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Composite Muscle Structure Found in M. Flexor Digitorum Superficialis of Slow Loris, *Nycticebus*

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Abstract The flexor digitorum superficialis of Slow Loris (*Nycticebus coucang* and *N. pygmaeus*) was examined. Close observations both on the muscular composition and on the innervation under dissecting microscope revealed that this muscle is consisted of two distinct portions, the proximal and the distal. The proximal portion receives two nerve branches at the cubital fossa, one from the median nerve and the other from the ulnar, and the distal belly is innervated by a small twig of the median nerve, which bifurcates far distal from the aforementioned branch. This last branch, with which the exact identification of the muscle is achieved, has not been described in Prosimii by any preceding authors. Findings on the innervation imply that the proximal portion has intimate relation with the deep flexors of the forearm, whereas the distal portion is derived from the intrinsic flexors of the hand. Consequently, the forearm flexors of the Slow Loris are classified into three groups: 1) Elbow matrix, 2) Forearm matrix, and 3) Intrinsic hand matrix.

Introduction

The muscular portion of the mammalian flexor digitorum superficialis muscle had been understood as developed in situ from the deep flexor of the forearm (STRAUS, 1942). Despite almost unanimous acceptance of this view, sporadic attempts to re-evaluate the phylogenetical position of the muscle have been brought forth (HAINES, 1950; OHTANI, 1979), which indicate the interpretation mentioned above is not totally convincing. HAINES (1950) suggested that the mammalian flexor digitorum superficialis as being derived from the intrinsic hand flexor of reptiles and its gradual proximad migration up to the forearm. Whatever the conclusion may be, an untested assumption that the muscle is single and homogeneous had been a premise to these authors.

On the other hand, a duality of phylogenetical origin of the mammalian flexor digitorum superficialis was first raised by EISLER (1895), although he did not clearly illustrate the evidence of his conclusion. GRÄFENBERG (1906) proposed another duality on the ontogenetical origin of this muscle on the basis of his own embryological observation. The only problem he encountered was lack of evidence in the adult form. Finally, however, DYLEVSKÝ (1967) concluded, in human ontogeny, that a single muscle blastema migrated from the carpal region to the forearm which later formed the flexor digitorum superficialis, and no fusion of muscle primordia was observed. It seems, his conclusion put an end to the issue. Recently, however, based on a detailed observation of the human adult anatomy, YAMADA (1986) presented a new interpretation of the human forearm flexors. This was established by analyzing newly revealed facts that the flexor digitorum superficialis is not homogeneous but made up of two distinct portions. This interpretation essentially agrees with the embryological results obtained by GRÄFENBERG (1906). On the contrary, comparative descriptions available on the subject are not applicable to the phylogenetical confirmation of this hypothesis. An untested assumption that the muscle in question is single and homogenous had prevented further study (MILLER, 1943; MURIE & MIVART 1872). Therefore, a phylogenetical consideration has to be made on the basis of new observations.

The present paper provides findings on the M. flexor digitorum superficialis of the Slow Loris (*Nycticebus coucang* and *N. pygmaeus*), and add evidences indicating the phylogenetical duality of this muscle.

Materials and Methods

Two specimens of *Nycticebus coucang* and one of *N. pygmaeus* were used as materials. Findings on the flexor digitorum superficialis of these two species are fundamentally identical.

All the following procedures were carried out under dissecting microscope with each specimen being immersed in water to enable the exact discrimination of nerves and vessels from the connective tissue. The forearm flexors and the nerves of innervation were carefully dissected out and identified. The forearm flexors were observed in detail to clarify their internal composition. WEIGERT's variation of LUGOL's solution (BOCK & SHEAR, 1972) was used to stain muscular fibres to enhance the contrast between the muscular fibres and the connective tissues.

Branching patterns of the median and the ulnar nerves were observed after the epineuria were removed. The nerves of innervation were pursued into the nerve trunks which compose these nerves. These nerves were teased out to observe the fasciculization. Finally, the muscles were removed for further examinations of the intramuscular nerve distribution.

Nomenclatures after STRAUS (1942), WINDLE (1889), FROSE and FRÄNKEL (1908), and GRÄFENBERG (1906) were adopted for the description.

Results

Structure of the Flexor Digitorum Superficialis

The flexor digitorum superficialis (FDS) of *Nycticebus* was in the second layer of the forearm flexors, forming the ulnar border of the intermediate sector (Fig. 1-A, -B). Although it appeared as a flat elongated muscle, the muscle was divided into two portions, a proximal (FDS-P) and a distal (FDS-D). The boundary between these two portions was hardly confirmed unless observed with dissecting microscope (Fig. 2-A, -B).

FDS-P arose from the medial epicondyle of the humerus, ran down the forearm between the condylo-radialis (C-R) and the condylo-ulnaris (C-U) portions of the flexor digitorum profundus (FDP), beneath the palmaris longus (PL) and was partly under cover of the flexor carpi ulnaris (FCU). At about the

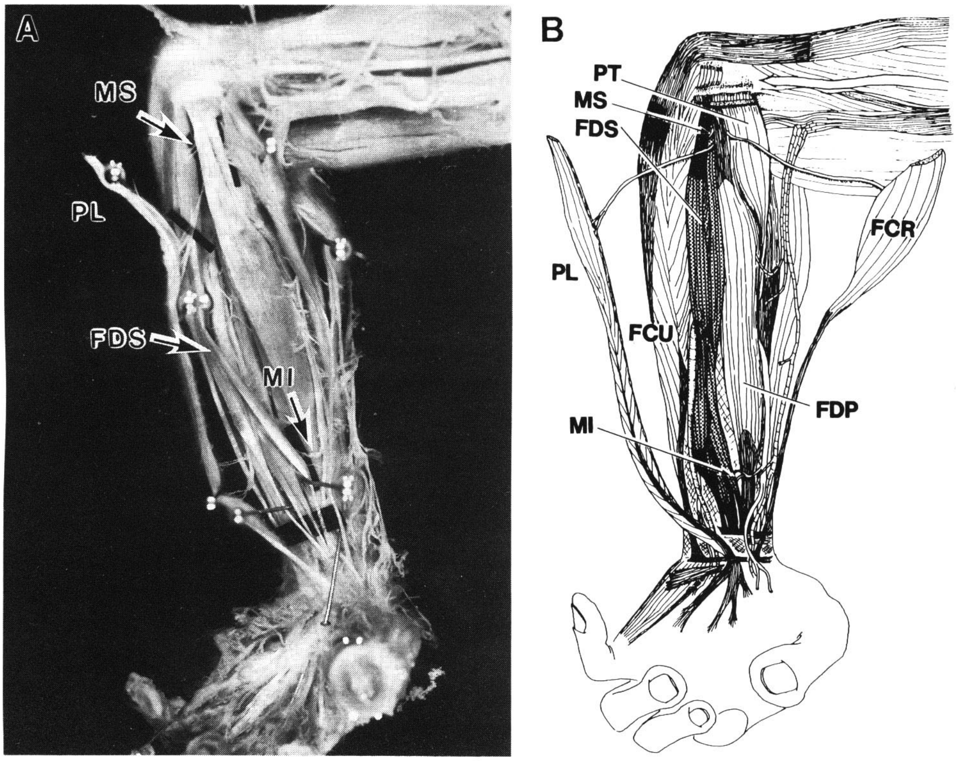

Fig. 1. A photograph (A) and a drawing (B) showing the flexor side of the left forearm of *Nycticebus coucang.* FCR and PL are cut at their origins and are turned over to show the second layer. FDS (dotted in B) receives two branches from the median nerve, MS and MI. MI has not been described in the former works.

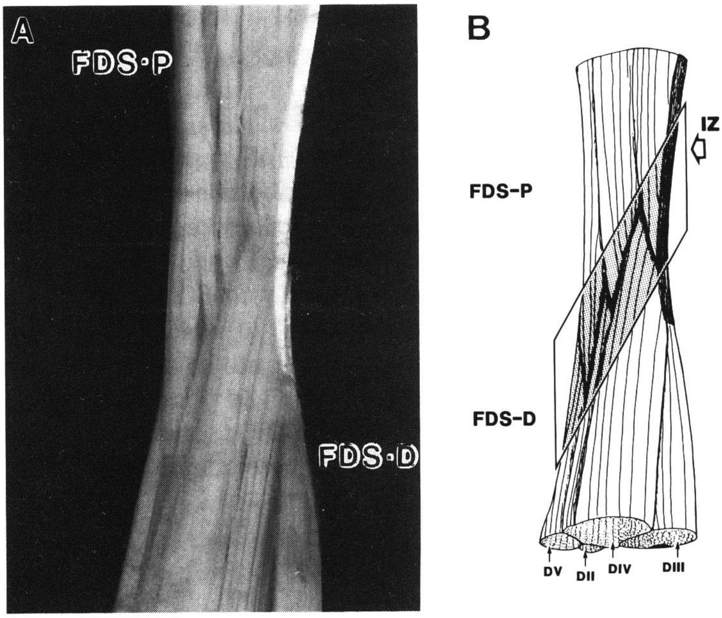

Fig. 2. A photograph (A) and a drawing (B) of the intermediate region of FDS. Apparently homogenous FDS of *Nycticebus* is partitioned, actually into FDS-P and FDS-D at IZ, where FDS-P insert to, and FDS-D originates from the aponeurotic fascia lining the deeper surface.

middle of the forearm was a narrow interrupting zone (IZ) which thoroughly traversed the muscle obliquely (Fig. 2-A, -B). Here, the muscle fibres of FDS-P terminated at an aponeurotic fascia investing the deeper surface of the muscle, whereas the fibres of FDS-D, in turn, arose from it. Thus, the muscle bundles of FDS-P which inserted to the aponeurotic fascia and those of FDS-D arising from it interdigitated each other at IZ (Fig. 2-A, -B). Distally, FDS-D splits into four muscle bundles (DII, DIII, DIV and DV), each destined to the ulnar four digits respectively. As a whole, a λ-shaped muscle was consisted of three muscle bellies, namely FDS-P, DIII, and DIV. Former two of these appeared as if they composed a digastric muscle (Fig. 3, 7).

The deeper surface of FDS-P (Fig. 3) was mostly fleshy but the distal half of the both lateral edges and the area proximally adjacent to IZ was invested by an aponeurotic sheet. It extended beyond IZ over the deep surface of FDS-D tapered and thickened to form the tendon of insertion of DII. A slender tendon emerged from the ulnar end of IZ, which joined the tendon of the deep flexor. Two muscle bundles of FDS-D took their origins from this tendon, one (DIV) was on the radial side and the other (DV) on the ulnar side.

The ulnar three tendons of insertion (DIII, DIV and DV) were perforated by

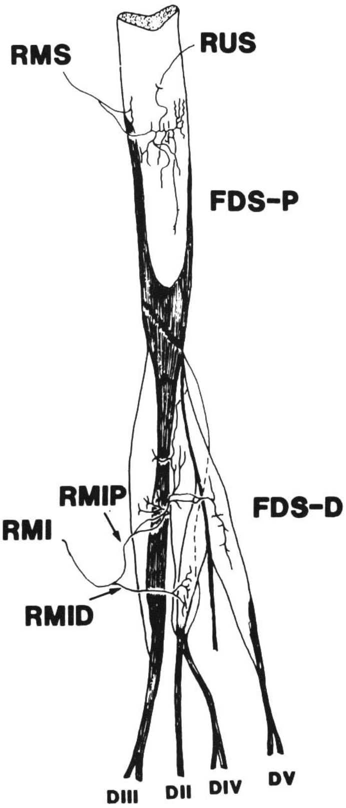

Fig. 3

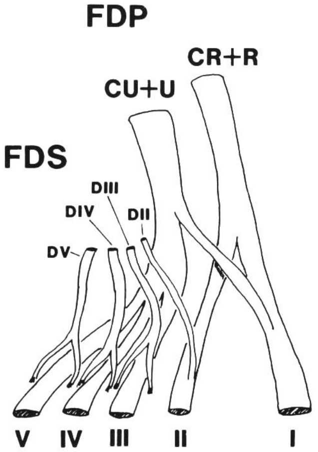

Fig. 4

Fig. 3. The deeper surface of FDS and the nerves of innervation are shown. The dark area indicate tendinous or aponeurotic portions. RMS and RUS are for FDS-P, and RMIP innervates D III, D IV and D V. D II is supplied by RMID.

Fig. 4. Tendons of insertion of FDS and FDP. Ulnar three tendons, D III to D V, are perforated by the corresponding tendons of FDP, while the tendon of D II simply joins the tendon of FDP.

the corresponding tendons of FDP. The most radial tendon of D II simply joined the tendon of FDP just proximal to its insertion (Fig. 4).

Nerves of Innervation

The fascicular formations of the median and the ulnar nerves were observed after the epineuria were removed carefully. The median nerve, at the elbow, was consisted of three major fasciculi (Fig. 5). The ulnar nerve was also made up of three divisions. These divisions were definitely defined by the perineurium sheaths.

The branches of these divisions from the median nerve are listed according to

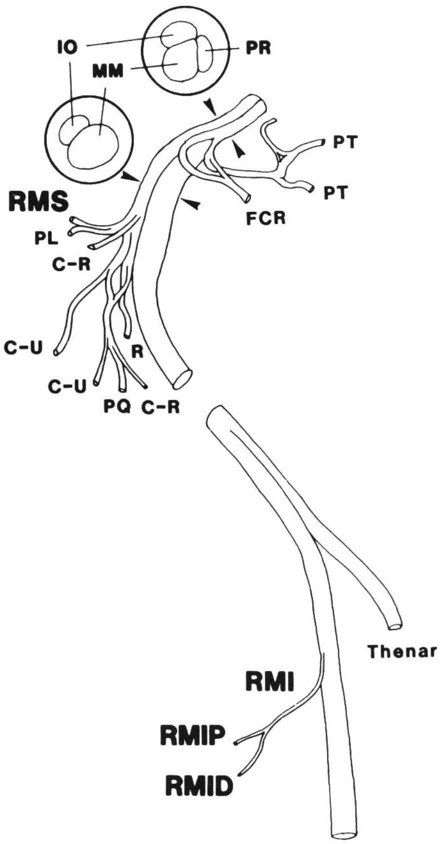

Fig. 5. Nerve branches from the median nerve to the forearm flexors. Cross sections at two different levels (indicated by two pairs of arrow heads) of the median nerve are shown in circles, where three divisions of the median nerve, A, B and C, are schematically drawn.

their destinations: (Fig. 5)

A, pronator teres (PT), and flexor carpi radialis (FCR)
B, FDS-P, palmaris longus (PL) and deep flexors
C, FDS-D and intrinsic hand muscles

Those from the ulnar nerve are:

D, epitrochleoanconaeus and flexor carpi ulnaris (FCU)
E, FDS-P and deep flexors
F, intrinsic hand muscles

FDS-P and FDS-D were innervated by three separate groups of nerve branches (Fig. 3, 5, 7). Two branches were confirmed to supply FDS-P, of which one (Ramus superior from the median nerve, RMS) was from the division A and the other (Ramus superior from the ulnar nerve, RUS) from the division E.

These two communicated with each other within FDS-P. RMS branched off in the cubital fossa together with a branch to PL. RMS and the branch for PL were inseparable even though the epineurium was removed. Four muscle bellies of FDS-D were innervated by a fine twig which bifurcated from the main trunk of the median nerve (the division C) at about the lower third of the forearm (Ramus inferior from the median nerve, RMI). A proximal division of RMI (RMIP) divided further into three twigs for DIII, DIV and DV. DII was supplied by a distal division (RMID) of RMI. This RMI in the prosimians has not clearly been described by the preceding authors.

Discussions

General Description of FDS, Historical Review

A homogeneity of the flexor digitorum superficialis (FDS) in mammals has been taken for granted although there was not any convincing proof (STRAUS, 1942; FROSE & FRÄNKEL, 1908; HAINES, 1950). EISLER (1895) maintained that the mammalian FDS is composed of two different muscles that are separately difined in urodeles. An embryological finding of GRÄFENBERG (1906) was an evidence which showed the dual ontogenetical sources of this muscle in human. According to his description, FDS is formed by a fusion of two completely independent muscle primordia, namely his flexor digitorum brevis (FDBG) and his flexor digitorum sublimis (FDSG). According to his description FDBG develops in the palm, migrates proximally to the forearm and joins FDSG forming the definite FDS. However, he did not specify any trace of a boundary where these two muscle primordia were fused in adult form. His monograph had been neglected probably because of the premise assuming the homogeneity of the muscle. The main subject of the phylogenetical research on the forearm flexors had been whether the muscle has its primordium originally in the palm or in the forearm. It was because HAINES (1950) suggested that amphibian or reptilian muscle components that are equivalent to mammalian FDS originate in the palm and these components migrate proximally to reach the humerus in mammals. This idea contradicted WINDLE (1889), STRAUS (1942) and many other authors. Anyway, it appeared DYLEVSKÝ (1967) put an end to the latent suspicion concerning the duality of FDS, with his embryological interpretation in which FDS had a sole anlage originally in the carpal region.

As a result of detailed studies of the human adult anatomy, YAMADA (1986) proposed a hypothesis that this muscle is made up of two different portions (Fig. 6). Both the muscle composition and the mode of innervation show two distinctive portions in the FDS. One is the so-called proximal belly of the deep layer of this muscle (FDS-P), and the other is composed of the rest of the muscle (FDS-D). Although human FDS had been interpreted as single and homogenous

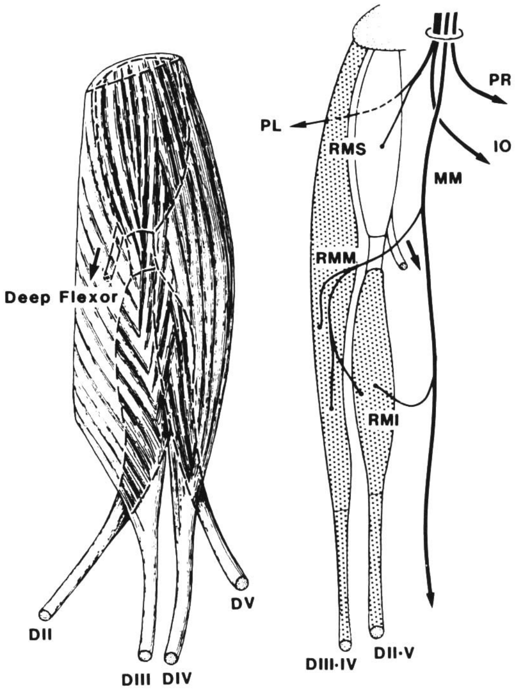

Fig. 6. A schematic drawing of FDS of *Homo*. FDS-D is indicated by dotted area. Note that FDS-P is overlaid by the superficial layer of FDS-D. It inserts on the intermediate tendon, from which the deep layer of FDS-D arises.

without any reasoning nor confirmation, the independency of FDS-P and FDS-D was proved. A general belief that the median nerve within the forearm has little constancy in its branching pattern, and hence the nerves of innervation can not be a determinant criterion for the myological study, was also refuted because the nerve fasciculi sheathed by perineuria showed striking constancy in their fasciculization, only if the epineurium is carefully removed (BORCHARDT & WJAMENSKI, 1917; HOMMA, 1980, and YAMADA, 1986). FDS-P is innervated by the Ramus superior (RS), which is a branch close to the interosseous nerve and closest to the nerve to PL. On the contrary, muscle bundles of FDS-D are supplied by R. medius (RM) and R. inferior (RI), and these two nerves are bound up by the same perineurial sheath. It was thus shown that findings on the innervation is a trustworthy criterion and FDS-P and FDS-D were proved to be independent in their structure and their nerve supply. Since the duality of at least human FDS was pointed out (YAMADA, 1986), re-evaluation of FDS became necessary, both onto- and phylogenetically. GRÄFENBERG's result (1906) is a positive evidence for the above-mentioned interpretation. Phylogenetical descriptions available, on the other hand, were based on the premise that FDS is single and homogenous (STRAUS, 1942; HAINES, 1950). This necessitated my own comparative investigations.

FDS of Nycticebus

That FDS has digastric form was already described in *Nycticebus cinereus*, *N. borneanus* and *Loris lydekkerianus*, but without mentioning its innervation and muscle composition (MILLER, 1943; NAYAK, 1933). MURIE and MIVART (1872) did not refer to any division of this muscle in Lemuroidea.

HAINES (1950) described a nerve branch equivalent to RMI in *Felis*, but the presence of RMI had generally been neglected in comparative anatomy. This indifference brought forth above-mentioned assumption that FDS is homogenous, and, vice versa, the premise prevented RMI from being described.

The present work shows two distinct portions in FDS of *Nycticebus*. Findings of both the muscular structure and the innervation are fundamentally identical with those of the human FDS. Two portions of FDS are independent in their muscular structures and innervations (Fig. 7). That RMS supplies FDS-P and is from the branch B (the nerve fasciculus for the deep flexors of the forearm,

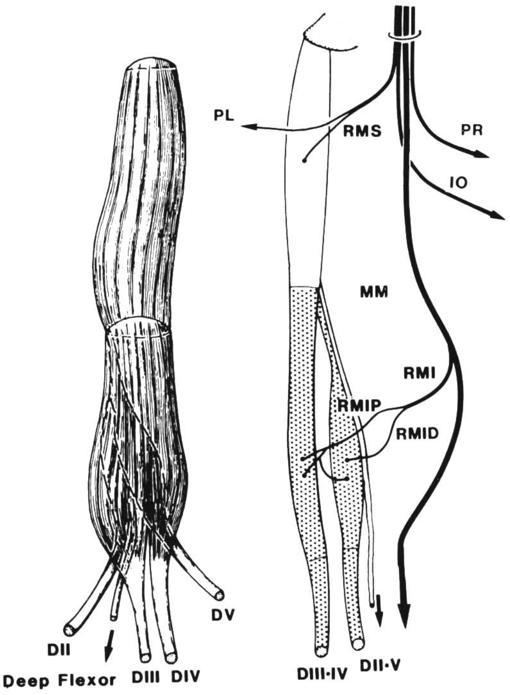

Fig. 7. A schematic presentation of FDS of *Nycticebus*. FDS-P and FDS-D (dotted) are arranged in a proximo-distal sequence. These two components alternate at the intermediate region.

namely the interosseus nerve) implies the close relationship of FDS-P to the deep flexors of the forearm. RMI for FDS-D is from the branch C (the main trunk of the median nerve mainly for the hand muscles). This indicates that FDS-D is related to the intrinsic hand muscles.

Comparison of FDS in *Homo* and *Nycticebus*

Apparently different findings in *Homo* and *Nycticebus* are, on the contrary, proved to be identical when corresponding characters are compared as follows:

1) FDS are made up of two portions in both species, namely FDS-P and FDS-D. In spite of the findings in which the proximal end of the superficial layer of FDS-D in *Homo* reaches the epicondylus medialis of the humerus, covering FDS-P superficially, and those of *Nycticebus* remains at the middle of the forearm together with the deep layers.

2) The innervations of these two portions are independent in both species. In *Nycticebus* FDS-P is innervated by RMS (and RUS), while the branches of RMM and RMI enter the four muscle bellies of FDS-D. In *Homo*, RS distributes to FDS-P, and FDS-D is supplied by RM and RI. RMS plus RUS of *Nycticebus* corresponds to RS of *Homo*, and RMI of *Nycticebus* is equivalent to RM plus RI of *Homo.*

3) The fasciculi consisting the median nerve are clearly distinguished by the perineuria enveloping them. Both in *Homo* and *Nycticebus* the median nerve in the forearm can be classified into three major divisions: A) the Elbow, B) the Interosseus, and C) the Main divisions.

Thus, the findings in *Nycticebus* are fundamentally homologous with those of *Homo.* As a result, following classification of the forearm flexors is established:

1 Elbow matrix
Pronator teres
Flexor carpi radialis
2 Forearm matrix
Proximal portion of Flexor digitorum superficialis
Palmaris longus
Flexor digitorum profundus (Flexor pollicis longus)
Pronator quadratus
3 Intrinsic hand matrix
Distal portion of Flexor digitorum superficialis

Further phylogenetical investigation is expected to examine the validity of this hypothesis. The ulnar innervation of, at least, a part of FDS-P in *Nycticebus* is a matter of debate. A similar case of PL was interpreted by STRAUS (1942) as follows: He recognized three types of PL in mammals. Two of them, intermediate and radial, are innervated by the median nerve and the ulnar one by the ulnar. His conclusion was that these two types are fundamental. These three types of PL are variously represented in certain animals. If this logic is applied to the present subject, we must assume two fundamental muscles, the median and the ulnar FDSs.

On the other hand, HOWELL (1936) was of opinion that the nerve composition of different animal species varies species to species. Whether a muscle is supplied by a certain nerve or by another depends mainly on the course chosen by the fibres in question. To establish convincing interpretation of this will require further investigations.

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Abbreviations

Muscles:

- C-R: condylo-radialis portion of FDP
- C-U: condylo-ulnaris portion of FDP
- D II, D III, D IV and D V: tendon of insertion to the second, the third, the fourth and the fifth digits (FDS-D)
- FCR: flexor carpi radialis
- FCU: flexor carpi ulnaris
- FDBG: flexor digitorum brevis (of Gräfenberg)
- FDP: flexor digitorum profundus
- FDS: flexor digitorum superficialis;
- FDSG: flexor digitorum sublimis (of Gräfenberg)
- FDS-D: distal portion of FDS
- FDS-P: proximal portion of FDS
- IZ: intermediate zone of FDS
- PL: palmaris longus
- PQ: pronator quadratus
- PT: pronator teres
- R: radialis portion of FDP
- U: ulnaris portion of FDP.

Nerves:

to FDS

- from the median nerve
- RMS(MS): superior ramus (FDS-P)
- RMM: middle ramus (FDS-D)
- RMI(MI): inferior ramus (FDS-D)
- RMIP: proximal division of RMI (FDS-D)
- RMID: distal division of RMI (FDS-D)

from the ulnar nerve
RUS: superior ramus (FDS-P)
Thenar: Thenar sensory branch from the median nerve divisions of the median nerve
A: elbow division
B: forearm division
C: intrinsic hand division (or the main trunk)