Incomplete Functional Subdivision of the Human Multitendoned Finger Muscle Flexor Digitorum Profundus: An Electromyographic Study

Karen T. Reilly and Marc H. Schieber
Department of Neurobiology and Anatomy and Department of Neurology, University of Rochester School of Medicine and Dentistry, Rochester, New York 14642

Submitted 24 March 2003; accepted in final form 17 June 2003

INTRODUCTION

Mammalian skeletal muscles vary widely in their architectural and functional complexity. At one end of the spectrum are anatomically simple muscles that act as one pool of motor units (MUs) all contributing to a single mechanical action. At the opposite end of the spectrum are muscles that are clearly divided into multiple anatomical compartments. In such muscles a separate nerve branch innervates each compartment, which frequently reflects an ability to independently recruit different compartments, allowing the muscle to produce a variety of mechanical actions on the skeleton (Balice-Gordon and Thompson 1988; Chanaud et al. 1991a,b; English and Letbetter 1982; English and Weeks 1984; Schieber et al. 2001; Segal et al. 1991; Serlin and Schieber 1993). In the middle of the spectrum are muscles with varying degrees of anatomical heterogeneity, without complete subdivision into structurally distinct, separately innervated compartments. Functionally, these heterogeneous muscles have varying degrees of regional specialization, enabling them to produce a variety of mechanical actions by differential recruitment of MUs in separate regions (Chanaud et al. 1991b; Herrmann and Flanders 1998).

The multitendoned extrinsic muscles that control the human fingers, such as the 4-tendoned human flexor digitorum profundus (FDP), commonly are assumed to achieve independent mechanical actions at each of the fingers by selective activation of a separate compartment within the muscle serving each finger. Indeed, magnetic resonance (MR) imaging has shown that the activated region of the human FDP varies depending on which finger is flexed (Fleckenstein et al. 1992; Jeneson et al. 1990). Neurophysiologically, MUs in the human FDP have been found to be recruited at low forces during flexion of one of the 4 fingers and to exert force selectively on that digit (Kilbreath and Gandevia 1994; Kilbreath et al. 2002). These studies support the notion that the human FDP consists of 4 compartments, each activated selectively during flexion of only one digit.

Four considerations suggest, however, that the human FDP might not be so completely compartmentalized. First, close examination of published MR images (Fig. 3 of Fleckenstein et al. 1992) reveals that the proximal region of FDP activated during exercise of the ring finger overlaps considerably with regions activated during exercise of either the middle finger or little finger. Second, MUs recruited at low force during flexion of a particular finger are recruited again during flexion of adjacent fingers at only slightly higher forces (Kilbreath and Gandevia 1994). Third, studies of MU physiology have excluded data from recording sites where MUs were active during movement of more than one finger, potentially confining the data to highly selective regions of the muscle (Kilbreath and Gandevia 1994; Kilbreath et al. 2002). Fourth, and finally, recent anatomical studies suggest that although the human FDP has some features of a subdivided muscle, it does not contain 4 distinct anatomical compartments (Bhadra et al. 1999; Segal et al. 2002). Taken together, these considerations raise the question of whether the functional organization of the human FDP is subdivided.


The human flexor digitorum profundus (FDP) sends tendons to all 4 fingers. One might assume that this multitendoned muscle consists of 4 discrete neuromuscular compartments each acting on a different finger, but recent anatomical and physiological studies raise the possibility that the human FDP is incompletely subdivided. To investigate the functional organization of the human FDP, we recorded electromyographic (EMG) activity by bipolar fine-wire electrodes simultaneously from 2 or 4 separate intramuscular sites as normal human subjects performed isometric, individuated flexion, and extension of each left-hand digit. Some recordings showed EMG activity during flexion of only one of the 4 fingers, indicating that the human FDP has highly selective core regions that act on single fingers. The majority of recordings, however, showed a large amount of EMG activity during flexion of one finger and lower levels of EMG activity during flexion of an adjacent finger. This lesser EMG activity during flexion of adjacent fingers was unlikely to have resulted from recording motor units in neighboring neuromuscular compartments, and instead suggests incomplete functional subdivision of the human FDP. In addition to the greatest agonist EMG activity during flexion of a given finger, most recordings also showed EMG activity during extension of adjacent fingers, apparently serving to stabilize the given finger against unwanted extension. Paradoxically, the functional organization of the human FDP—with both incomplete functional subdivision and highly selective core regions—may contribute simultaneously to the inability of humans to produce completely independent finger movements, and to the greater ability of humans (compared with macaques) to individuate finger movements.

Address for reprint requests and other correspondence: M. H. Schieber, University of Rochester Medical Center, 601 Elmwood Ave, Box 673, Rochester, NY 14642 (E-mail: mhs@cvs.rochester.edu).

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.
possibility that FDP might not be organized into 4 completely separate functional subdivisions.

To examine further the functional organization of the human FDP, we therefore recorded electromyographic (EMG) activity by bipolar fine-wire intramuscular electrodes inserted at various positions throughout the radioulnar extent of the muscle belly. EMG activity was recorded as normal subjects produced isometric flexion and extension forces of each of the 4 fingers and of the thumb. These recordings confirm the presence of 4 core regions, one selectively active during flexion of each finger, while also revealing regions in which EMG activity, unlikely to have resulted from MUs in adjacent compartments, was recorded while either of 2 adjacent fingers produced flexion forces. Part of this material was presented previously in abstract form (Reilly and Schieber 2001).

METHODS

Subjects

Four right-handed subjects (3 female and 1 male; mean age, 37.5 yr; range, 26–49 yr) each participated in 3 separate recording sessions after giving written informed consent according to the Declaration of Helsinki. The Research Subjects Review Board of the University of Rochester Medical Center approved the study protocol. None of the participants had any history of trauma or degenerative or neurological disease affecting the upper limbs.

Electromyographic recordings

We recorded intramuscular EMG activity from 2 or 4 bipolar fine-wire electrodes placed in the left FDP while participants performed isometric individuated flexion and extension of each left-hand digit. The intramuscular electrodes were made of 2 Teflon-insulated stainless steel wires (100 µm diameter). The wires were threaded through the lumen of a 25-gauge disposable needle (3.8 cm length), twisted, and heated to fuse the Teflon coating of the 2 wire strands. Only the cut ends of the wire were exposed and the distance between the centers of the tips was about 100 µm. An almost 5-mm section of the wire tips was bent back over the bevel of the needle to make a small hook, after which the electrode and needle were sterilized.

We extensively sampled the left FDP of 4 individuals. Each electrode was inserted percutaneously from the medial aspect of the forearm at a proximodistal level between 20 and 60% of the distance from the olecranon process to the wrist crease. The proximo-distal electrodes were inserted at different staggered positions along the forearm horizontally on a table with their elbow flexed to approximately 130° relative to their humerus, the forearm in neutral pronation/supination, and the wrist extended approximately 45°. A vacuum cast stabilized the forearm and elbow. The distal phalanges of the 5 digits were secured into 5 small plastic rings with a thumbscrew over the fingernail. The rings were arranged such that the shape of the hand was similar to that used to grasp a medium-sized spherical object (see Fig. 2). Each ring was mounted on a stationary rod by a load cell (Omega LCL-010) that transduced flexion/extension forces. Forces were amplified with a strain gauge amplifier (Omega DMD–465 WB) and sampled at 0.5 kHz per channel.

Once the participant’s hand was arranged comfortably in the apparatus, resting forces in each fingertip were measured for 1 min as the participant sat quietly. A baseline force window for each digit then was set as the mean resting force in that digit ±0.6 N. A criterion force level was set 1 N beyond the limits of the baseline force window in either the flexion or extension direction.

The participant viewed a display on which each digit was represented by a row of 5 light-emitting diodes (LEDs). The middle (yellow) LED in a row was illuminated when the force exerted by the digit was less than the criterion force for flexion or extension. One of 2 green LEDs on either side of the middle LED was lit whenever the force exerted by the digit exceeded the criterion flexion (rightward green LED) or extension (leftward green LED) force. Red LEDs at either end of the row were illuminated one at a time, under computer control, instructing the participant with which digit to produce a criterion flexion (rightward red LED) or extension (leftward red LED) force.

The participant initiated a trial by maintaining the force exerted by each digit within its baseline force window for 500 ms. After a randomly varied initial hold period of 1,000 to 1,500 ms, during which the participant maintained each finger within its baseline force win-
TABLE 1. Means (and SDs) of force in instructed and noninstructed fingers (N)

<table>
<thead>
<tr>
<th>Noninstructed Finger</th>
<th>Instructed Finger</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Flexions</td>
</tr>
<tr>
<td>Thumb</td>
<td>Index</td>
</tr>
<tr>
<td>Thumb</td>
<td>2.12 (0.16)</td>
</tr>
<tr>
<td>Index</td>
<td>0.19 (0.12)</td>
</tr>
<tr>
<td>Middle</td>
<td>0.16 (0.09)</td>
</tr>
<tr>
<td>Ring</td>
<td>0.19 (0.20)</td>
</tr>
<tr>
<td>Little</td>
<td>0.24 (0.18)</td>
</tr>
</tbody>
</table>

Bold numbers represent force produced by instructed digit.
control or test period) on any correct trial. Normalized δEMG values then were averaged across all correctly performed trials of the same instructed finger force to produce a mean normalized change in EMG activity (δEMG) for each of the 10 instructed finger forces.

Using the δEMG values associated with each of the 4 instructed flexion forces (2f, 3f, 4f, 5f) we calculated a selectivity index (SEL) to quantify the degree to which EMG activity in each recording was associated with one instructed flexion force versus all 4 instructed flexion forces. We also calculated the center of activity (COA) of the EMG activity recorded by each electrode across the 4 instructed flexion forces. Both indices were adapted from those described by Schieber et al. (2001), using the δEMG values associated with each of the 4 instructed flexion forces (2f, 3f, 4f, 5f) in place of the tension values used previously. (The output index described previously is equivalent to the present center of activity index.) To calculate these indices, the amount of EMG activity recorded during each of the 4 instructed finger flexion forces was normalized as a fraction of the sum of the δEMG values from all 4 flexion forces

\[ \tau_i = \frac{\delta EMG_i}{\sum_{i=1}^{4} \delta EMG_i} \]

where \( \delta EMG_i \) is the δEMG during the \( i \)th instructed finger flexion force, \( n \) is the number of instructed finger flexion forces (here \( n = 4 \)), and \( \tau_i \) is the fractional EMG change during the \( i \)th instructed finger flexion force. The COA then is calculated as

\[ COA = \frac{\sum_{i=1}^{n} \tau_i w_i}{\sum_{i=1}^{n} w_i} \]

where \( \tau_i \) is the fractional EMG change during the \( i \)th instructed finger flexion force, \( n \) is the number of instructed finger flexion forces, and \( w_i \) is a constant that provides a rank-ordered weighting of the instructed finger flexion forces

\[ w_i = \frac{(2i-n-1)(n-1)}{n(n-1)} \]

The fractional EMG activity of a completely unselective recording would be \( \tau_i = 1/n \), whereas the fractional EMG activity of an ideally selective recording that was active only during the instructed flexion of a single digit would be \( \tau_1 = 1, \tau_2 = 0, \cdots, \tau_4 = 0 \). In an \( n \)-dimensional fractional EMG space, the linear distance between these 2 points would be

\[ d_{max} = \sqrt{(1 - \tau_1)^2 + \sum_{i=2}^{4} (0 - \tau_i)^2} \]

and the linear distance \( d \) between the point representing any other recording and the completely unselective recording would be

\[ d = \sqrt{\sum_{i=1}^{n} (\tau_i - \tau_i)^2} \]

The SEL of a given recording then is calculated as

\[ SEL = \frac{d}{d_{max}} \]

Analysis of cross-talk between the EMG recordings

Although our bipolar electrodes were designed to record relatively selectively from muscle fibers within a radius of only a few hundred micrometers of the electrode tips (Andreasen and Rosenfalck 1978), we frequently recorded EMG activity through a given electrode during flexion of 2 or more contiguous digits (see RESULTS). Such recordings from FDP commonly have been assumed to indicate placement of the electrode near the border between 2 compartments, so that MUs from one compartment are recorded during flexion of one finger and MUs from an adjacent compartment during flexion of the other finger. We reasoned that if an electrode in compartment A picked up MUs from compartment B as well, then a second electrode relatively nearby in compartment B would be likely to record some of the same compartment B MUs, producing appreciable cross-talk between the recordings from the 2 electrodes. The incidence of cross-talk between our recordings then should be similar to the incidence of recordings showing EMG activity during flexion of more than one finger.

We therefore estimated the extent of cross-talk between each pair of simultaneously recorded EMGs using the technique described by Buys and colleagues (1986). We discriminated the largest MUs within a given EMG channel, and used these units as triggers to create a motor unit–triggered average (MUTA) of the unrectified EMG in each channel. The ratio of the peak-to-peak amplitude of the average motor unit action potential (MUAP) in a test channel to that in the trigger channel provides an estimate of cross-talk from the trigger to the test channel. On a trial-by-trial basis, we considered that the EMG activity recorded in a test channel might be attributable to cross-talk from MUs recorded in the trigger channel if the ratio of the δEMG in the test channel to the δEMG in the trigger channel was less than twice the ratio of the average MUAP in the test channel to that in the trigger channel (Buys et al. 1986).

Figure 3 illustrates this analysis using recordings from a special session in which we placed 4 electrodes at the same depth, 1 cm apart, in the ulnar aspect of FDP. In this session we aimed to place multiple electrodes in the same region of FDP so that adjacent electrodes would be more likely to record the same MUs. We recorded simultaneous EMG activity from all 4 electrodes during 17 trials of each of the 5 flexion movements (1f, 2f, 3f, 4f, and 5f). At each electrode the EMG activity recorded during 5f was substantially greater than that during any of the other movements, confirming that all 4 electrodes were in the digit 5 region of FDP. The first column in Fig. 3 shows the MUTA from each channel, triggered from the largest MUs recorded in channel C. The ratio of the peak-to-peak MUAP amplitude in channel B (the test channel) to that in channel C (the trigger channel) was 0.124. The second column shows EMG activity recorded simultaneously in the 4 channels during a single 5f trial. The ratio of the
δEMG in channel B to that in channel C was 0.215, less than 2 times 0.124. We therefore concluded that cross-talk from channel C could have contributed to the EMG in channel B on this trial. The final column shows the same 4 EMG channels for a trial in which we decided that the EMG activity at channel B was too large to have resulted mainly from cross-talk from the MUs recorded at channel C because the ratio of the δEMG in channel B to that in channel C was 0.614, more than 2 times 0.124. With 4 electrodes there are 6 possible electrode pairs, and MUs from either electrode can be used as triggers, generating 12 possible trigger-test pairs for each trial. The number of trigger-test-trial combinations with sufficient EMG recorded in both electrodes to look for cross-talk in this special session was 107. In 35% of these trigger-test-trial combinations, according to our criteria, the same MUs could have contributed to the EMG recorded at both the trigger and test electrodes. The recordings from this special session, however, were not included in the results presented below.

We therefore performed the same analysis on the recordings from each of the regular sessions in which electrodes were placed at different depths to record from different regions of FDP. The number of electrode trigger-test-trial combinations with sufficient EMG to look for cross-talk in these regular sessions ranged from 0 to 702 per session (median = 202), and EMG that might have been attributable to cross-talk was detected in only 71 of the 3,031 (2%) trigger-test-trial combinations from all 12 sessions. Moreover, instances of cross-talk were detected in only 3 of the 12 recordings sessions, each from a different subject. In 2 subjects possible cross-talk was detected on only one trigger-test-trial combination, whereas for the third subject possible cross-talk was detected on 69 of the 398 (17%) trigger-test-trial combinations from all 12 sessions. Conversely, whereas electrode A recorded EMG activity only during 2f, the other electrodes each recorded EMG activity during more than one instructed flexion force. Electrode C, for example, recorded activity during both 3f and 4f. Furthermore, some recordings also showed activity in FDP during extensions. Electrode C, for example, recorded activity during both 2e and 4e. Rather than each electrode recording activity during force production in only one instructed finger, the EMG activity at most electrodes varied with the instructed finger.

The variability of EMG activity at electrode C is examined in more detail in Fig. 5, which shows the rectified EMG averaged across all 20 trials of each instructed finger force (top row), as well as the unrectified EMG activity recorded during 5 single trials (bottom rows) of each of the 10 instructed forces. During flexions, EMG activity was recorded consistently during all 3f trials, and the amount of activity during the 3f trials was greater than that during any other instructed finger force. A smaller amount of activity also was recorded during 4f, but in contrast to the 3f trials, EMG activity was not present on every 4f trial. These observations suggest that this region of FDP acted primarily to flex digit 3, but also was activated to some degree during flexion of digit 4. During extensions, this electrode consistently recorded EMG activity during 2e and 4e, but not during 3e. Rather than acting as an antagonist during 3e, this region of FDP thus appeared to stabilize digit 3 against exerting extension force during 2e or 4e.

Figure 4 shows an example of the raw EMG and force data from one trial of each of the 10 instructed finger forces, collected in a single session. The instructed force on each trial is indicated at the top of the figure. The individual finger force traces at the bottom show that the subject performed each trial by producing force rather selectively with the instructed digit. Four EMG electrodes (A, B, C, D) were placed at different radioulnar depths in FDP. For some instructed forces, like flexion of the index finger and flexion of the little finger (2f and 5f), EMG activity occurred in only one of the 4 electrodes. In contrast, during flexion of the middle and ring fingers (3f and 4f) EMG activity was recorded in electrodes B, C, and D. Thus during flexion of some fingers only one of the electrodes recorded activity, whereas during flexion of other fingers multiple regions of the muscle were active to various degrees. Conversely, whereas electrode A recorded EMG activity only during 2f, the other electrodes each recorded EMG activity during more than one instructed flexion force. Electrode C, for example, recorded activity during both 3f and 4f. Furthermore, some recordings also showed activity in FDP during extensions. Electrode C, for example, recorded activity during both 2e and 4e. Rather than each electrode recording activity during force production in only one instructed finger, the EMG activity at most electrodes varied with the instructed finger.
The selectivity of regions within FDP during flexion of the fingers

We recorded EMG activity from 48 sites within the left FDP of 4 individuals. Some recordings showed EMG activity during the isometric flexion of only one of the 4 fingers. The majority of recordings (65%), however, showed substantial EMG activity during the flexion of more than one finger. To examine the selectivity of the EMG activity recorded at each electrode we expressed the ΔEMG value for each instructed finger flexion (2f, 3f, 4f, and 5f) as a percentage of the sum of the 4. Figure 6 shows these percentages for each of the 48 recordings, separated into 3 arbitrary categories based on the maximum percentage ΔEMG associated with any one instructed finger force. Recordings were classified as highly selective if the ΔEMG associated with any one instructed finger force was ≈80%; moderately selective, 60–79%; and minimally selective, <60%. Highly selective recordings (17 of 48) are shown in Fig. 6A. Recordings that were highly selective for 2f, 3f, and 5f were found in all 4 participants, but highly selective recordings for 4f were obtained from only one participant (cf. Kilbreath and Gandevia 1994). Moderately selective recordings (21 of 48) are shown in Fig. 6B. In these recordings, flexion of one of the 4 digits clearly was associated with the most EMG activity, whereas flexion of one or both adjacent digits was associated with a smaller, but still substantial, amount of EMG activity. Minimally selective recordings (10 of 48) are shown in Fig. 6C. In these recordings 2 or more instructed forces were associated with similar amounts of EMG activity. Because the EMG activity recorded by a single electrode during multiple instructed flexion forces was unlikely to have resulted from pickup of MUs in adjacent compartments of the muscle (see METHODS), these observations suggest that some regions of FDP might be activated during individuated flexion forces of more than one digit.
Quantification of SEL and COA of EMG activity during flexion of the fingers

Based on the instructed finger force (2f, 3f, 4f, or 5f) associated with the greatest amount of EMG activity, each recording from FDP might be categorized as originating from one of 4 discrete compartments acting on a given finger. We examined the possibility, however, that recording sites within FDP do not fall into 4 discrete categories. We calculated a selectivity index (SEL) to quantify the degree to which EMG activity in each recording was associated with one instructed flexion force versus all 4 instructed flexion forces. We also calculated the COA of the EMG activity recorded by each electrode across the 4 instructed flexion forces. Although the 2 indices are not independent, each quantifies a different aspect of the pattern of EMG activity in a given recording. SEL quantifies the degree to which EMG activity occurred selectively during only one instructed flexion force (SEL = 1), to completely unselectively, with equal activity during all 4 instructed flexion forces (SEL = 0). SEL is unaffected by which particular instructed forces were associated with different levels of EMG activity. In contrast, COA quantifies the particular instructed forces for which EMG activity was recorded. COA can range from −1 to +1, where −1 represents a recording in which EMG activity occurred only during 2f, −0.33 represents a recording in which the EMG activity recorded during the 4 instructed flexion forces was centered around 3f, +0.33 represents a recording in which EMG activity was centered around 4f, and +1 represents a recording in which EMG activity occurred only during 5f. In a scatter plot of SEL versus COA for each recording, the presence of 4 discrete neuromuscular compartments in FDP, each active for only one instructed flexion force, ideally would be evident as 4 clusters of points centered near COAs of −1, −0.33, +0.33, and +1, all with high SEL values.

Figure 7 shows a scatter plot of SEL versus COA for each of the 48 recordings. Rather than 4 clusters at high SEL values, the present data show many recordings scattered at intermediate COAs and lower SEL values. The 3 parabolic lines represent theoretical curves on which points would lie if EMG activity were recorded only during instructed flexion forces produced by 2 adjacent digits. For example, points lying on the leftmost parabolic curve would represent recordings in which EMG activity occurred in different proportions during 2f and 3f, but in which no EMG activity occurred during 4f or 5f. Points lying along the limb ascending toward “2f” would represent recordings in which more EMG activity occurred during 2f than during 3f. Conversely, points lying along the limb ascending toward “3f” would represent recordings in which more EMG activity occurred during 3f than during 2f. Points at the top of the left peak of the curve would represent recordings in which all of the EMG activity was recorded during 2f. Similarly, those at the right peak of the curve would represent recordings in which all of the EMG activity was recorded during 3f. Examining the data along all 3 parabolic curves thus indicates that the region of FDP most active during 2f was also active to a lesser degree during 3f, the region most active during 3f was also active to a lesser degree during 4f, the region most active during 4f was also active to a lesser degree during 3f and/or 5f, and the region most active during 5f was also active to a lesser degree during 4f.

Although many of the data points fall close to the theoretical curves, others reveal some noteworthy asymmetries and deviations. Approximately 20% of the recordings have SEL and COA indices that place them appreciably below the theoretical curves. In most of these recordings near-equivalent EMG activity levels were recorded during all 4 instructed flexion forces. For example, in the recording represented by the inverted triangle in Fig. 7 very similar amounts of EMG activity were associated with each of the 4 instructed flexion forces. Other recordings were minimally selective because appreciable EMG activity was recorded during flexion of 3 adjacent digits (e.g., open square in Fig. 7). Still other recordings were minimally selective because EMG activity was recorded during 3 instructed flexion forces, but less activity was recorded during flexion of the central digit that during flexion of the 2 digits adjacent to it on either side (e.g., open diamond in Fig. 7). These recordings suggest that some regions of FDP were active during as many as 3 or even 4 instructed finger flexions, consistent with previous observations that a single electrode in FDP could record 3 separate MUs, each associated with flexion of either the middle, ring, or little finger (Kilbreath and Gandevia 1994). Indeed, most of the present recordings fail to cluster into the discrete groups that would be expected if FDP were organized into 4 discrete regions, each active during a different instructed finger flexion. These data suggest instead that FDP, although containing regions highly selective for a given finger, also contains less-selective regions in which EMG activity occurs during instructed flexion of more than one digit.

EMG activity in FDP during all 10 movements

Figures 4 and 5 show that FDP was active not only during finger flexions but also during other instructed finger forces. To examine the activity of FDP during production of these other forces we summed the ΔEMG values from all 10 instructed finger forces and expressed the ΔEMG for each force as a percentage of this summed value. Figure 8 shows the percent-

![Figure 7. Selectivity (SEL) vs. center of activity (COA). Each recording is represented by a single point plotted at coordinates of SEL (selectivity of EMG activity for one of 4 instructed flexion forces) vs. COA (center of activity of EMG activity across 4 instructed flexion forces) for that recording. The three parabolic lines indicate ideal curves on which points would lie if EMG activity were recorded only during flexion of 2 adjacent digits. Highly, moderately, and minimally selective recordings of Fig. 6 are plotted as small open triangles, small filled squares, and small open circles, respectively. Large open square, diamond, and triangle correspond to 3 recordings in Fig. 6C plotted with the same special symbols and are described in text.](http://jn.physiology.org/DownloadedFrom/)
age summed ΔEMG values associated with each instructed finger force. Here, to group the recordings according to the instructed flexion force associated with the greatest ΔEMG, we included only moderately and highly selective recordings; as many minimally selective recordings had similar amounts of EMG activity associated with 2 or more flexion forces and were therefore difficult to categorize precisely. As described earlier in RESULTS, many recordings in all 4 categories (2f, 3f, 4f, and 5f) showed considerable EMG activity during flexion of adjacent digits. In addition, many recordings showed activity during finger extensions. EMG activity tended to be larger during extension of fingers adjacent to the finger with the greatest ΔEMG during flexion. Recordings in which the most activity occurred during 2f tended to show more activity during 3e than during other finger extensions; 3f recordings showed more activity during 2e and 4e; 4f recordings during 3e and 5e; and 5f recordings during 4e. We suggest that the activity in FDP during extensions acted to reduce the extension force exerted by noninstructed digits. During 4e, for example, activity in a region of FDP most active during 5f (Fig. 8, bottom right panel) acted to minimize extension force at the digit 5 fingertip. Besides stabilizing fingers during extension of adjacent digits, many recordings, with the exception of those showing the most activity during 3f, also showed appreciable activity during 1f. Activity in FDP during 1f might reflect an opposition synergy, in which the fingers stiffened or flexed slightly in opposition to the forces exerted by the thumb.

**Discussion**

Our intramuscular EMG recordings during individuated production of isometric finger forces are consistent with prior anatomical, clinical EMG, single MU, and MR imaging studies indicating a general organization of the human FDP into 4 functional subdivisions, each serving primarily to flex a different finger (Brand and Hollister 1993; Jeneson et al. 1990; Kilbreath and Gandevia 1994). From radial to ulnar, these 4 subdivisions are activated to the greatest extent during individuated flexion of the index, middle, ring, and little fingers. In many of the present recordings, however, although the greatest EMG activity appeared during flexion of a given finger, substantial EMG activity also was present during flexion of adjacent fingers. Although these observations should be interpreted with consideration of certain technical limitations, we infer that EMG activity recorded so frequently during flexion of more than one finger indeed reflects the functional organization of the human FDP.

**Technical limitations**

Two technical limitations of electromyography in human subjects should be considered in interpretation of the present findings (Loeb and Gans 1986). First, the exact location of the electrode tips within the muscle belly (e.g., index finger region vs. middle finger region of FDP) cannot be confirmed by direct visualization. In experimental animals, EMG electrodes can be placed on or within the muscle belly under direct visualization at surgery. Here, we considered the possibility of using ultrasound or magnetic resonance imaging to confirm electrode placement, but found visualizing the fine-wire electrodes and defining compartment boundaries impractical with these techniques. We also considered using constant current electrical stimulation through each electrode to identify its position within FDP, but with such small and closely spaced recording surfaces we found we were not able to evoke visible finger movement. We therefore have relied on the depth of the electrode from the ulnar skin surface, and observing motion of the placement needle and EMG recorded from the electrode during flexion of each fingertip, to assess placement of each electrode. Furthermore, our analysis has focused on the EMG activity recorded from each electrode, independent of any assumptions about the location of the electrode.

Second, the spatial radius over which EMG electrodes record MUAPs is difficult to define precisely. Larger potentials
Functional subdivision of the human FDP

In the periphery, FDP might contain subpopulations of 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. Such multigemt MUs have been demonstrated with single-MU stimulation in the cat extensor digitorum communis (Fritz et al. 1992) and macaque extensor digiti quarti et quinti (Schieber et al. 1997). Motor unit–triggered averaging (MUTA) of finger forces suggests that multigemt MUs might also be present in the human FDP (Kilbreath et al. 2002; Reilly and Schieber 2002) and extensor digitorum communis (Keen and Fuglevand 1999; Keen et al. 1998), although MUTAs with forces on more than one digit might result in part from short-term synchronization between single-digit MUs acting on different fingers (Keen and Fuglevand 2001). EMG activity recorded by the same electrode during flexion of different fingers could therefore result from the presence of multigemt MUs that are activated during flexion of each of the fingers on which they act.

A second peripheral factor that might contribute to recording EMG activity at one electrode during flexion of different fingers would be overlapping territories of single-digit MUs that put tension on different digits. Previous studies of the human FDP have shown that single intramuscular, fine-wire, bipolar electrodes can record different low-threshold MUs recruited during flexion of digits 3, 4, and 5 (Kilbreath and Gandevia 1994). This observation raises the possibility that muscle fibers of single-digit MUs acting on adjacent finger tendons are, to some extent, intermingled. Anatomically, as fascicles of muscle fibers are followed back from their insertion on the FDP finger tendons to their origin from the interosseus membrane, the cleavage planes between fibers serving adjacent tendons become indistinct and muscle fascicles serving adjacent tendons appear interdigitated at their origins (Reilly, Gardinier, Schieber, unpublished observations). If these fascicles serving adjacent tendons are composed of single-digit MUs, then the intramuscular territories of MUs serving adjacent tendons overlap spatially. Electrodes in the vicinity of these overlapping MU territories would record EMG activity during flexion of more than one finger, but the individual MUs contributing to the EMG activity would differ depending on which finger was flexed.

A third factor that could contribute to our observations is central coactivation of MUs serving adjacent digits. Even if FDP consists entirely of single-digit MUs, with no overlap between territories of MUs serving adjacent digits, the human nervous system might be unable to activate MUs acting on one finger without activating some MUs acting on adjacent fingers, even when producing individuated flexion forces. Short-term synchronization between FDP MUs indicates that FDP motoneurons acting on different fingers do receive common inputs (Garland and Miles 1997; Huesler et al. 2000). Indeed, FDP MUs first recruited at low threshold during flexion of a given fingertip also are recruited during flexion of adjacent fingertips at slightly higher force (Kilbreath and Gandevia 1994). Recruitment of a set of MUs during individuated flexion of the finger to which those MUs are mechanially linked, as well as during flexion of an adjacent finger to which those MUs are not mechanically linked, would produce EMG activity during flexion of adjacent digits like that which we observed. Distinguishing the extent to which these 3 factors contribute to the present observations will require future studies in which the activity of single motor units is followed through the production of instructed forces by each finger.

In summary, we suggest the following picture of functional organization in the human FDP. Four core regions each act selectively on a single digit. In addition, other less-selective regions contain MUs that are active during flexion of adjacent fingers as a result of their biomechanical connections, overlapping territories, and/or central coactivation. If MUs in the selective core regions can be viewed as having “preferred directions” pointing to a single digit, MUs in the less-selective regions can be viewed as having “preferred directions” intermediate between 2 adjacent digits. FDP then might be considered to have MUs with a spectrum of preferred directions from index to little finger, similar to the human biceps brachii and deltoid (Herrmann and Flanders 1998). In addition to producing the patterns of EMG observed in the present study, the activity of MUs within these less-selective regions would contribute to the features of FDP MU recruitment observed elsewhere (Kilbreath and Gandevia 1994) and to the incomplete individuation of human finger forces and finger movements (Häger-Ross and Schieber 2000; Reilly and Hammond 2000; Zatsiorsky et al. 2000).

The role of FDP in the production of individuated finger movements

FDP is the only muscle that attaches to the distal phalanx of each of the 4 fingers and is therefore important for the production of both individuated finger forces and movements. Our recordings suggest that this importance extends beyond the agonist role of FDP in flexing the fingers, given that almost all of our recordings showed EMG activity in FDP during extension of certain fingers and/or during flexion or extension of the
thumb. For example, a recording most active during 3f typically also showed activity not during 3e, but during 2e and 4e. Rather than acting as an antagonist during extension of digit 3, this region of FDP presumably stabilized digit 3 to limit its extension force during the instructed extension of the adjacent digits 2 and 4. Thus during production of individuated finger forces in humans, as in the macaque (Schieber 1993 1995), functional subdivisions of FDP act not only as agonists for finger flexion but also as stabilizers against unwanted extension.

Comparison of the functional organization of the human and macaque FDP

In macaque monkeys FDP is anatomically compartmentalized. The macaque FDP muscle belly consistently has 4 anatomically distinct regions, each of which receives a separate primary nerve branch, and hence can be defined as a neuromuscular compartment (Serlin and Schieber 1993). Stimulation of the primary nerve branch entering each of the 4 compartments demonstrates that, although each compartment produces a different pattern of tension across the 5 tendons, no compartment puts tension on only one tendon (Schieber et al. 2001). The action of each compartment on multiple digits results in part from the heavy interconnections between the tendons to different digits, and in part from the insertion of muscle fascicles from a single compartment onto the region of the proximal insertion tendon serving multiple digits. Nevertheless, intramuscular EMG recordings from the 2 largest compartments during voluntary movements of the fingers and wrist have shown that these 2 compartments consistently produce categorically distinct patterns of EMG, as would be expected of discrete compartments (Schieber 1993). The radial compartment consistently is most active during 2f and is also active during 3f, whereas the ulnar compartment consistently is most active during 5f but also produces some activity during both 3f and 4f. The macaque FDP thus is compartmentalized, although functionally each of the 4 neuromuscular compartments acts on multiple digits.

In comparison, the human FDP appears less completely compartmentalized than that of the macaque. Anatomically, the innervation of some regions within the muscle is variable, with 2 primary nerve branches innervating a number of regions (Bhadra et al. 1999; Segal et al. 2002; Sunderland 1945). Distinct fascicular boundaries between muscle fibers inserting onto each of the 4 tendons are also difficult to identify. Prior EMG studies at low forces (Kilbreath and Gandevia 1994), as well as the present study, have failed to show the 4 categorically distinct patterns of EMG recruitment that would be expected from 4 discrete compartments.

Paradoxically, even though the human FDP muscle belly may be less anatomically compartmentalized than that of the macaque FDP, humans have a greater ability to produce individuated finger movements (Häger-Ross and Schieber 2000; Schieber 1991). Two major aspects of the functional organization of FDP contribute to this difference. First, the 5 insertion tendons of the macaque FDP are much more interconnected than the 4 insertion tendons of the human FDP. In the macaque all 5 distal tendons arise from a single common insertion tendon that continues through the carpal tunnel and divides into clearly separate tendons for each digit only within the palm (Serlin and Schieber 1993). In humans, separate tendons are present proximal to the wrist. Second, regions within the muscle belly that are exclusively active during the flexion of only one digit are absent in the macaque FDP but present in the human FDP. Thus the anatomically compartmentalized macaque FDP does not contain any neuromuscular regions that put tension on only one tendon. In contrast, humans do have the ability to selectively activate core regions of the muscle that serve to flex a single digit (along with other less-selective regions serving multiple digits) and so can achieve relatively selective tension on a single digit. In part because of these differences in the functional organization of FDP, human finger movements can be more highly individuated than those of macaques.

DISCLOSURES

This work was supported by R01-NS-36341 and R01-NS-27686 from the National Institute of Neurological Disorders and Stroke and P41-RR-09283 from the National Center for Research Resources.

REFERENCES


J Neurophysiol • VOL 90 • OCTOBER 2003 • WWW.jn.org

Downloaded from http://jn.physiology.org/ by 10.220.33.6 on June 22, 2017


