



Neuromuscular Compartments of the Macaque Flexor Digitorum Profundus Distribute Tension to Multiple Digits. J. Gardinier, J.Liu & M.H. Schieber*.

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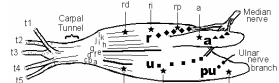


1. Abstract

The macaque flexor digitorum profundus (FDP) sends tendons to all 5 fingers. Different primary nerve branches innervate 4 regions of the muscle belly. To determine the extent to which these different regions exert tension selectively on a single digit or distribute tension to multiple digits, we stimulated each nerve branch while recording the tension on all 5 tendons. Though no region exerted tension on only one digit, each region produced a different distribution of tension among the tendons. Distribution of tension to multiple digits might result simply from interconnections between the FDP tendons to different digits. We therefore applied a 1 kg proximally-directed load at different radioulnar locations on the FDP tendon proximal to the wrist, while again recording the tension in all 5 FDP finger tendons. These passively produced tensions were distributed more selectively than those produced by active contractions. Stimulation repeated after ligation of the median and ulnar nerves in the upper arm, and again after cutting each primary nerve branch off its parent nerve trunk, excluded the possibilities that the broader distribution of active tension resulted either from spinal reflexes or from branching of motor axons proximal to the muscle, respectively. EMG recordings from each region indicated that stimulation of each primary nerve branch activated a different region of the muscle belly. We conclude that 4 neuromuscular compartments in the macaque FDP each produce a different tension distribution that results both from passive mechanical interconnections between the 5 tendons and from the arrangement of active contractile elements. Support: NINDS R01-NS36341

2. Introduction

When performing tasks that require individualized finger movements, the nervous system produces finger movements through contraction of hand and forearm muscles. Several of the muscles activated during individualized finger movements send multiple tendons to different fingers. Contraction of a multidendroned muscle during movement of an individual finger might produce movement of all the fingers on which its tendons insert. Alternatively, a multidendroned muscle might consist of separate neuromuscular compartments, each acting on a single finger. An intermediate possibility would be that compartments in a multidendroned muscle act differentially on its tendons without being completely selective for a single digit.



The macaque flexor digitorum profundus (FDP), shown in the figure above, sends tendons to each of the five fingers. Our previous studies have shown that FDP typically consists of four regions, a radial region (FDP_{rd}), an ulnar region (FDP_{ul}), an accessory region (FDP_a) and a proximal ulnar region (FDP_{pu}). Each region is innervated by a separate nerve branch. EMG studies have indicated that two of these regions, FDP_{rd} and FDP_{ul}, are functional subdivisions within the muscle. FDP_{rd} can be activated without activation of FDP_{ul}, and vice versa (Schieber, 1993). It is unknown whether all four neuromuscular regions each represent a functional subdivision, and if so whether each region produces a different distribution of tension on the tendons. We therefore examined the distribution of tension across the 5 FDP tendons produced by contraction of each neuromuscular region.

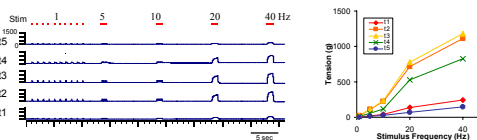
3. Methods

Studies were performed on 5 male pigtail monkeys (*Macaca nemestrina*, 2 to 4 kg). Once the monkey was surgically anesthetized, the tendons of FDP were dissected free in each digit of the right hand. The flexor carpi radialis (FCR), palmaris longus (PL) and flexor digitorum superficialis (FDS) muscles were dissected proximally. Median nerve branches innervating FCR, PL, FDS, FDP, and pronator teres (PT), as well as the anterior interosseous nerve (AIN) were dissected and identified with electrical stimulation. Branches of the ulnar nerve innervating flexor carpi ulnaris (FCU) and FDP were identified in the same manner. All forearm muscles other than FDP were denervated. The median and ulnar nerves were cut just proximal to the wrist, denervating the intrinsic hand muscles. The dissected forelimb was fixed ventral side up, and a protective mineral oil pool was constructed with skin flaps. Each FDP tendon then was tied to a separate tension transducer (Load Cell BG-1000 gm, Kulite Semiconductor Products, Inc.) mounted on a custom-made miniature rack and pinion, and the length of each digital tendon was adjusted such that the resting tension was approximately 100 gm in each tendon. A diagram of the experimental set up is shown in the figure below.

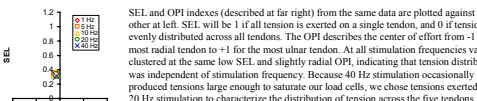
Each FDP primary nerve branch was placed in turn on a bipolar hook electrode, elevated into the mineral oil pool, and stimulated. Recordings were made while stimulating with twice the current needed to produce maximal tension output.



4. Effects of Stimulation Frequency



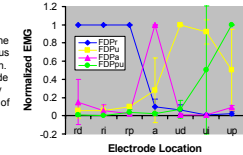
An original recording of tension in each FDP tendon and 1, 5, 10, 20 and 40 Hz stimulation of FDP is shown above. Contraction of FDP produced the most tension on tendon 3 and the least tension on tendon 5 at each frequency of stimulation.



SEL and OPI indices (described at far right) from the same data are plotted against each other at left. SEL will be 1 if all tension is exerted on a single tendon, and 0 if tension is evenly distributed across all tendons. The OPI describes the center of effort from -1 for the most radial tendon to +1 for the most ulnar tendon. At all stimulation frequencies values clustered at the same low SEL and slightly radial OPI, indicating that tension distribution was independent of stimulation frequency. Because 40 Hz stimulation occasionally produced tensions large enough to saturate our load cells, we chose tensions exerted during 20 Hz stimulation to characterize the distribution of tension across the five tendons.

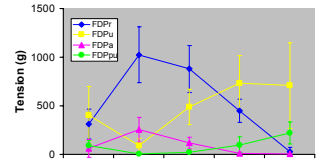
5. Primary Nerve Branch Stimulation Activated Each Neuromuscular Region Separately

In four of the present experiments we recorded compound muscle action potentials from bipolar intramuscular electrodes inserted at 7 sites in the FDP muscle belly (stars in the map up and to the left). The average level of rectified EMG activity from 6 to 25 msec after stimulus onset was normalized for maximum activity at each electrode location. The figure at right shows normalized EMG activity from each electrode averaged across these four experiments. Stimulation of each primary nerve branch produced electrical activation of the appropriate region of the FDP muscle belly, with little evidence of activity in other regions.

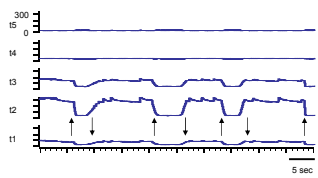


6. Each Neuromuscular Region Has a Different Tension Distribution

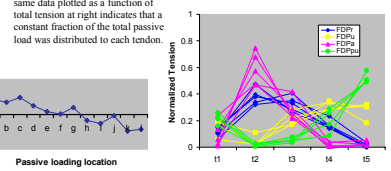
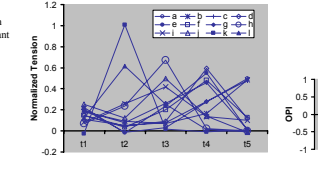
Simulation of each primary nerve branch produced a different distribution of tension across the 5 FDP tendons. Similar distributions were obtained for each nerve branch in all monkeys. The mean 1 second tension for a 20 Hz stimulus averaged across monkeys is shown in the figure to the left. Contraction of FDP_{rd} resulted in the greatest amount of tension on tendons 2 and 3 with less tension on tendons 4 and 1, and little if any tension on tendon 5. FDP_{ul} produced the greatest tension on tendons 4 and 5, less on tendons 3 and 1, and very little on tendon 2. FDP_a produced tension on tendon 2, less on tendon 3, and very little tendon 1; the tension FDP_{pu} produced on tendons 2 and 3 always was less than that produced by FDP_{ul} in the same animal. FDP_{rd} produced more tension on tendon 5 than 4, though in all cases less than that produced by FDP_{ul}.



7. Tension Distribution by Neuromuscular Regions Does Not Result Only From Passive Mechanical Interconnections

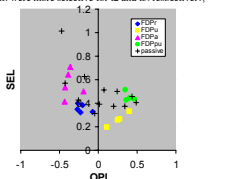


The macaque FDP tendons originate from the muscle belly as a single sheet-like aponeurosis, which then divides into separate digital tendons within the palm. These mechanical interconnections will cause tension exerted at one point on the proximal aponeurosis to be distributed among multiple distal finger tendons. The original record at left shows the tension in the 5 tendons as a 1 kg load was exerted passively at one location on the proximal aponeurosis by lowering and raising weight. The same data plotted as a function of total tension at right indicates that a constant fraction of the total passive load was distributed to each tendon.



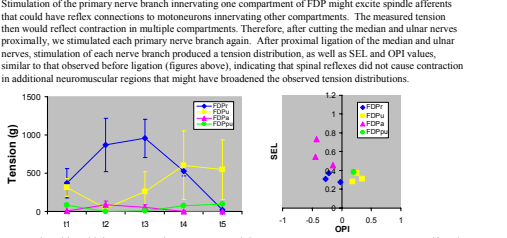
The tension distributions produced by passive loading at twelve radioulnar locations on the proximal tendon sheet each had a relatively sharp peak on a single tendon that shifted stepwise from 12 to 15 (above left), as the point of loading was moved progressively from the radial to the ulnar aspect of the proximal insertion aponeurosis ("a" to "j"). Concurrently, the OPI shifted progressively from more negative to more positive values (above center). The sharp peaks produced by passive loading contrast with the broader peaks spanning two or three tendons produced by active contraction of FDP_{rd} and FDP_{ul} (above left). These broader peaks indicate that FDP_{rd} and FDP_{ul} each exerted active tension at a range of radioulnar locations on the proximal insertion aponeurosis. The tension distributions produced by active contraction of FDP_{rd} and FDP_{ul} were more selective for 12 and 15, respectively, similar to the passive loading distributions.

To compare the tension distributions produced by passive loading versus active contractions more quantitatively, we calculated the SEL and OPI for both conditions and plotted them against one another at right. The SEL and OPI from active contraction of FDP_{rd} and FDP_{ul} were comparable to those from passive loading of the most radial and most ulnar aspect of the proximal insertion aponeurosis, respectively. The SEL of FDP_{rd} was slightly lower than passive loading for similar OPIs and the SEL of FDP_{ul} was considerably lower. FDP_{rd} and FDP_{ul} must therefore each exert active tension at multiple radioulnar locations on the proximal insertion aponeurosis.



8. Spinal Reflexes and Axon Collaterals Did Not Distribute Tension to Multiple Tendons

Stimulation of the primary nerve branch innervating one compartment of FDP might excite spindle afferents that could have reflex connections to motoneurons innervating other compartments. The measured tension then would reflect contraction in multiple compartments. Therefore, after cutting the median and ulnar nerves proximally, we stimulated each primary nerve branch again. After proximal ligation of the median and ulnar nerves, stimulation of each nerve branch produced a tension distribution, as well as SEL and OPI values, similar to that observed before ligation (figures above), indicating that spinal reflexes did not cause contraction in additional neuromuscular regions that might have broadened the observed tension distributions.



In muscles with multiple neuromuscular compartments, it is commonly assumed that motor axons ramify only after the axon has entered the muscle. We wished to exclude the possibility that axons might give off collaterals in the parent nerve, such that collaterals of the same axons enter more than one primary nerve branch. Stimulating one primary nerve branch then would cause contraction in more than one compartment, via axon reflexes in such collaterals, producing a broader distribution of tension. By stimulating each primary nerve branch a third time after it had been cut away from the nerve trunk, we eliminated any contribution of proximal axon branching. Since the tension distribution was not altered from both previous recordings and SEL and OPI values were again similar (figures above), no evidence for axon collaterals innervating more than one region was found.

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9. Conclusions

- 1) The macaque FDP has four neuromuscular compartments each innervated by a separate primary nerve branch: FDP_{rd}, FDP_{ul}, FDP_a and FDP_{pu}.
- 2) Each of these neuromuscular compartments exerts tension on multiple FDP tendons.
- 3) Tension distribution is independent of stimulation frequency.
- 4) Each neuromuscular compartment produces a different distribution of tension on the five tendons.
- 5) The tension distribution to multiple tendons by each neuromuscular compartment is influenced by both the biomechanical structure of the tendons and the distribution of muscle fibers inserting on the proximal tendon.
- 6) Passive tension distribution by the complex insertion tendons is highly linear.
- 7) Neither spinal reflexes nor axon collaterals proximal to the primary nerve branches contributed appreciably to the distribution of tension by FDP's neuromuscular compartments.

Appendix: OPI and SEL Indexes

Tension measurements were used to calculate the SEL and OPI for each FDP region. The OPI is calculated as follows:

$$OPI = \frac{\sum_{i=1}^n T_i \cdot W_i}{\sum_{i=1}^n T_i}$$

where T_i is the tension on tendon i and W_i is the weight of tendon i . The SEL is calculated as follows:

$$SEL = \frac{\sum_{i=1}^n T_i^2}{\sum_{i=1}^n T_i}$$

The SEL and OPI are calculated as follows:

$$SEL = \frac{\sum_{i=1}^n T_i^2}{\sum_{i=1}^n T_i}$$

$$OPI = \frac{\sum_{i=1}^n T_i \cdot W_i}{\sum_{i=1}^n T_i}$$

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