adjacent subdivisions also showed short-term synchronization. Figure 3B shows an example in which one MU was in the digit 5 subdivision and the other was in the digit 4 subdivision (separation = 1). Although these two MUs were in FDP subdivisions acting on different digits, the narrow peak in the cross-correlogram indicates that these MUs had a tendency to fire synchronously. Figure 3, C and D, illustrates the same tendency toward synchronous firing for a pair of MUs with a separation value of 2 (digit 5 and 3 subdivisions), and for a pair with a separation value of 3 (digit 5 and 2 subdivisions), respectively.

To examine the distribution of synchrony according to the regions of FDP acting on particular fingers, we categorized each MU as acting on a given finger, on the basis of the COA value derived from its parent EMG. This produced 10 possible (4 within- and 6 between-) subdivision combinations. Figure 3A shows the mean k value from all MU pairs (including both significant and nonsignificant peaks) for each of the 10 possible MU subdivision combinations. The combinations are arranged from left to right with increasing separation between subdivisions. A one-way ANOVA with subdivision combination as
the factor showed a main effect of combination \( F_{0.478} = 15.44, P < 0.05 \); post hoc tests revealed that the \( k' \) values for each of the 5/5, 4/4, and 5/4 combinations were significantly greater than the \( k' \) values for at least four of the remaining seven combinations. None of the other seven combinations were significantly different from each other. The strength of synchrony as quantified by \( k' \) was significantly higher \( (t_{284} = 7.22, P < 0.05) \) on the ulnar than on the radial side of the muscle; the average \( k' \) value for ulnar pairs (5/5, 5/4, and 4/4 combinations) was 1.35 ± 0.02, and for radial pairs (2/2, 2/3, and 3/3 combinations) was 1.23 ± 0.01. Figure 4B shows that the mean \( k' \) values for the four levels of separation also varied significantly \( F_{3,484} = 22.86, P < 0.05 \). Two units situated in the same or adjacent subdivisions (separation 0 or 1) tended to have a similar amount of synchronization, which was higher than that of MU pairs separated by more than one subdivision (separation of 2 or 3). The distributions of \( k' \) values in each of the four separation categories were not significantly different from normal (Kolmogorov-Smirnov test, \( P > 0.05 \)).

The strength of synchronization measured by \( k' \) is affected by the firing rate of the MUs. To ensure that the observed effects of subdivision combination and separation level on synchrony strength (Fig. 4, A and B) were not due to firing rate differences, we examined the mean firing rates of the MU pairs for the 10 different subdivision combinations. A one-way ANOVA revealed some differences in the mean firing rates \( F_{3,484} = 5.10, P < 0.05 \). Post hoc testing revealed that the firing rate for 5/4 pairs was significantly higher than for 3/2, 4/2, 5/2, 4/3, and 5/5 pairs, and the firing rate of 3/2 pairs was higher than that of 4/3 pairs. These firing rate differences, however, fail to account for the significant differences in \( k' \) values.

Figure 4, C and D, shows the percentage of cross-correlograms for which the synchrony peak was deemed significant using the method described by Wiegner and Wierzbicka (1987). Figure 4C shows that a cross-correlogram was more likely to have a significant peak when both MUs were in the digit 5 (5/5), digit 4 (4/4), or digit 3 (3/3) subdivisions, or if one was in digit 5 and one in digit 4 (5/4). With the exception of the 3/3 combinations, significant peaks occurred more often when both units were in the ulnar side of the muscle compared with both in the radial side or one in the radial side and one in the ulnar side. Figure 4D shows the percentage of significant peaks as a function of the separation between the subdivisions containing the two MUs of a pair. The prevalence of significant synchrony peaks in the cross-correlograms generally decreased with increasing separation between the two subdivisions.

The likelihood of detecting a significant peak is influenced by the mean bin count of the cross-correlogram (Wiegner and Wierzbicka 1987). To assess whether differences in mean bin count might have influenced the prevalence of significant peaks (Fig. 4, C and D), we compared the mean bin count for cross-correlograms from MU pairs with different levels of separation. The mean bin count for combinations with separation values of 0–3 were 18.1 ± 1.62, 14.6 ± 1.04, 15.4 ± 3.09, and 20.7 ± 4.83, respectively. These values did not differ significantly from each other. Thus differences in mean bin count failed to account for the higher prevalence of significant

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**TABLE 1. The number of motor unit pairs recorded from each subdivision combination**

<table>
<thead>
<tr>
<th>Separation Value</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Pairs</td>
<td>30</td>
<td>82</td>
<td>24</td>
<td>85</td>
</tr>
<tr>
<td>Pairs with significant ( k' ) values</td>
<td>18</td>
<td>82</td>
<td>24</td>
<td>85</td>
</tr>
<tr>
<td>Percentage significant pairs</td>
<td>60</td>
<td>91</td>
<td>25</td>
<td>11</td>
</tr>
</tbody>
</table>

Pairs are shown with the number of pairs that showed significant synchrony in their cross-correlograms and the percentage of pairs with significant synchronous peaks.

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**Fig. 3.** Examples of 4 cross-correlograms and their corresponding cusums from pairs of MUs with separation values of 0–3.

One unit of each pair was from the digit 5 subdivision of the muscle and the other was from digit 5 (separation = 0, \( k' = 1.18 \)), digit 4 (separation = 1, \( k' = 1.20 \)), digit 3 (separation = 2, \( k' = 1.20 \)), and digit 2 (separation = 3, \( k' = 1.18 \)).
MU synchrony in pairs with separation values of 0 and 1. Rather, the pattern of significant peak prevalence (Fig. 4, C and D) closely follows the pattern of synchrony strength (Fig. 4, A and B) across the different subdivision combinations and separation levels.

Differences in peak width may reflect different patterns of connectivity in last-order inputs to motoneurons, and particularly broad peaks may reflect synchrony of the last-order inputs themselves (Kirkwood 1979). The duration of the significant peaks varied significantly for MU pairs from the various subdivision combinations \([F_{(9,191)} = 4.71, P < 0.05]\). Figure 4E shows mean peak width for all significant synchrony peaks, grouped by subdivision combination. Post hoc tests showed that peaks from 5/4 cross-correlograms were significantly broader than peaks from 3/2 and 4/2 combinations, and that peaks from 4/4 pairs were broader than those from 4/2 pairs. Within the 0–2 separation categories in Fig. 4E there appears to be a general trend whereby peaks were wider for subdivision combinations containing at least one unit in the ulnar side of the muscle. A Spearman’s rank correlation analysis, however, revealed that this tendency was not significant (Spearman’s \(\rho = -0.079, P > 0.05\)). Likewise, when grouped according to separation value (Fig. 4F), no significant variation in peak width was found \([F_{(3,197)} = 2.06, P > 0.05]\).

**DISCUSSION**

The present study confirms previous reports that pairs of MUs in FDP display short-term synchronization (Garland and Miles 1997; Huesler et al. 2000). We have extended these findings by demonstrating that the degree of MU synchrony is not uniform across the functional subdivisions of FDP that act on different fingers. MUs acting on ulnar digits \((d5, d4)\) were significantly more synchronized than MUs acting on radial digits \((d2, d3)\). Synchrony was observed between MU pairs in which each unit acted on a different digit, indicating that the CNS does not exert completely independent control over the different functional subdivisions of FDP. Pairs of units in the same subdivision or in adjacent subdivisions were significantly more synchronized on average than pairs of units in nonadjacent subdivisions. The degree of MU synchrony between subdivisions generally declined with increasing separation between the digits, indicating more independent CNS control of FDP subdivisions supplying more anatomically distant fingers.

**Technical limitations**

To sample the functional subdivisions of FDP as thoroughly as possible, we included MUs, the parent EMG of which showed activity during flexion of more than one fingertip. Each
MU then was assigned to a functional subdivision based on the pattern of parent EMG during individuated flexion of the four fingers (see METHODS). Although as reported previously (Reilly and Schieber 2003) we have found little objective evidence that our electrodes in one functional subdivision pick up MUs in adjacent subdivisions, some of the present MUs assigned to a given subdivision conceivably might have belonged to an adjacent subdivision. Such misclassifications would tend to diminish differences in the average strength of synchrony we measured for MU pairs in different subdivision combinations, particularly those differences for pairs in the same or adjacent subdivisions. We therefore may have failed to demonstrate some differences in synchronization that in fact were present, but those differences found to be significant are unlikely to have arisen from inaccurate assignment of MUs to the wrong functional subdivision. Given the large number of MU pairs examined (n = 488), our results are likely to be representative of the MU synchronization gradient that exists within FDP.

At high forces, the action potentials of individual MUs become obscured in the interference pattern generated by the numerous MUs recruited. Our sample was, therefore confined primarily to low-threshold MUs. Although our findings cannot necessarily be extrapolated to situations involving high forces, the low-threshold MUs studied here are perhaps the most important MUs for fine manipulative tasks involving the digits.

Inputs to motoneurons responsible for synchrony

The contralateral primary motor cortex and the corticospinal system make a major contribution to the generation of MU synchronization (Conway et al. 1995; Datta et al. 1991; Farmer et al. 1991, 1993a,b, 1997; Salenius et al. 1997). Corticomo-
toneuronal (CM) cells have widely divergent monosynaptic excitatory connections within the motoneuron pools of single muscles and among the motoneuron pools of multiple synergistic muscles, especially the distal muscles of the upper limb (Porter and Lemon 1993). CNS lesions that affect the cortico-
spinal tract and/or its CM cells alter the strength and time course of MU synchronization (Farmer et al. 1993b). Thus the differences in synchrony that we observed here are likely to reflect in large part differences in the distribution of branched-
axon inputs from CM cells to motoneurons.

Differences in the strength of synchrony between various pairs of MUs can arise from anatomical factors (number of shared, branched-axon inputs from last-order neurons) and/or from different activation patterns of the last-order neurons responsible for synchrony as evidenced by the task-dependent nature of synchrony (Bremner et al. 1991a; Garland and Miles 1997; Schmied et al. 2000). As the task in our experiment was similar for all four digits (simultaneous flexion), we suggest that our results reflect differences in the anatomical distribution of shared last-order inputs rather than task-related differences in corticospinal neuronal activity.

Furthermore, while the strength of synchrony (k') for MU pairs with separation values of 0 and 1 on average was higher than for pairs with separation values of 2 or 3, the k' values were normally distributed for each separation level. This indicates that the mean k' is a reliable estimate of central tendency for comparison of the strength of synchrony between functional subdivisions of FDP. The physiological processes responsible for MU synchrony are less effective with increasing separation of the MUs within FDP, but there do not appear to be fundamental differences in the pattern of organization of the synchronizing inputs acting on MUs in the same or separate subdivisions.

Strength of synchrony between FDP MUs acting on the same or different digits

If the corticospinal system accesses all MUs in a multiten-
doned muscle as a single homogeneous motoneuron pool, the strength and prevalence of short-term synchrony between all MU pairs should be similar, regardless of the functional subdivision(s) in which the two MUs lie. In contrast, if the corticospinal system accesses the motoneurons as distinct sub-
 pools, each acting on a different digit, then synchrony between pairs of MUs that both lie within the same functional subdivision should be more prominent than synchrony between pairs in which the two MUs lie in different functional subdivisions. This latter pattern recently has been reported for the human extensor digitorum communis (EDC) (Keen and Fuglevand 2004a).

The distribution of short-term synchrony found here in the human FDP falls somewhere in between that of a homoge-
 nous motoneuron pool and that of four distinct subpools. We found that pairs of MUs both within the d5 or both within the d4 subdivision of FDP were significantly more synchronized on average than pairs within the d3 or within the d2 subdivision (Fig. 4A). Furthermore, pairs with one MU in the d5 and one in the d4 subdivision were as highly synchronized on average as pairs with both MUs within either the d5 or the d4 subdivision. In contrast, pairs with one MU in the d3 and one in the d2 subdivision showed less synchronization, similar on average to that of 3/3 or 2/2 pairs. We infer that motoneurons of the d4 and d5 subdivisions of FDP receive relatively more shared, branched-axon last-order inputs—both within and between the two subdivisions. Access of the corticospinal system to the d5 and d4 subdivisions of FDP thus may be less independent than its access to the d2 and d3 subdivisions.

We also found that synchrony was significantly stronger between pairs of MUs in the same or in adjacent functional subdivisions of FDP than between MU pairs in nonadjacent subdivisions. One therefore might expect that when forces or movements are generated by FDP, noninstructed force or movement would be greatest in digits adjacent to the instructed digit and would decline with increasing distance from the instructed digit. Such patterns indeed have been observed during isometric force production (Reilly and Hammond 2000; Reilly and Schieber 2003; Zatsiorsky et al. 2000). For example, when the little finger was instructed to flex in isolation Reilly and Hammond (2000) reported the largest noninstructed force in the ring finger. Similarly, when the ring finger was instructed to flex in isolation, Reilly and Schieber (2003) found that the little finger produced the greatest noninstructed force. These noninstructed forces were the largest recorded in either study; this is consistent with our observation that the highest between-subdivision synchrony occurred between the ring and little finger subdivisions of FDP.

It is interesting to note, however, that the pattern of between-subdivision synchronization we observed does not match ex-
actly the pattern of force in noninstructed digits. In particular, the presence of short-term synchronization between MUs in
different subdivisions of FDP would suggest that the two digits served by those subdivisions would have a tendency to flex simultaneously. Frequently, however, the limited independence of an instructed digit is caused by extension forces in some noninstructed digits (e.g., Reilly and Hammond 2000; Reilly and Schieber 2003). Thus the pattern of synchronization between different subdivisions of FDP does not directly parallel differences in the independence of the digits, probably because digit independence is affected by a variety of interacting factors. We suggest that synchrony between MUs in different subdivisions of FDP is one of these factors, and therefore contributes to the inability to produce completely independent force in, or movements of, the digits.

For 4 of the 10 subdivision combinations, one MU of a pair was in the radial half of the muscle (the d2 and d3 subdivisions) and the other in the ulnar half (the d4 and d5 subdivisions). For the adjacent subdivision combination of 4/3, the strength of synchrony was similar to that observed when both MUs of a pair were within the radial side of the muscle. For the other three radial-ulnar subdivision combinations (5/3, 4/2, and 5/2), however, the strength of synchrony tended to be slightly lower than when both MUs were within the radial side of the muscle. Of course, these nonadjacent combinations were also those with larger separations between functional subdivisions (separation value = 2 or 3), and the strength of synchrony did vary significantly with separation. The present data therefore are unable to disambiguate whether these relatively low levels of synchrony reflect relatively independent corticospinal access to subdivisions of FDP acting on nonadjacent digits or relatively independent access to the radial versus ulnar portions of the muscle.

Nevertheless, our findings in FDP are consistent with radial-ulnar differences that have been observed in other finger muscles. In EDC, Keen and Fuglevand (2004a) found that the strength of synchrony when both MUs were within the digit 2 or within the digit 3 compartment was lower than when both MUs were within the digit 4 or within the digit 5 compartment. Bremner et al. (1991c) examined synchronization between MUs acting on adjacent fingers and reported that in various finger flexors, extensors, and abductors, pairs of MUs acting on the ulnar fingers were more synchronized than pairs acting on the radial fingers. Regardless of the muscle group, pairs of MUs acting on the ulnar fingers are more synchronized than pairs acting on the radial fingers, suggesting less independent corticospinal control of the ulnar than the radial fingers.

**MU synchronization in the finger flexors versus other finger muscles**

Our results show that the extent of MU synchrony depends both on the functional subdivision(s) of FDP in which the MUs lie (higher for d4 and d5) and on the level of separation between the functional subdivisions (higher for same or adjacent subdivisions). MU pairs exhibiting higher synchrony are thought to receive a greater proportion of common inputs in their net excitatory drive (Bremner et al. 1991a,b; Datta and Stephens 1990; Nordstrom et al. 1992). It is interesting, therefore that the mean strength of synchrony between MU pairs in FDP was lower (mean $k' = 1.27$) than values previously reported for MU pairs within FDI (mean $k'$ for 7 subjects = 1.39) (Nordstrom et al. 1992) or for MU pairs within and between subdivisions of EDC (Schmied et al. 1993). Bremner and colleagues (1991c) compared the strength of synchrony between finger flexors, extensors, and abductors, all within the same subjects. Although these authors did not identify the extrinsic finger flexor muscle(s) they studied, they found that pairs of MUs in the finger flexors were less synchronized than pairs in either the finger abductor or finger extensor muscles. Taken all together, these observations suggest that MU synchrony is generally lower in the finger flexors than in the extensors or abductors.

Lower synchrony between MU pairs within the finger flexors suggests that the motoneurons of muscles that flex the digits are controlled more independently by the CNS than the motoneurons of muscles that extend or abduct the fingers. More independent control over the flexor motoneurons parallels common movement patterns of the hand and fingers. The fingers tend to extend and abduct together when opening the hand, but relatively independent flexion of the fingers is employed when shaping the hand to the contours of an object, when manipulating objects or, for example, when using a keyboard. Moreover, these functions of the hand may require finer grading of flexion than extension forces at the different fingertips.

**Conclusion**

Previous studies have shown that the ability to independently move the digits is limited by peripheral as well as central factors. Some potential peripheral factors could be connections between tendons, the anatomical and functional organization of the muscles, and the lateral distribution of force within the muscle. The present study demonstrates a central limitation with widespread MU synchrony within and between various functional subdivisions of FDP. This is a consequence of the divergent nature of the last-order inputs to the FDP motoneuron pool, which limits the independence of the CNS command signals controlling movements of each finger. CM cells in the motor cortex, which have widely divergent connections within spinal motoneuron pools, are likely to play a major role in this MU synchronization and the consequent limits that such synchronization places on the ability to flex the digits completely independently of each other.

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