Motor-Unit Synchrony Within and Across Compartments of the Human Flexor Digitorum Superficialis

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McIsaac TL, Fuglevand AJ. Motor-unit synchrony within and across compartments of the human flexor digitorum superficialis. J Neurophysiol 97: 550–556, 2007. First published November 8, 2006; doi:10.1152/jn.01071.2006. An interesting feature of the muscular organization of the human hand is that the main flexors and extensors of the fingers are compartmentalized and give rise to multiple parallel tendons that insert onto all the fingers. Previous studies of motor-unit synchrony in extensor digitorum and flexor digitorum profundus indicated that synaptic input to motor neurons supplying these multitendioned muscles is not uniformly distributed across the entire pool of motor neurons but instead appears to be partially segregated to supply subsets of motor neurons that innervate different muscular compartments. Little is known, however, about the organization of the synaptic inputs to the motor neurons supplying another multitendoned finger muscle, the flexor digitorum superficialis (FDS). Therefore in this study, we estimated the extent of divergence of last-order inputs to FDS motor neurons by measuring the degree of short-term synchrony among motor units within and across compartments of FDS. The degree of synchrony for motor-unit pairs within the same digit compartment was nearly twofold that of pairs of motor units in adjacent compartments and more than fourfold that of pairs in nonadjacent compartments. Therefore like other multitendoned muscles of the hand, last-order synaptic inputs to motor neurons supplying the FDS appear to primarily supply subsets of motor neurons innervating specific finger compartments. Such an organization presumably enables differential activation of separate compartments to facilitate independent movements of the fingers.

INTRODUCTION

Motor neurons supplying the hand muscles of humans and other higher-order primates are thought to receive substantial synaptic input directly from the motor cortex (Bennett and Lemon 1996; Heffner and Masterton 1983; Lawrence and Kuypers 1968; Palmer and Ashby 1992; Porter and Lemon 1993). This privileged monosynaptic input from the cerebral cortex is thought to underlie the adaptability and unique dexterity associated with voluntary movements of the hand (see review by Lemon and Griffiths 2005). In general, these inputs appear to diverge extensively to contact many neurons within a motor nucleus (Lawrence et al. 1985; Mantel and Lemon 1987) and may also ramify to contact multiple motor nuclei, particularly those supplying extrinsic hand muscles (Asanuma et al. 1979; Buys et al. 1986; Fetz and Cheney 1980; Hocken-smith et al. 2005; Shinoda et al. 1981). However, the precise organization of these descending inputs to motor neurons supplying specified hand muscles, and in particular to multitendoned muscles that serve as the main finger flexor and extensor, is not fully understood.

In humans there are three multitendon extrinsic finger muscles, two flexors [flexor digitorum superficialis (FDS); flexor digitorum profundus (FDP)], and one extensor [extensor digitorum (ED)], located in the forearm, that give rise to four parallel tendons that cross multiple joints and insert onto the four fingers. These muscles, and homologous muscles in nonhuman primates, appear to be composed of relatively distinct compartments (Keen and Fuglevand 2003, 2004a; Kilbreath and Gandevia 1994; Schieber 1991), each of which operates on a separate digit. Recent studies of ED (Keen and Fuglevand 2004b) and FDP (Reilly et al. 2004; Winges and Santello 2004) indicate that the subsets of motor neurons that innervate different muscular compartments within these multitendoned muscles do not receive entirely segregated synaptic inputs. Instead, last-order inputs that are primarily destined to supply motor neurons innervating one compartment also appear to ramify to contact motor neurons innervating other compartments. Such divergence of synaptic input may limit the ability to differentially activate separate muscular compartments in these multitendoned muscles and thereby contribute to the lack of fully independent actions of the fingers (Aoki et al. 2003; Häger-Ross and Schieber 2000; Kilbreath and Gandevia 1994; Reilly and Hammond 2000; Schieber 1991; Zatsiorsky et al. 2000).

Comparative information about the extent of such divergence for the different multitendoned muscles of the hand would be beneficial for understanding the facility with which each muscle potentially contributes to fractionated movements of the digits. Work done in nonhuman primates indicates a greater degree of divergence in corticospinal projections across motor nuclei supplying extensor muscles compared with flexor muscles of the hand (Fetz and Cheney 1980), implying less independence for extensor muscles. For the two extrinsic flexor muscles, there appears to be an enhanced capacity in humans to selectively activate compartments of the FDS compared with FDP (Butler et al. 2005; Kilbreath and Gandevia 1994). On this basis then, we hypothesized that the breadth of divergence of last-order synaptic inputs would be greatest for ED motor neurons and least for FDS. To address this hypothesis, we estimated the extent of divergence of last-order inputs to FDS motor neurons by measuring the degree of short-term synchrony between motor units residing in different compartments of FDS. These data were then compared, using the same metric, to those previously reported for ED (Keen and Fuglevand 2004b) and FDP (Winges and Santello 2004).

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METH O D S

Subjects and test muscle

Forty-two experiments were performed on the right FDS muscle in 28 healthy human volunteers (20 women, eight men, ages 19–54 yr). Five subjects participated in three experimental sessions, five other subjects participated in two sessions, and the remaining subjects participated in one session. Based on the Edinburgh Handedness Inventory (Oldfield 1971), 26 of the subjects were right-hand dominant (laterality quotient range 0.47–1.0), of which 18 were strongly right-hand dominant (laterality quotient ≥0.75), one subject had no hand preference (laterality quotient = 0.0), and one subject was left-hand dominant (laterality quotient = −0.67). Procedures were approved by the Institutional Human Investigation Committee at the University of Arizona. All subjects gave informed consent as required by the Helsinki Declaration.

The FDS originates from the humerus and proximal ulna and typically gives rise to four tendons that insert on the middle phalanges of the index (digit 2, D2), middle (D3), ring (D4), and little (D5) fingers. One of the main functions of FDS is thus to flex the proximal interphalangeal (IP) joint without concurrent flexion of the distal IP joint, which is controlled by FDP. There are a number of anatomical anomalies noted for FDS, especially related to the tendon to the little finger, including absence of the tendon (Furnas 1965; Gonzalez et al. 1997; Kaplan 1969). An absent FDS tendon to the little finger precludes the ability to isolate volitional flexion to the proximal IP joint, leaving flexion to occur through the action of the FDP. There is a number of anatomical anomalies noted for FDS, especially related to the tendon to the little finger, including absence of the tendon (Furnas 1965; Gonzalez et al. 1997; Kaplan 1969). An absent FDS tendon to the little finger precludes the ability to isolate volitional flexion to the proximal IP joint, leaving flexion to occur through the action of the FDP. There is a number of anatomical anomalies noted for FDS, especially related to the tendon to the little finger, including absence of the tendon (Furnas 1965; Gonzalez et al. 1997; Kaplan 1969).

Experimental setup

Subjects were comfortably seated in a dental chair with the right arm supported on a horizontal platform and the proximal forearm and elbow stabilized in a padded trough. The hand was held in a vertical orientation, midway between full supination and pronation, by padded vertical posts placed in contact with the dorsal and palmar aspects of the hand. An additional narrow vertical post was placed just distal to the metacarpophalangeal (MCP) joints to contact the volar surface of the proximal phalanges of digits 2–5 and served to hold the MCP joints in a neutral orientation. The proximal IP joints of each finger were maintained in slightly flexed configurations (about 30° flexed from full extension) by narrow leather bands around the middle phalanges of each digit that were attached to separate force transducers.

A
Little
Ring
Middle
Index

B

C

D

2 s

2 s

2 s

2 s

2 s

FIG. 1. Example isometric force responses recorded simultaneously from the middle phalanges of the index, middle, ring, and little fingers in response to intramuscular electrical stimulation verifying placement of the microelectrode in the (A) index, (B) middle, (C) ring, and (D) little finger compartments of flexor digitorum superficialis (FDS).

Force and electromyographic recording

Flexion forces of the digits were measured by four force transducers (model FT-10, range 0–5 N, sensitivity 780 mN/mV; Grass Instruments, Warwick, RI) mounted in a custom-built manipulandum. Each transducer was aligned with the direction of pull orthogonal to the long axis of the middle phalanges of each digit. Force signals were amplified (×1,000) (World Precision Instruments, Sarasota, FL) and displayed on an oscilloscope.

Single-unit electromyographic (EMG) activity was recorded with sterilized, lacquer-coated tungsten microelectrodes inserted percutaneously into the FDS muscle (1- to 5-μm-tip diameter, 5- to 10-μm uninsulated length, 250-μm shaft diameter, about 200-kΩ impedance at 1,000 Hz after insertion; FHC, Bowdoinham, ME). Surface electrodes (4 mm diameter Ag–AgCl) attached to the skin overlying the radial styloid served as reference electrodes for each intramuscular electrode. Two microelectrodes were inserted into FDS at different locations to record the activity of separate motor units on each electrode. In some trials, the two electrodes were placed into the same compartment, and in other trials the electrodes were placed in separate compartments. Weak electrical stimulation (1.0-ms pulses, 1 Hz, 0.2–6.0 mA) was used initially and between each trial to identify, based on the evoked force responses, the compartment location of each electrode and to verify microelectrode placement in FDS (Hockensmith et al. 2005; Keen and Fuglevand 2004b). Each microelectrode was adjusted in depth and angle until an individuated response of the proximal IP joint of the target digit was elicited on stimulation. Figure 1 depicts example force responses in each of the four fingers to such electrical stimulation in the index (Fig. 1A), middle (Fig. 1B), ring (Fig. 1C), and little (Fig. 1D) finger compartments of FDS.

In an attempt to minimize inadvertent reanalysis of the same motor-unit pairs recorded on separate trials, pairs of surface electrodes were applied to the skin overlying each muscle compartment within which the microelectrodes were placed. The EMG signals detected with these surface electrodes were subsequently spike-triggered averaged in off-line analysis (see following text) to extract the surface EMG signature associated with discharge of recorded motor units (Johns and Fuglevand 2005; Lemon et al. 1990). The intramuscular and surface EMG signals were amplified (×2,000), band-pass filtered (100–3,000 and 10–1,000 Hz, respectively; Grass Instruments), and displayed on oscilloscopes. Intramuscular EMG signals were also routed to a two-channel audio amplifier.

Protocol

Subjects were instructed to perform low-force isometric flexion of all four digits primarily at the proximal IP joint to activate the FDS muscle. The microelectrodes were gently manipulated during the contraction until action potentials of motor units could be clearly identified on each electrode. Subjects were then instructed to sustain
weak isometric flexion of all four fingers such that both units remained active. This instruction was the same regardless of the compartment locations of the microelectrodes. During the contractions, the forces exerted by individual fingers were not specified; rather, subjects were instructed to maintain a low rate of discharge of the two motor units while maintaining some degree of flexion force on each finger. Intramuscular EMG signals were recorded for 5 min or until the action potentials could no longer be clearly discriminated. Subjects received visual and audio feedback of the motor-unit discharges and 1–2 min of rest between trials. After each trial at least one of the two microelectrodes was adjusted until a presumed different motor unit was identified. Occasionally this required removal and reinsertion of the microelectrode into a new site, after which placement was verified with electrical stimulation as described above. Successive trials were performed for up to 2 h. Flexion force of each finger, surface EMG, and intramuscular EMG signals were digitally sampled at about 2.0, 2.5, and 12.5 kHz, respectively, using the Spike2 data-acquisition and data-analysis system (Cambridge Electronics Design (CED), Cambridge, UK).

Data analysis

The extent of common, last-order synaptic input was estimated from the level of short-term synchrony in the discharge times of simultaneously recorded pairs of motor units (Kirkwood and Sears 1978; Sears and Stagg 1976). Accordingly, in off-line analysis, simultaneously recorded pairs of motor units (Kirkwood and Sears 1978; Sears and Stagg 1976). In all, 393 FDS motor units were recorded during 164 trials involving flexion of all four digits and were used to generate 234 cross-correlation histograms. In 59 trials, more than one motor unit was discriminated on an electrode, yielding multiple correlations. On average, data for about six cross-correlations were obtained per experiment (±2.9, range 1–17). Sampling of motor-unit pairs involved only one to four compartment combinations out of a possible 10 combinations for an individual subject. This was done primarily for the sake of expediency and to minimize the discomfort associated with multiple electrode penetrations needed to sample multiple compartment combinations in a single subject. Weak isometric contractions were performed in all trials with an average force per finger across all trials of 0.56 ± 0.49 N (range 0.0–2.4 N), and thus the entire sample of motor units in this study is presumably composed of low-threshold weak motor-unit types only. Based on our functional test, FDS tendons to digit 5 (D5) were found in only 12 of 28 (43%) subjects tested. Therefore the total number of trials involving recordings from the D5 compartment was less than that for the other compartments of FDS. The mean firing rate for all recorded motor units was 10.2 ± 1.6 Hz and the mean coefficient of variation (CV) in the interspike intervals was 0.15 ± 0.03. The average number of events used to generate the cross-correlograms was 2,270 ± 737. Of the 234 cross-correlograms generated, 115 had significant synchrony peaks using the criteria described in METHODS. The average peak duration assessed from the cusum of these cross-correlograms with significant peaks was 8.9 ± 3.0 ms. The average CIS for all pairs of FDS motor units, including those with nonsignificant peaks, was 0.32 ± 0.26, whereas the mean CIS for just those pairs with significant peaks was 0.51 ± 0.23.

Figure 2A shows four examples of intracompartmental cross-correlograms for each compartment of FDS and their respective CIS values. The labels at the top indicate the compartments within which the microelectrodes were located.

RESULTS

In all, 393 FDS motor units were recorded during 164 trials involving flexion of all four digits and were used to generate 234 cross-correlation histograms. In 59 trials, more than one motor unit was discriminated on an electrode, yielding multiple correlations. On average, data for about six cross-correlations were obtained per experiment (±2.9, range 1–17). Sampling of motor-unit pairs involved only one to four compartment combinations out of a possible 10 combinations for an individual subject. This was done primarily for the sake of expediency and to minimize the discomfort associated with multiple electrode penetrations needed to sample multiple compartment combinations in a single subject. Weak isometric contractions were performed in all trials with an average force per finger across all trials of 0.56 ± 0.49 N (range 0.0–2.4 N), and thus the entire sample of motor units in this study is presumably composed of low-threshold weak motor-unit types only. Based on our functional test, FDS tendons to digit 5 (D5) were found in only 12 of 28 (43%) subjects tested. Therefore the total number of trials involving recordings from the D5 compartment was less than that for the other compartments of FDS. The mean firing rate for all recorded motor units was 10.2 ± 1.6 Hz and the mean coefficient of variation (CV) in the interspike intervals was 0.15 ± 0.03. The average number of events used to generate the cross-correlograms was 2,270 ± 737. Of the 234 cross-correlograms generated, 115 had significant synchrony peaks using the criteria described in METHODS. The average peak duration assessed from the cusum of these cross-correlograms with significant peaks was 8.9 ± 3.0 ms. The average CIS for all pairs of FDS motor units, including those with nonsignificant peaks, was 0.32 ± 0.26, whereas the mean CIS for just those pairs with significant peaks was 0.51 ± 0.23.

Figure 2A shows four examples of intracompartmental cross-correlograms for each compartment of FDS and their respective CIS values. The labels at the top indicate the compartments within which the microelectrodes were located.
FIG. 2. Common input strength (CIS) values for intracompartamental pairs of motor units in FDS. A: example cross-correlograms for motor-unit pairs residing in the Index (D2–D2), Middle (D3–D3), Ring (D4–D4), and Little (D5–D5) finger compartments of FDS. Trace above each correlogram is the cusum used to delineate the correlogram peak (dotted lines). B: median ± SD CIS values for all intracompartamental unit pairs as in A. *Significantly different (*P < 0.05) from all other intracompartamental pairs.

The mean (SD) intracompartamental CIS values for each compartment are shown in Fig. 2B. A total of 94 motor-unit pairs were recorded from within the same compartment. These had substantial mean CIS values of 0.43 ± 0.40 (n = 28), 0.34 ± 0.19 (n = 28), 0.45 ± 0.24 (n = 28), and 0.75 ± 0.23 (n = 10) for D2–D5 compartments, respectively (Table 1). A Kruskal–Wallis test revealed a significant difference (P = 0.004) between compartments in CIS values for intracompartamental pairs. Post hoc analysis using the Dunn’s method identified this difference to include only comparisons involving the D5 compartment (between D2 and D5 and between D3 and D5). No other intracompartamental comparisons of CIS were significantly different from one another. Furthermore, there were no significant differences in durations of the cross-correlogram peaks, firing rates, or CVs across the four intracompartamental combinations (Table 1).

In all, 140 extracompartamental motor-unit pairs were recorded from FDS. As a group, these extracompartamental pairs exhibited significantly (P < 0.001) less synchrony (CIS = 0.23 ± 0.19) than did intracompartamental pairs (CIS = 0.45 ± 0.30). Inexplicably, motor-unit firing rates were significantly lower (P < 0.001) and discharge variability was significantly greater (P = 0.01) for trials involving extracompartamental pairs (firing rate = 9.8 ± 1.6 Hz; CV = 0.15 ± 0.03) compared with those involving intracompartamental pairs (firing rate = 10.7 ± 1.6 Hz, CV = 0.14 ± 0.03). CIS was previously shown to be relatively unaffected by differences in discharge rate but to be modestly and positively correlated with discharge variability (Nordstrom et al. 1992). Despite the slightly higher discharge variability for trials involving extracompartamental pairs, the associated CIS values were still appreciably lower than those obtained during trials involving intracompartamental pairs.

Extracompartamental pairs were further categorized according to the respective locations of each recorded motor unit in the pair and the degree of separation between compartments. The adjacent group included the motor-unit pairs of D2–D3 (CIS = 0.26 ± 0.81, n = 35), D3–D4 (CIS = 0.27 ± 0.17, n = 39), and D4–D5 (CIS = 0.26 ± 0.18, n = 10) (Table 1). The two-apart group included the motor-unit pairs of D2–D4 (CIS = 0.16 ± 0.15, n = 31) and D3–D5 (CIS = 0.36 ± 0.28, n = 13). The three-apart group included the motor-unit pairs of D2–D5 (CIS = 0.10 ± 0.13, n = 12). Figure 3A shows four examples of cross-correlograms, one for an intracompartmen-

![Diagram](http://jn.physiology.org/)

TABLE 1. **Synchrony and discharge properties for pairs of FDS motor units residing in various compartment combinations**

<table>
<thead>
<tr>
<th>Compartment Location</th>
<th>Number of Subjects*</th>
<th>Number of Pairs</th>
<th>Percentage Significant Peaks</th>
<th>CIS</th>
<th>k’</th>
<th>Peak Duration, † ms</th>
<th>Firing Rate, Hz</th>
<th>CV ISI‡</th>
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</thead>
<tbody>
<tr>
<td>Same</td>
<td></td>
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<td></td>
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<tr>
<td>D2–D2</td>
<td>8</td>
<td>28</td>
<td>50</td>
<td>0.43 ± 0.40</td>
<td>1.54 ± 0.35</td>
<td>10.3 ± 4.2</td>
<td>10.7 ± 2.0</td>
<td>0.14 ± 0.03</td>
</tr>
<tr>
<td>D3–D3</td>
<td>4</td>
<td>28</td>
<td>61</td>
<td>0.34 ± 0.19</td>
<td>1.53 ± 0.37</td>
<td>7.9 ± 2.5</td>
<td>10.8 ± 1.3</td>
<td>0.14 ± 0.02</td>
</tr>
<tr>
<td>D4–D4</td>
<td>7</td>
<td>28</td>
<td>82</td>
<td>0.45 ± 0.24</td>
<td>1.65 ± 0.26</td>
<td>7.6 ± 2.7</td>
<td>10.4 ± 1.2</td>
<td>0.15 ± 0.04</td>
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<tr>
<td>D5–D5</td>
<td>3</td>
<td>10</td>
<td>90</td>
<td>0.75 ± 0.23</td>
<td>1.79 ± 0.17</td>
<td>9.8 ± 2.7</td>
<td>11.1 ± 1.9</td>
<td>0.16 ± 0.02</td>
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<tr>
<td>1 apart</td>
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<tr>
<td>D2–D3</td>
<td>7</td>
<td>35</td>
<td>51</td>
<td>0.26 ± 0.18</td>
<td>1.53 ± 0.34</td>
<td>9.4 ± 0.26</td>
<td>9.6 ± 1.5</td>
<td>0.15 ± 0.03</td>
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<tr>
<td>D3–D4</td>
<td>7</td>
<td>39</td>
<td>51</td>
<td>0.27 ± 0.16</td>
<td>1.50 ± 0.26</td>
<td>9.1 ± 0.28</td>
<td>9.4 ± 0.20</td>
<td>0.14 ± 0.02</td>
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<tr>
<td>D4–D5</td>
<td>2</td>
<td>10</td>
<td>30</td>
<td>0.26 ± 0.18</td>
<td>1.40 ± 0.23</td>
<td>8.2 ± 0.9</td>
<td>10.2 ± 1.5</td>
<td>0.15 ± 0.03</td>
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<tr>
<td>2 apart</td>
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<td>D2–D4</td>
<td>8</td>
<td>31</td>
<td>13</td>
<td>0.16 ± 0.15</td>
<td>1.32 ± 0.20</td>
<td>9.7 ± 0.20</td>
<td>9.8 ± 1.4</td>
<td>0.15 ± 0.03</td>
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<tr>
<td>D3–D5</td>
<td>3</td>
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<td>46</td>
<td>0.36 ± 0.28</td>
<td>1.52 ± 0.17</td>
<td>10.0 ± 0.7</td>
<td>11.0 ± 1.2</td>
<td>0.18 ± 0.04</td>
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<td>3 apart</td>
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<tr>
<td>D2–D5</td>
<td>2</td>
<td>12</td>
<td>8</td>
<td>0.10 ± 0.13</td>
<td>1.27 ± 0.35</td>
<td>8.3</td>
<td>10.4 ± 1.0</td>
<td>0.18 ± 0.04</td>
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Values are means ± SD. *Number of subjects contributing data to particular compartment combination. Many subjects (20 of 28) contributed data to more than one compartment combination. †Duration of cross-correlogram peak measured only for those histograms exhibiting a significant peak. ‡Coefficient of variation in interspike intervals.
Figure 3. CIS values for all intracompartmental and extracompartmental unit pairs of different degrees of separation in FDS. A: example cross-correlograms for motor-unit pairs residing in the same compartment (D2–D2), adjacent compartments (D3–D4), 2 compartments apart (D2–D4), and 3 compartments apart (D2–D5). B: mean ± SD CIS values for combinations of unit pairs as in A. *Significantly different (P < 0.05) from intracompartment pairs. Significantly different (P < 0.05) from adjacent-compartment pairs.

There were no significant differences in the durations of the cross-correlogram peaks associated with different degrees of separation between pairs of units. This comparison, however, included only intracompartmental pairs (mean duration 8.6 ± 3.2 ms), pairs in adjacent compartments (9.1 ± 2.6 ms), and pairs two compartments apart (10.0 ± 2.7 ms). For the three-compartment–apart condition, only one pair of units exhibited a significant peak in the cross-correlogram from which a reliable measure of peak duration could be made (8.3 ms). In terms of firing rate, trials involving intracompartmental pairs exhibited slightly but significantly (P < 0.05) higher rates (10.7 ± 1.6 Hz) than trials involving pairs in adjacent compartments (9.5 ± 1.7 Hz). The firing rates for trials involving pairs of units two compartments apart (10.2 ± 1.5 Hz) and three compartments apart (10.4 ± 1.0 Hz) were not significantly different from one another or from trials involving intra- or adjacent-compartment pairs of units. Interestingly, there was a tendency toward greater discharge variability in trials involving greater separation between motor-unit pairs. For example, the CV in interspike intervals was significantly greater for trials involving units three compartments apart (0.18 ± 0.04) compared with intracompartmental (0.15 ± 0.03) and adjacent-compartment (0.15 ± 0.03) trials. Likewise, trials involving units two compartments apart had significantly higher values of CV (0.16 ± 0.04) than trials involving intracompartmental pairs.

Figure 4 depicts the mean CIS values obtained for various extracompartment combinations of motor-unit pairs for the three extrinsic multitendoned finger muscles: FDP (Winges and Santello 2004), FDS (present study), and ED (Keen and Fuglevand 2004b). Insufficient or no data were available from ED for combinations of motor-unit pairs two and three compartments apart and therefore ED is not depicted for those combinations in Fig. 4. From Fig. 4, it can be seen that the average level of synchrony is greater in FDP (black bars) than in FDS (hatched bars) for all extracompartmental combinations of motor-unit pairs. For adjacent-compartment pairs (i.e., those “one apart”), the average level of synchrony tends to be higher in ED (open bars) than in the flexors for combinations involving ulnar compartments (D3–D4 and D4–D5), whereas ED synchrony appears to be somewhat less than that in the flexors for the most radially situated compartment combination (D2—D5).
The functional implications of these apparent differences in synchrony across muscles are highlighted in the following discussion.

DISCUSSION

The present study demonstrates that the degree of synchrony for motor units in the FDS follows a general pattern such that the greatest synchrony occurs for pairs of units within compartments and less synchrony is seen for pairs of units residing in separate compartments. Therefore like other multitendoned muscles of the hand, last-order projections to FDS motor neurons do not appear to be uniformly distributed across the entire FDS motor nucleus, but instead tend to be segregated to supply subsets of motor neurons innervating different compartments. This presumably enables differential activation of motor neurons supplying specific compartments of FDS to facilitate movements of individual fingers. Nevertheless, significant extracompartamental synchrony was also observed, which is indicative of some across-compartment divergence of synaptic input that may contribute to the inadvertent movement of adjacent fingers during intended movement of only one finger (Butler et al. 2005; Häger-Ross and Schieber 2000; Kilbreath and Gandevia 1994; Zatsiorsky et al. 2000).

Anatomical complexity of the FDS muscle

The FDS anatomy is unique when compared with the other multitendoned muscles of the hand, having a more complex arrangement of the digital compartments and greater variation and anomalies across subjects (Brand and Hollister 1999; Ohtani 1979; Wood Jones 1941). For instance, the deep layer of the muscle typically consists of a single proximal belly that gives rise distally to an intermediate tendon from which two muscle bellies emerge, one of which gives rise to the tendon inserting on the index finger and the other gives rise to the tendon inserting on the little finger. In the present experiments, we sampled primarily from the distal, single-digit compartments. Future work is needed to evaluate the organization of the intriguing proximal belly and how its activity is coordinated with that of its two daughter bellies.

In addition to the complex arrangement of the muscle-belly components, there is a surprisingly high proportion of anomalies associated with the FDS tendon to the little finger. Indeed, only 43% of our sample population had a functional FDS tendon to the little finger of the right hand. This is in agreement with the percentage (42%) reported by Stein and colleagues (1990) using more extensive clinical tests of FDS. It remains for future investigations to determine whether the absence of an FDS tendon to the little finger leads to detectable functional impairment in certain types of manipulative tasks. From a practical standpoint, this relatively low incidence of digit 5 tendons limited the number of trials we were able to record involving motor units in the little-finger compartment of FDS.

Functional consequences of extracompartement synchrony

When human subjects attempt to voluntarily flex an individual finger, significant motor unit activity is detected in compartments other than that associated with the targeted compartment in multitendoned flexor muscles (Butler et al. 2005; Kilbreath and Gandevia 1994). This inadvertent activity is particularly prominent in FDP compared with FDS (Butler et al. 2005; Kilbreath and Gandevia 1994). On this basis, Butler and colleagues (2005) suggested that descending pathways destined for the FDS motor nucleus might be more selective for subsets of motor neurons supplying individual compartments of FDS than the pathways that target the FDP motor nucleus. Consonant with this idea, we have shown here that the degree of extracompartement synchrony was less for FDS than that for FDP (Winges and Santello 2004) for every extracompartement combination of motor-unit pairs tested (Fig. 4). Because such extracompartement synchrony can be considered to reflect the extent of neural coupling across motor units acting on different digits, these results imply that FDS has the potential to exert more selective control over individual digits than FDP.

From a functional perspective, it would seem reasonable to suspect that multitendoned flexor muscles might possess a greater capacity for selective control over the digits compared with the multitendoned extensor muscle. One manifestation of such an enhanced capacity for digit individuation should be a lower degree of extracompartement synchrony for multitendoned flexors compared with the extensor. Although this seems to be the case for compartments inserting on digits 3 and 4, and on digits 4 and 5 (Fig. 4), the extensor muscle (ED) appears to exhibit less neural coupling (i.e., extracompartement synchrony) between digits 2 and 3 compared with either of the flexors (Fig. 4).

Interestingly, there is some evidence to indicate a parallel between those patterns of extracompartement synchrony and the relative independence of finger movements for flexion and extension (Robinson and Fuglevand 1999). In that study, subjects were instructed to attempt to flex or extend just one finger while movements of the instructed finger and noninstructed fingers were recorded (Robinson and Fuglevand 1999). The movement that exhibited the greatest independence was index-finger extension, whereas the least independent movement was ring-finger extension. Likewise, the lowest level of adjacent-compartment (i.e., “one apart”) synchrony depicted in Fig. 4 is associated with the index-finger compartment of the extensor, ED, whereas the greatest extracompartement synchrony also involves the ED but when associated with the ring finger. Although the high degree of independence associated with index-finger extension could certainly arise from selective activation of the extensor indicis muscle, the behavioral results are nevertheless intriguingly consistent with the predicted patterns of finger independence based on the extent of extracompartement synchrony for different multitendoned muscles.

Finally, the pattern of extracompartement synchrony we found for FDS in which synchrony tended to be greatest for unit pairs in adjacent compartments and to decrease with increasing physical separation between units (Fig. 3) was consistent with previous observations in the ED and FDP (Bremner et al. 1991; Keen and Fuglevand 2004; Reilly et al. 2004; however, see Winges and Santello 2004). Likewise, Kilbreath and Gandevia (1994) and Butler et al. (2005) showed similar patterns of coactivation across compartments in multitendoned flexor muscles when subjects attempted to exert force with a single digit. Furthermore, behavioral studies also showed that the greatest degree of unintended force development (Reilly and Hammond 2000; Zatsiorsky et al. 2000) or digit movement (Aoki et al. 2003; Hager-Ross and Schieber 2000; Schieber 1991) occurs in the digits immediately adjacent...
to the digit subjects attempt to move in isolation. Although such inadvertent movements of neighboring digits during finger-individuation tasks might partly be related to biomechanical coupling between adjacent digits (e.g., Lang and Schieber 2004), it seems likely that divergence of descending inputs, particularly across submotor nuclei supplying neighboring muscle compartments, may also limit the ability to move the digits independently (Keen and Fuglevand 2004b; Kilbreath and Gandevia 1994).

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