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1. Introduction

We routinely use our hands in numerous daily tasks, such as typing and manipulating objects. After having learned a specific task, most of us act without realizing the complexity of the required motor control. Fine hand motor skills require coordinated movements of fingers relative to each other, but individual fingers can only to a limited extent move or exert force independently. When asked to move one finger, involuntary movements of neighboring fingers are commonly observed. The same is true for the voluntary exertion of force by one finger. This limited finger independency has been termed enslaving (Zatsiorsky et al., 1998). To understand finger force and movement enslaving, all structures that are involved (from the motor cortex to the muscles) need to be considered. Several features of the central and peripheral nervous system have been described constraining the independent control of fingers, such as the spatial overlap of motor cortex areas for movements of different fingers, as well as anatomical characteristics of the musculoskeletal system, such as connective tissue linkages between muscle bellies and tendons (see review by Van Duinen and Gandevia, 2011). Despite many years of research in this area, the relative importance of neural and musculoskeletal factors for the finger enslaving phenomenon is still under debate.

In the summer of 2016, we organized a symposium at the XXI Congress of the International Society of Electromyography and Kinesiology (ISEK, see https://isek.org/past-conferences/) entitled “Muscle mechanics and neural control determining fine hand-motor tasks”. This symposium brought together scientific contributions from the disciplines of biomechanics, neuroscience, and orthopedics, covering different determinants of hand motor control, including both basic science and clinical studies. This special issue is based on the talks and discussions of the symposium as well as on additional contributions to the topic of hand motor control.

Before presenting the content of the special issue, we briefly discuss the anatomy of the extrinsic finger muscles to illustrate their complexity.

2. Complex anatomy of extrinsic muscles actuating the fingers

In advanced prosthetic hands, each finger is moved by a separate actuator (so called independently motorized digits). Also in musculoskeletal models of the human hand (e.g., Mirakhorlo et al., 2016), fingers are controlled by separate muscle-tendon units (Fig. 1; showing only one extrinsic finger muscle). However, the human system actuating finger movements is built differently. Next to the above described connections between the tendons of the extrinsic finger muscles, most extensively described for the m. extensor digitorum communis (EDC) (von Schroeder and Botte, 2001), the four tendons of these muscles are not linked in series with four separate, independent muscle bellies. At the origin of these muscles, the muscle fibers form an inseparable muscle belly, while distinct muscle heads can be identified only near the distal musculotendinous junction. It has been shown for a muscle in the rat with similar morphology, the m. extensor digitorum longus, that if only one muscle head is lengthened, force is transmitted between the different muscle heads via their connective tissue interface (Huijing et al., 1998; Maas and Huijing, 2005; Maas et al., 2003).

The m. flexor digitorum superficialis (FDS) (or sublimis) has a far more complex structure than the EDC and the m. flexor digitorum profundus, maybe the most complex in our body. In the early 20th century, two German anatomists (Frohse and Fränkel, 1908) provided a detailed drawing (Fig. 2) and description of FDS morphology. More recently, we studied the morphology of nine FDS muscles obtained from human cadavers (unpublished). In this study the description of Frohse and Fränkel was confirmed. In addition, some variations were found (see Fig. 3) that have been reported earlier (Ohtani, 1979). The main implications of this architecture are that for every finger a unique set of FDS muscle fibers is present, but that some muscle fibers act *in series* with multiple (2–4) distal FDS tendons. Activating those fibers will inevitably lead to forces exerted onto more than one finger. Based on the morphology of the extrinsic finger muscles, it can be considered quite surprising that we can independently move our fingers to a large degree (van den Noort et al., 2016). At least, it is clear that this will require a more complicated control paradigm than used, for instance, in prosthetic hands. From a biological-evolutionary perspective, some advantages of such a morphology might be expected, but these advantages have not yet been identified.

3. Special issue content

Besides four papers from the speakers at the symposium, the special issue includes three contributions from other authors. A variety of topics is presented, ranging from the neuromechanics of finger independence (May and Keir, in press; Van Beek et al., 2017a), the effects of training or learning finger force modulation tasks (Godde et al., in press; Yoshitake et al., in press), and the pathophysiology of carpal tunnel syndrome (Grandy

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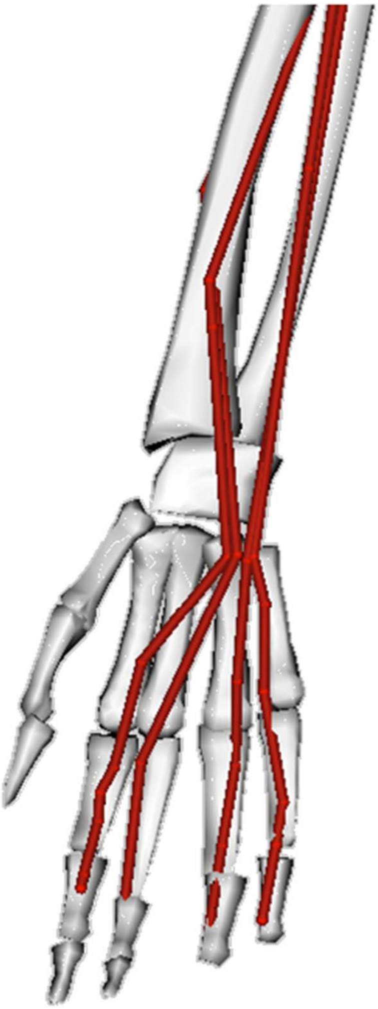

Fig. 1. Flexor digitorum superficialis muscle as represented in an OpenSim model of the hand and wrist of which a preliminary version was presented recently (Mirakhorlo et al., 2017b).

et al., 2017; Mansiz-Kaplan et al., 2017; Schrier and Amadio, in press).

In contrast to many previous studies on finger enslaving, the experiments presented in this special issue combine kinematic or kinetic measurements with assessment of activity patterns, measured with electromyography (EMG), of the different regions of FDS and EDC associated with each finger (May and Keir, in press; Van Beek et al., 2017a). For some conditions, enslaving effects were independent of muscle activity patterns. This was interpreted as evidence for a critical role of mechanical connections between muscle-tendon structures. For other conditions, however, a clear correlation between finger enslaving and activity of the corresponding muscle region was observed. This was interpreted as evidence for a predominantly neural origin of enslaving. From these and other recent studies on finger enslaving (Mirakhorlo et al., 2017a; Sanei and Keir, 2013; van den Noort et al., 2016), the view emerges that both neural and musculoskeletal characteristics impose constraints on finger motor control, but that their relative importance depends on the specific conditions of the task.

Two papers of this special issue investigate effects of training a finger force task to improve fine hand motor performance, for example in elderly. There are only a few studies that have investigated the effects of aging on finger enslaving. During static finger pressing tasks, an increased finger force independency with aging has been reported (Kapur et al., 2010; Oliveira et al., 2008; Shinohara et al., 2003). In contrast, recently a decreased finger force and movement independency in elderly during single finger movement tasks was found (Mirakhorlo et al., submitted for publication; Van Beek et al., 2017b). Yoshitake et al. (in press) present a robotic system that can be used to apply random force perturbations to a single finger with the goal to improve finger postural steadiness and hand dexterity. Testing this in young adults, two-weeks of this training reduced fluctuations of index finger metacarpophalangeal joint angle and increased the score on a pegboard test, while this was not found in the control groups. In addition, improvements in finger steadiness were strongly correlated with improvements in hand dexterity. In the study by Godde et al. (in press), effects of learning a force tracking task on young and older adults are compared. Besides assessing motor performance (accuracy and variability), functional magnetic resonance imaging was used to assess activities in the brain areas involved with motor learning. Performance improved similarly in both groups, which was associated with decreased activity in certain brain areas. As a result of this, the brain activation pattern (assessed using functional MRI) of the older adults approached the pattern of the young adults before training. An absence of age differences in the training improvement slopes is explained in terms of compensatory strategies in older adults (Godde et al., in press).

Many pathological conditions and traumata affect fine hand motor skills, including the frequently encountered carpal tunnel syndrome (CTS). CTS is the result of an increased pressure in the carpal tunnel compressing the median nerve (Schrier and Amadio, in press). In some cases, the symptoms appear to be spread outside the median nerve territory. Mansiz-Kaplan et al. (2017) hypothesize that in patients with such extramedian spreading, the cross-sectional area of the ulnar nerve would be higher than in patients without extramedian symptoms. However, no differences between groups for neither ulnar nor median nerves were found, suggesting that these extramedian symptoms are not related to peripheral nerve

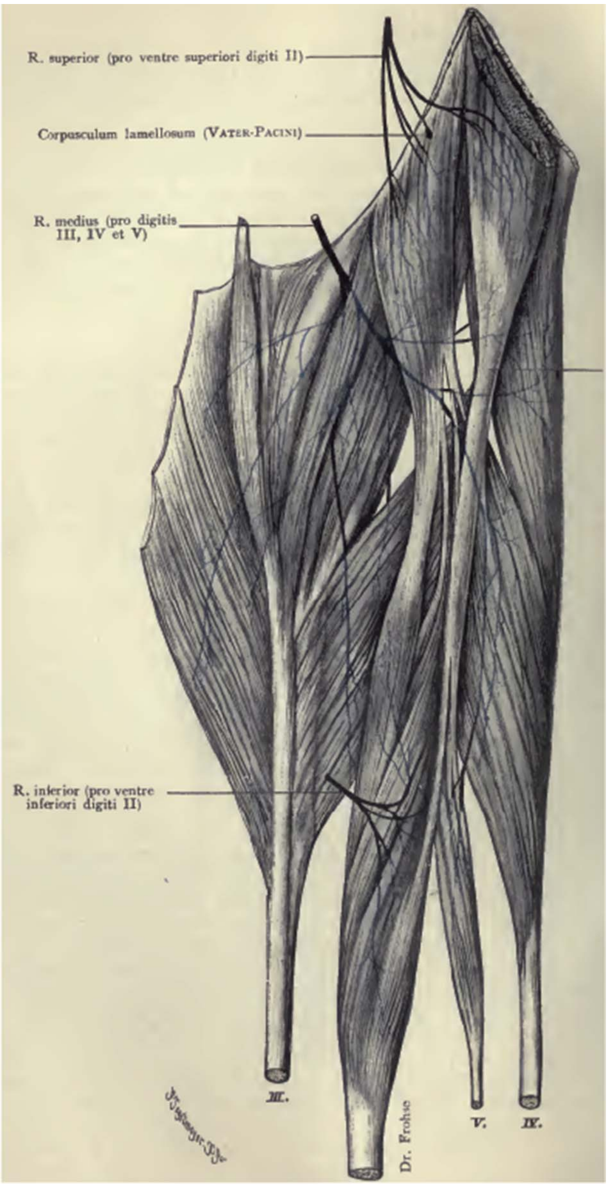

Fig. 2. Drawing of m. flexor digitorum superficialis (Fig. 60 in Frohse and Fränkel, 1908).

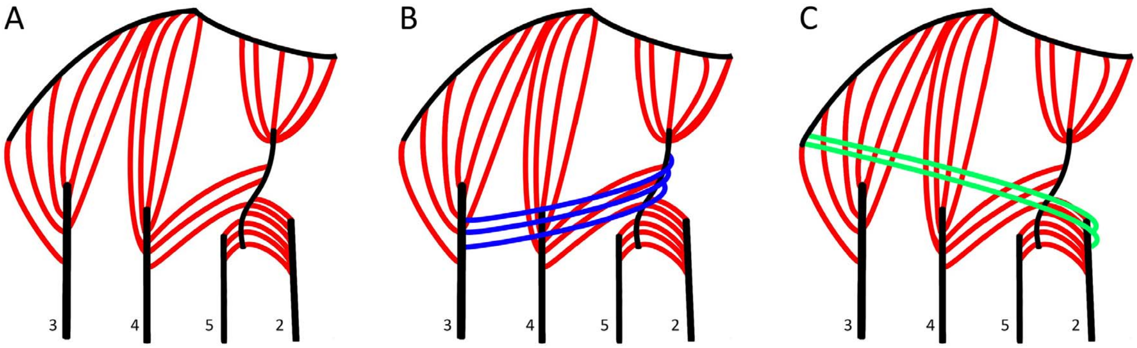

Fig. 3. Schematic drawings of variations in m. flexor digitorum superficialis (FDS) morphology. The tendons are numbered after their insertions on the digits of the hand. The number of red lines represent the approximate volume of the different heads. In vivo, a superficial layer (muscle fibers linked to digit 2 and 5) and a deep layer (muscle fibers linked to digit 3 and 4) can be distinguished. Here, a folded out view is shown. (A) In all muscles investigated, muscle fibers of a proximally located muscle belly insert on an intermediate tendon that is connected in series with muscle bellies inserting on the second, fourth and fifth fingers. This structure had been defined as type II (Ohtani, 1979). (B) In five of the nine muscles, an additional fiber bundle was running between the intermediate tendon and the distal tendon inserting on the third finger, which has been defined as type III. (C) In also five muscles, in two cases in combination with the bundle shown in B, a fiber bundle between the tendon of origin associated with the third finger and the tendon of insertion of the second finger was found.

characteristics. Schrier and Amadio (in press) focus on a different structure that appears to be involved in the etiology of CTS, the subsynovial connective tissue (SSCT). This tissue connects the different tendons and nerve, imposing some constraints on differential tendon movement. Normally, these constraints do not impair hand and finger movements. However, it is not clear whether the SSCT provides a sufficiently strong mechanical linkage between tendons to cause finger enslaving, which is not discussed in the review paper of Schrier and Amadio. In most CTS patients, fibrosis of the SSCT is observed. This results in stiffer connections between the tendons and the nerve, limiting differential tendon and nerve movements. The formation of fibrotic tissue may also increase carpal tunnel pressure and, thereby, play a critical role in the pathophysiology of CTS, as proposed by Schrier and Amadio (in press). A similar chain of events and vicious cycle, but then leading to scar tissue formation between muscle heads of extrinsic finger muscles, has been proposed earlier as a mechanism for the development of muscle disorders in the forearm associated with repetitive work (Maas and Huijing, 2005). The effects of CTS on finger motor control is the topic of a third paper on CTS in this special issue (Grandy et al., 2017). For a task in which subjects had to stop a suddenly sliding plate with their index finger, longer latencies of muscle activity and finger force responses were found in the CTS patients. Several disruptions of peripheral and central sensorimotor circuits of the nervous system are discussed as possible explanations for these findings.

From the above, it is clear that the contribution of the different constraints of finger motor control varies with the specific task requirements. Because it is impossible to fully exclude a certain type of constraint (anatomical characteristics of the musculoskeletal system or features of the central and peripheral nervous system) using an experimental approach, combining different sources of data (such as finger kinetics and kinematics, EMG derived muscle activation patterns) with inverse and forward dynamical modeling may provide a means to distinguish between the different factors involved. For this, first a model of the hand and wrist is needed that includes the complex anatomy of the extrinsic and intrinsic muscle apparatus, with which the mechanical constraints can be separated from the neural factors. To this end, combining EMG with modeling results, or even using EMG as a partial control parameter in inverse modeling, appears to be essential. The added value of EMG would be considerable, providing that muscle activation data are recorded at a sufficient level of specificity regarding the muscles' anatomy. An approach in which EMG is recorded with multichannel arrays, such as presented in this special issue (Van Beek et al., 2017a), in combination with source localization methods (e.g., Urbanek and van der Smagt, 2016) might be a necessary next step.

Fine hand motor skills are critical for many activities in daily life. Their deterioration has major consequences. Therefore, it essential that we improve our understanding of hand and finger motor control in health, but certainly also in cases in which such skills are deteriorated such as with aging, following stroke or CTS. Such knowledge will help to design tailored rehabilitation strategies and treatment plans to improve or restore normal manual dexterity.

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