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**FINGER INTER-DEPENDENCE: LINKING THE KINETIC AND KINEMATIC
VARIABLES**

A Thesis in
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by
Sun Wook Kim

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The thesis of Sun Wook Kim was reviewed and approved* by the following:

Mark L. Latash
Distinguished Professor of Kinesiology
Thesis Advisor

Vladimir M. Zatsiorsky
Professor of Kinesiology

Stephen J. Piazza
Associate Professor of Kinesiology

John Challis
Professor of Kinesiology
Graduate Program Director

*Signatures are on file in the Graduate School

ABSTRACT

The main goal of this dissertation has been to study the inter-dependence between actions of the fingers of the human hand. Earlier studies quantified finger inter-dependence in either isometric conditions using force production tasks, or in nearly isotonic conditions using finger movement tasks. We addressed a common situation when a person holds an object using a subset of the digits of the hand and moves one of the digits. Participants moved one of the fingers (task finger) of the right hand trying to follow a cyclic, ramp-like flexion-extension template at different frequencies. The other fingers (non-task fingers) were restricted from moving; their fingertip pressing forces were recorded and analyzed. The index finger motion caused the smallest force production by the non-task fingers. Larger forces were produced by the neighbors of the task finger; these forces showed strong modulation over the range of motion of the task finger. The forces were higher during the flexion phase of the movement cycle as compared to the extension phase. The index of enslaving expressed in N/rad depended on the movement speed and was higher when the task finger moved through the more flexed postures. These observations suggest an important role of central, neural mechanisms in the patterns of finger interdependence. They also suggest that methods of analysis of finger coordination based on an assumption of universal matrices of finger interdependence should consider the specific features of the studied tasks.

Key words:

Hand Finger Force production Enslaving Kinetics Kinematics

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CHAPTER 1. Introduction

1.1 Problem Statement

The human hand is an excellent form of versatile architecture that can accomplish numerous tasks with effortless execution in everyday life. Many tasks in our daily living require seemingly simple actions, such as pointing, picking up objects, and buttoning shirts. In addition, we partake in more complex actions as well, such as drawing, sculpting, eating with chopsticks, and playing musical instruments. Although they require different levels of intensity, all of these tasks are common human tasks and all require coordinating the action of the digits in the hand.

Although the human hand is quite capable, the skilled manual activities that require the control precise and the interaction of individual finger forces and movements can be difficult for even dexterous hands, especially in terms of individuated finger movements. For example, when a person tries to move a single finger of the hand or to press down with one finger, other fingers of the hand move or generate force (Kilbreath and Gandevia, 1994; Kinoshita, Murase, and Bandou, 1996; Lang and Schieber, 2004; Li, Dun, Harkness, and Brininger, 2004; Li, Latash, and Zatsiorsky, 1998). This phenomenon has been referred to as enslaving (Li et al. 1998; Zatsiorsky, Li, and Latash, 2000) or lack of individuation (Lang and Schieber, 2003; Schieber and Santello, 2004). This phenomenon has also been analyzed by kinematic approaches that study the movement of individual digits (Fish and Soechting, 1992; Flanders and Soechting, 1992; Fleckenstein et al. 1992; Hager-Ross and Schieber, 2000; Kimura and Vanderwolf, 1970; Schieber, 1991, 1995).

Enslaving has been discussed as a consequence of both peripheral and neural

factors. In particular, the presence of multi-tendon, multi-digit muscles and of passive connective tissue links between adjacent fingers can be expected to contribute to enslaving (Kilbreath and Gandevia, 1994; Leijnse et al. 1993). In addition, projections of fingers in the primary motor cortex show substantial overlaps (Schieber, 1999; Schieber and Hibbard, 1993; Schieber and Santello, 2004), suggesting a neural contribution to enslaving. Besides, enslaving of a comparable magnitude has been documented in experiments when the participants produced flexion forces by pressing with their proximal phalanges (Latash, Li, Danion, and Zatsiorsky, 2002). Primary agonists of this action are intrinsic hand muscles that are digit specific. Hence, these findings support the idea of a central neural origin of the enslaving.

Enslaving has been usually characterized using percentages of maximal forces produced by non-instructed fingers when one finger of the hand (the “task finger” or the “master finger”) was instructed to produce maximal force (maximal voluntary contraction, MVC) (Li et al. 1998; Zatsiorsky, Li, and Latash, 1998, 2000). In other studies enslaving was quantified during submaximal force production by master fingers (Latash, Scholz, Danion, and Schöner, 2001, 2002; Scholz, Danion, Latash, and Schöner, 2002). These studies have revealed, in particular, that unintended forces show nearly linear changes with the force produced by the master finger. This finding has allowed for the use of matrices of enslaving indices for analysis finger coordination over a variety of tasks and force magnitudes (reviewed in Latash, Scholz, and Schöner, 2002, 2007). The force enslaving effects have been reported to be large, nearly symmetrical, non-additive, and dependent on the distance between fingers (Zatsiorsky et al. 1998). Other common kinematic approaches study the movement of individual digits (Fish and Soechting 1992;

Flanders and Soechting, 1992; Fleckenstein et al. 1992; Hager-Ross and Schieber, 2000; Kimura and Vanderwolf, 1970; Li et al. 2004; Schieber, 1991, 1995). When a subject performs flexion and extension of one digit, the simultaneous movement of the remaining digits was evaluated, and the results show that the ability for individual digit movement was limited and movements of instructed digits were accompanied by unintended movement in the other digits. This observation suggests that individuated finger movements are produced, not by independent sets of muscles acting on each digit, but by the activity of several muscles, many of which act on more than one digit (Schieber, 1993; Schieber et al. 1997; Serlin and Schieber, 1993). In particular, the thumb and index finger are the most independent digits, while the ring and middle fingers are the least independent ones (Hager-Ross and Schieber, 2000). In other studies, the enslaving characteristics of multiple fingers was quantified during isolated flexion of the distal interphalangeal joints (DIP). Studying the fingers independence of the DIP joint movement has demonstrated that enslaving effects are mainly generated in neighboring fingers and among the compartments of the FDP (Li et al. 2004). Enslaving matrices have also been addressed as finger interconnection matrices and have been used for the computational modeling of finger interactions over a variety of subject subpopulations and tasks (Gao, Li, Li, Latash, and Zatsiorsky, 2003; Zatsiorsky et al. 1998).

1.2 Research Question

In some everyday actions, an object is grasped with only a subset of fingers, for example in the precision grip with the thumb and one of the fingers or in the tripod grip, while other fingers are free to perform other movements. In such actions, the intended

force production by the grasping digits may lead to unintended motion of other digits of the hand, while motion of free fingers may lead to changes in the grasping force.

Until now, studies have only tried to quantify the independence/interdependence of fingers using either kinetic or kinematic variables. This study presents a novel approach to extend previous studies that link to the two classes of variables. The main purpose of the current study has been to provide quantitative estimates of the enslaving effects between the kinematic and kinetic variables in the individual digit forces. In particular, we were interested in the following questions:

- (1) Does the motion of a finger in flexion and in extension bring about symmetrical changes in forces produced by other (non-task) fingers of the hand?
- (2) Are quantitative indices of enslaving similar over the range of flexion and extension motion of the instructed finger?

This study investigates the dependence between voluntary motion of a finger and pressing forces produced by the tips of other fingers of the hand. To answer the first question, we quantified the unintended finger force production by three fingers of the hand during the instructed flexion-extension cyclic movements of the fourth finger at different frequencies. To address the other question, indices of enslaving were compared over different phase intervals within the flexion-extension cycle and across different movement frequencies (different movement speeds).

This line of research will contribute to the current understating of the hand control in general, as well as to modeling relations between the kinematics and kinetics during

hand action with possible implications to other areas, such as changes in hand function with age and neurological disorders, hand rehabilitation, and prosthetics.

Chapter 2. Background and Literature Review

2.1 Motor Redundancy/Abundance Problems

Human movement coordination is produced by a complex system that interacts and integrates multiple segments, approximately hundreds of joints, thousands of muscles, and numerous neural systems, which allow us to engage with our environment adequately and with flexibility. For example, when a person touches his/her nose with the tip of his/her right index finger, or even tries to move his/her arm without losing contact between the finger and nose, he/she can perform this movement using a wide variety of individual joint angle trajectory patterns, which produce a certain, desired trajectory of the endpoint of the limb. The redundancy problem is similar to mathematically solving a system of equations where the number of equations describing the system behavior is smaller than the number of unknown variables in the equation. The central nervous system (CNS) seems to be always confronted with the problem of selecting a solution from the redundant degrees of freedom. Thus the questions arise: how does the CNS choose a solution from the infinite number of seemingly equal possibilities? This problem of motor redundancy was introduced by Nikolai Bernstein, a Russian physiologist, (Bernstein, 1947, 1967) and has been termed *the Problem of Motor Redundancy* or *Bernstein's Problem* (Turvey, 1990; Latash, 1996)

Redundancy problems at each analysis of the human voluntary movement system are characterized by involvement of a large number of elements contributing to performance rather than only those absolutely necessary for performing a task. In the earlier example of a person touching his/her nose, the trajectory of the endpoint of the finger does not define the unique solution for the joint angle trajectories (the problem of

inverse kinematics, Mussa-Ivaldi et al. 1989) and a unique pattern of joint torque that would ensure a certain trajectory of the end point (the problem of inverse dynamics, Atkeson 1989). Similar problems may be formulated at other levels of the human system for movement production. A value of joint torque does not define a unique combination of activation levels of muscles crossing the joint, and many patterns of motor unit recruitment can produce a certain level of activation of a given muscle (cf. Latash 1996).

The fact that humans can easily perform voluntary movements shows that the CNS is able to organize apparently redundant sets of effectors, such as muscles, joints, digits, and limbs, to perform tasks that impose relatively few constraints. There have been two major approaches to solve the motor redundancy problem. The first approach follows the traditional attempts by Bernstein's formulation that a unique solution is selected by the CNS each time it faces a redundancy problem. This is commonly done by adding constraints to the system or by selecting a cost function and optimizing its value (reviewed in Latash, 1993; Rosenbaum et al. 1995). The second approach follows the traditions of Gelfand and Tsetlin (1967), who state that the CNS does not eliminate the DOF and does not select a unique solution but rather uses the whole available DOFs to facilitate families of solutions that are equally successful for solving the task. Later Gelfand and Latash (1998) suggested "*The principle of abundance*," which states that the apparently redundant DOFs always contributes to a task, rather than apparently redundant DOFs being eliminated, which allows the controller to ensure both stability and flexibility in the performance of the motor system (Latash et al. 2004, Gelfand and Latash, 2002).

2.2 Motor Synergies

The notion of synergy originated from Hughlings Jackson (1899), Babinski (1899), and Sherrington (1910). Hughlings Jackson (1988) wrote “the CNS knows nothing about muscles, it only knows movements.” In his view, the body is controlled by hardwired pathways from the brain to individual muscles. The notion of “muscle synergy” was developed by Babinski (1899), who studied the coordinated activity of muscles united into groups or “synergies,” which the controller activates simultaneously. Following Babinski, Sherrington (1910) assumed that muscle synergies were organized in the spinal cord and that reflex arc was the basis of synergic muscle groupings, which views synergies as an anatomical morphological concept (Vinjamuri, 2004). His concept of synergies is linked to low-level neural elements (cf. reflex arcs), only one step away from the muscle. An alternative view of synergies that stresses higher-level neural processes was developed by Bernstein (1967) who developed functional and operational concepts for synergies that were counter to Sherrington’s anatomical morphological concept. Bernstein defined a synergy as a higher-level organizing principal of movements, which in turn causes CNS to group several variables into functional synergies, while each synergy is controlled by a single central command. Bernstein proposed that the mechanical DOF problem is partly solved by muscle linkages or synergies and also suggested that the control system was built on a hierarchical principle (Bernstein, 1947, 1967; Gelfand and Latash, 2002; Turvey, 1990).

Gelfand and Tsetlin (1966) formulated the idea of synergy by proposing two principles of motor control: the principle of non-individualized control and the principle of minimal interaction. The principle of non-individualized control states that the

elements of complex systems are divided into task-specific, or intention-specific, structural units, commonly termed “synergies” in the contemporary literature. They also introduced the principle of minimal interaction (PMI), which states that the interaction among elements at a lower level of a hierarchy is organized in such a way that the external input to each of the elements is minimized (Gelfand and Tsetlin 1966; cf. Latash et al. 2004). Later, Gelfand and Latash (1998) reformulated this principle and referred it to two salient features of synergies, stable sharing patterns and error compensation. These features reflect the fact that elements within a synergy interact in such a way that each of them tries to maintain a stable performance (sharing pattern) while at the same time maintaining the overall functional output at a desired level such that no intervention from the higher level of the hierarchy are needed, even when one or more of the elements changes their contribution (cf. Latash et al, 2004)

Hand function is a very attractive example for addressing the problem of motor redundancy. As mentioned above, motor synergies have been described using two features: sharing patterns and error compensation. For example, a simple synergy occurs when two fingers press in parallel on an object to produce a certain level of total force; each finger contributes a percentage of the total force, which would be termed the sharing pattern (figure 2.1). If one finger accidentally produces a higher force, the other finger may do one of three scenarios: 1) do nothing—the two fingers act completely independently of each other (do not form a synergy), 2) increase its force proportionally to maintain the sharing pattern and change the force in the same direction (positive co-variation, potentially increasing the deviation of the total force from its planned level, no synergy between two fingers), or 3) decrease its force to keep the total force relatively

unchanged (negative force co-variation, force stabilizing synergy) (Latash et al. 2007). The synergy shown follow the third scenario: when a finger produces a higher force, then the other finger is more likely to produce less force so that the relation between the two finger forces reduces the error in the total force. In other words, the negative covariation of finger forces can be interpreted as a force-stabilizing synergy.

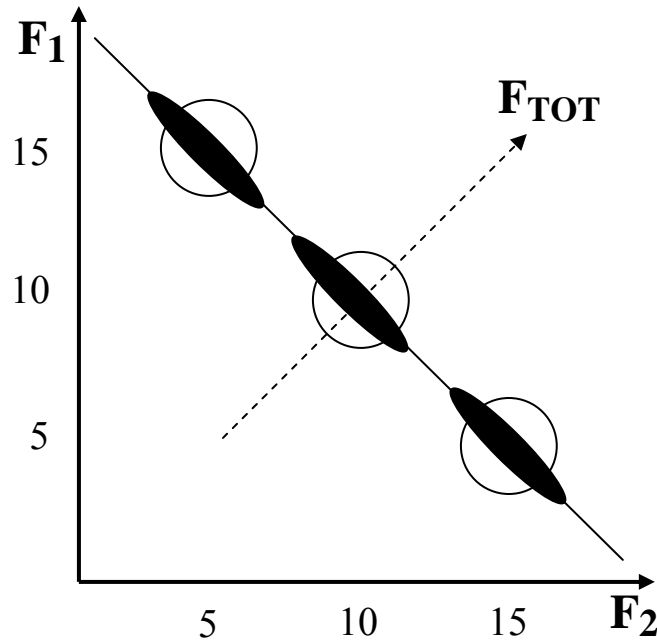


Figure 2.1 An examples of synergies during a two finger pressing task. Synergies can be characterized by sharing and error compensation. In this illustration, two fingers must press parallel to produce a total force of 20N. Three sharing patterns are illustrated: 5:15N, 10:10N, and 15:5 N. There are three sharing pattern (circles) that solve this problem. For each sharing pattern, there is a cloud of data points (shown as a black ellipse) that can change shape and either lead (the elliptical cloud, bold line) or not lead (the spherical clouds) to error compensation. This example indicates that synergies must be characterized not only by sharing patterns but also by patterns of co-variation reflecting the feature of stability/flexibility (Latash, 2007).

Apparently, a very narrow elliptical (*solid black*) cloud of data points on a force-force plane would correspond to a very strong synergy stabilizing the total force because force deviations of one finger would be nearly perfectly matched by changes in the force of the

other finger in the opposite direction in order to keep the desired total force at the required level; a wider ellipse would correspond to a weaker synergy (figure 2.1).

Numerous concepts of synergy have been discussed and have appeared in the literature. We will accept a definition that a synergy is a neural organization of a multi-element system that organizes the sharing of a task among a set of elemental variables and ensures covariation among the elemental variables in order to stabilize important performance variables (Latash et al. 2007).

2.3 The Anatomy and Biomechanics of the Hand

The human hand is a complex mechanical system. It consists of 27 bones and the 29 muscles located within the hand and forearm that control its movement. A complicated feedback system is also required to control the 21 degrees of freedom of movement in the hand and wrist simultaneously (Jones and Lederman, 2006). For humans, the versatile hand is used both for grasping objects and for individuated finger movements. Grasping objects of all shapes and sizes involves the entire hand, which needs the linked action of multiple fingers simultaneously. On the other hand, the individuated finger movements are needed for a large variety of creative and practical endeavors such as playing a musical instruments. The hands are also capable of very complex manipulative motions, such as those involved in skilled activities like microsurgery, watch-making, and playing musical instruments.

The human hand is defined as the region of the upper limb that lies distal to the wrist joint, which has eight carpal bones, the hand proper, which has five metacarpal bones, and the five digits. All five digits are made up of a collection of many of different

components, including bones, muscles, ligaments, tendons, fascia, nerves, and vascular structures, that are all encapsulated by skin. Overall, the hand can be divided into three sub-systems: the wrist, the metacarpus, and the digits.

2.3.1 Skeletal System:

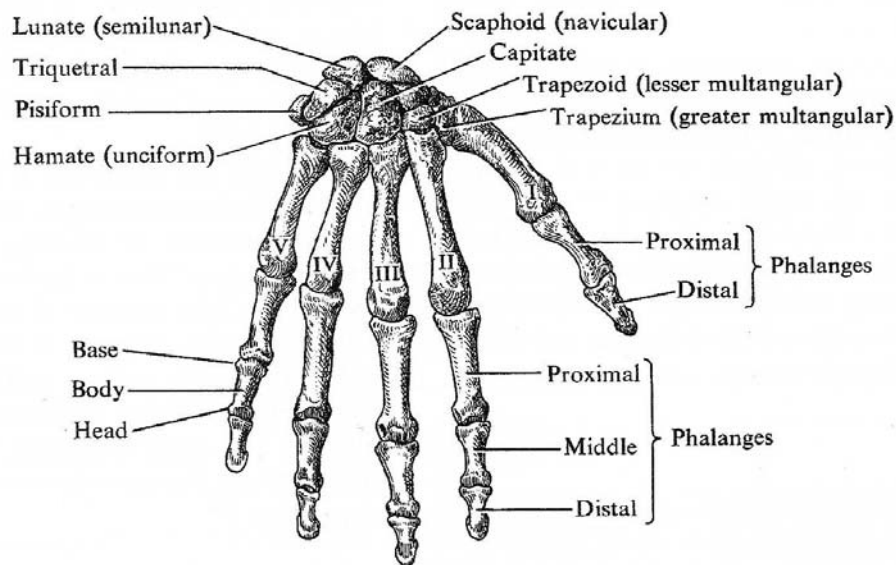
2.3.1.1 Bones of the Hand, Wrist, and Forearm

The bones are the structural basis of the hand, supporting the muscles and tendons and giving form to the hand itself. They are the structure of the articulated body with ligaments binding their ends together to guide their motion, thus preventing dislocation and excessive movement.

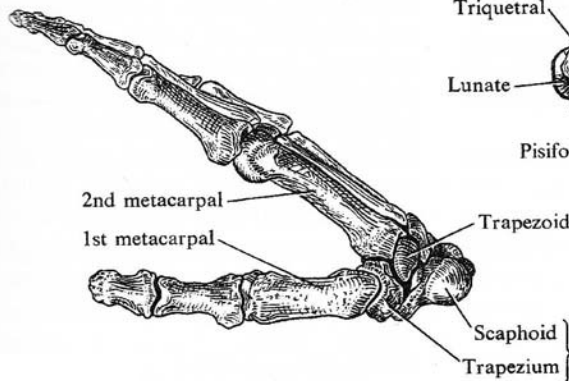
A normal hand has 27 bones divided into the three categories: the carpal bones (8), the metacarpal bones (5), and phalanges (14). The eight carpal, or wrist, bones are arranged in two rows of four. The bones of the proximal row are the scaphoid, lunate, triquetrum, and pisiform bones (seen lateral to medial), which connect to the two forearm bones, the radius (thumb side) and the ulna (little finger side). The distal row of bones are the trapezium, trapezoid, capitate, and hamate bones (seen lateral to medial), which join with the five metacarpal bones via the carpometacarpal (CMC) joint that make up the palm. All of these bones are independent of each other, but they are articulate and act as a solid block, making a progressive transition between the two wrist bones (radius and ulna) and the five metacarpal bones. Each digit has three phalanges (proximal, middle, and distal) while the thumb has just two. The metacarpophalangeal (MCP) joint connects the metacarpal bones and the proximal phalanges, the proximal interphalangeal (PIP) joint connects the the proximal and middle phalanges, and the distal interphalangeal

(DIP) joint connects the middle and distal phalanges. The thumb, having only two phalanges, has only one interphalangeal (IP) joint. Figure 2.2 shows an image of the bones and joints of the hand with their names as well as abbreviations used throughout the rest of this thesis. The digits are typically referred to by the numbers I - V for the thumb, index, middle, ring, and little fingers respectively (Drake, 2005; Jones et al. 2007).

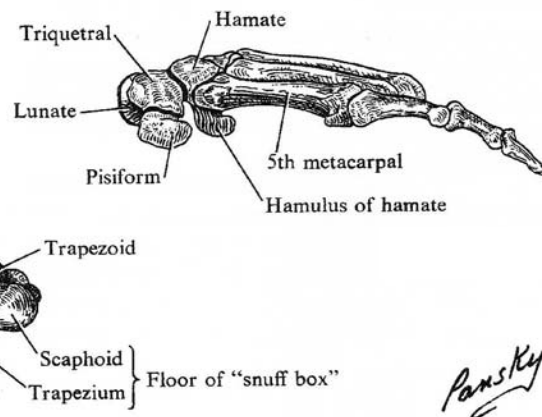
A. DORSAL VIEW



B. RADIAL VIEW



C. ULNAR VIEW



Pansky

Figure 2.2 Bones and joints of the right hand and wrist. Digits I to V represent the thumb, index, middle, and little finger, respectively. A) Dorsal, B) Radial, C) Ulnar views of hand bone.

2.3.1.2 Joints of the Hand and Wrist

The hand joints are formed by a large set of movable articulations between the bones in the hand. There are 20 joints in the hand that are divided into four categories: wrist joints, intercarpal joints, CMC joints, MCP joints, and IP joints.

The wrist joint, also termed the radiocarpal, is formed by the large articulated concave surface of the distal radius and the proximal carpal row, scaphoid, lunate, and triquetrum and is classified as a condyloid articulation. The condyloid joint provides a degree of freedom (DOF) that allows for flexion/extension and abduction/adduction (also termed radial and ulnar deviation).

The intercarpal joint is formed by the articulations of the proximal and distal rows of the wrist bones and is classified as an arthrodiarthral joint that only allows gliding motions between the bones. However, the mid-carpal joint where the two rows move with respect to one another is a combination of gliding joints and an articular cavity that creates a three-DOF, ball-and-socket type connection. Intercarpal motion is primarily in flexion/extension, but unlike the other carpal interactions, it only allows a very slight amount of rotation. The CMC joint is found between the metacarpals and the related distal row of carpal bones. The I, II, and III (presenting thumb, index, and middle fingers, respectively) metacarpal bones are articulated with the trapezium, trapezoid, and capitate respectively, while the IV and V (presenting ring and little fingers, respectively) metacarpal bones are fixed on the hamate due to the configuration of carpal bones. The joints between the carpals and the II-V metacarpal bones are all arthrodiarthral, which allow a small amount of gliding motion, increasing from the index to the little finger. However, the first CMC joint of thumb has unique saddle joints that are quite different from the

other fingers (II-V). These saddle joints provide two DOFs that allow for flexion/extension in the palm plane, abduction/adduction in the perpendicular palm plane, and opposition/reposition. The geometry of the thumb's CMC joint provides opposition/reposition, one of the primary factors that allows for a wide variety of grasps. Figure 2.3 shows the movements of the thumb. The MCP joints, also known as the knuckles, exist where the metacarpals meet the proximal phalanges of the digits. For digits II-V, these articulations are condyloid, which allow for flexion/extension, abduction/adduction (medical-lateral deviation), and circumduction (a slight degree of axial rotation). The abduction/adduction movement is in either direction with less ability for flexion than for extension. The first MCP joint is more of a ginglymoid, or hinge, joint that only allows for flexion and extension. IP joints articulation are the final joints, which are between the adjacent phalanges in the hand. The IP joints, along with the thumb MP joint, are all hinge joints that only allow for flexion and extension. The capability for flexion in these joints is much greater than extension. Digits II-V have two separate articulations: the proximal (PIP) and distal (DIP) interphalangeal joints, while the thumb has only one IP joint. The DIP joints have structure similar to PIP but are less stable and allow for some hyperextension.

Table 2.1 The Joints of the Hand and Wrist (Drake, 2005)

JOINT(s)	TYPE	DOF	MOVEMENT
Distal radioulnar	Pivot	1	Pronation/Supination
Radiocarpal	Condyloid	2	Flexion/Extension Abduction/Adduction Circumduction
Intercarpal	Plane/Gliding	Non-axial	Gliding Motion
Carpometacarpal (Thumb)	Saddle	2	Flexion/Extension Abduction/Adduction Opposition/Reposition
Carpometacarpal (Fingers)	Ellipsoid	2	Flexion/Extension Abduction/Adduction
Metacarpophalangeal (MCP)	Ellipsoid	2	Flexion/Extension Abduction/Adduction Circumduction
Interphalangeal (IP, PIP, DIP)	Hinge	1	Flexion/Extension

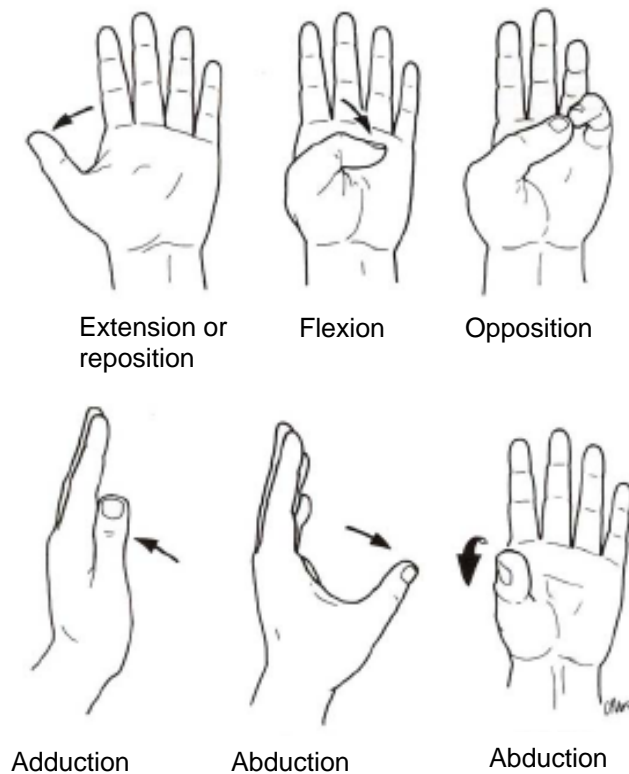


Figure 2.3 Movement of the Thumb (Smith, 2005)

2.2.3 Muscles of the Hand, Wrist, and Forearm

The forearm, wrist, and hand have 29 muscles that control hand movement. These muscles produce forces that are transmitted via tendons to the bones to generate motion. Although some of these muscles are divided into distinct parts with separate tendons, the flexor digitorum profundus (FDP) connects tendons to the distal phalanx of all four fingers (Jones and Lederman, 2006). If the subdivisions of multi-tendon muscles are counted separately, the number of muscles controlling the hand increases to 38 (Alexander 1992). This design provides illustrates the large number of muscles acting on the hand in a relatively small amount of space.

The muscles that actuate fingers are classified as intrinsic (originating in the hand) and extrinsic (originating in a forearm) muscles. Extrinsic muscles are generally larger and generate most of force of the hand, while intrinsic muscles are smaller and are associated with fine finger movements (Freivalds, 2004). The extrinsic muscles are functionally and structurally divided into two groups of muscles: anterior and posterior muscle groups. The anterior muscles group consists of flexors of digits and hand, while the posterior muscles are extensors (see figure 2.5). These long flexor and extensor muscles of the wrist and fingers originate from the bones in the arm, and then approaching the wrist, the muscle bellies are replaced by tendons (Kapandji, 1970). The three main extrinsic muscles for the fingers are the flexor digitorum profundus (FDP), the flexor digitorum superficialis (FDS), and the extensor digitorum communis (EDC). The FDS performs most of the unloaded finger flexion, while the FDP comes into play when extra strength is needed (Long et al. 1970). The FDS contributes to the flexion of the PIP joints of the fingers, especially when the wrist is flexed. The FDP contributes to the

flexion of the PIP joints, the MP joints, and the wrist joints and is the only muscle responsible for the flexion of the DIP joints. The FDP is divided into two bellies: the radial and the ulnar. The radial parts inserts into the index finger, while the ulnar parts insert into the middle, ring, and little fingers. Consequently, the latter three fingers tend to move together, while the index finger can function independently of the others.

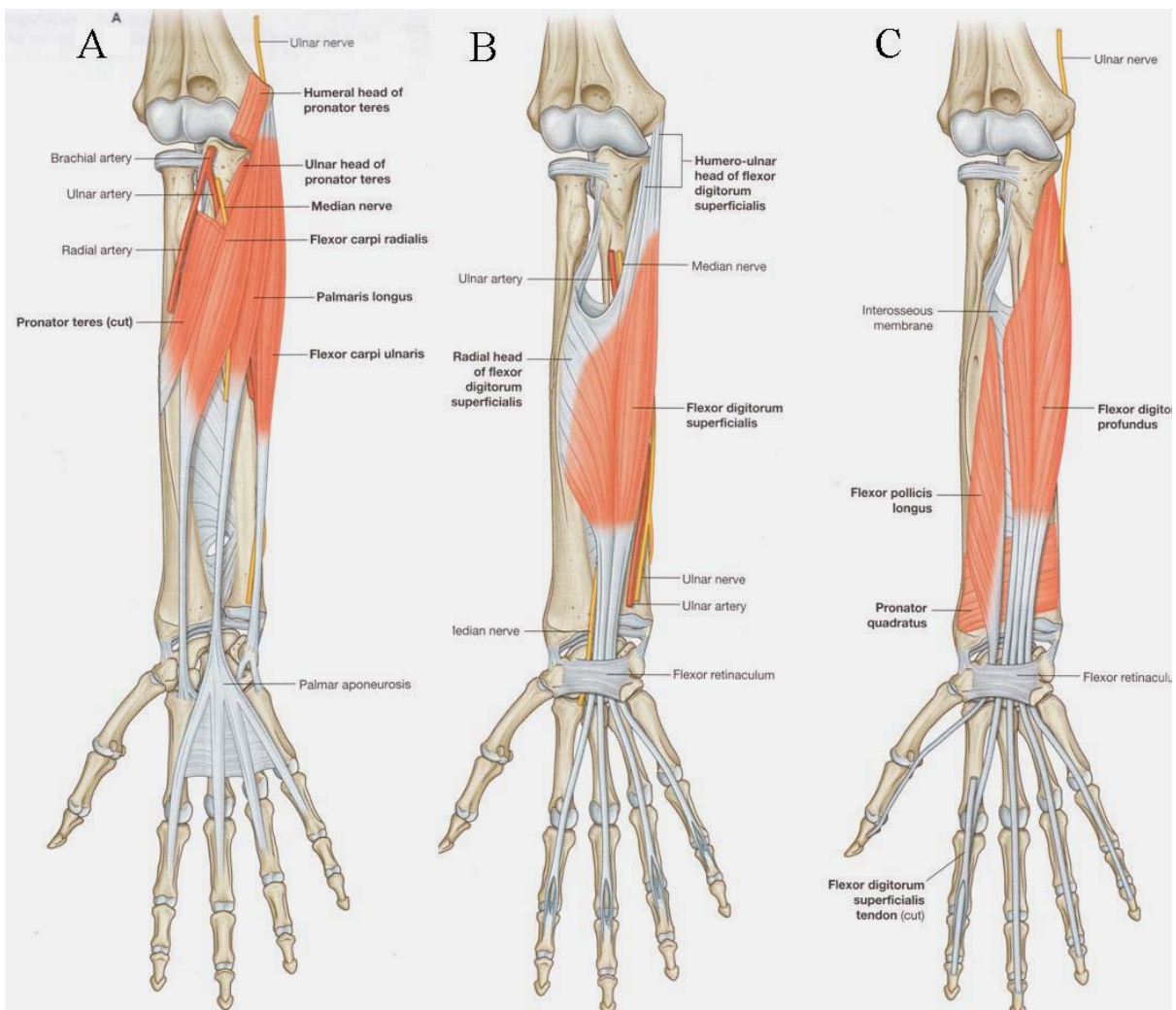


Figure 2.4 Extrinsic flexor muscles of the right forearm, A) Superficial layer; B) Intermediate layer; C) Deep layer (Drake et al. 2005)

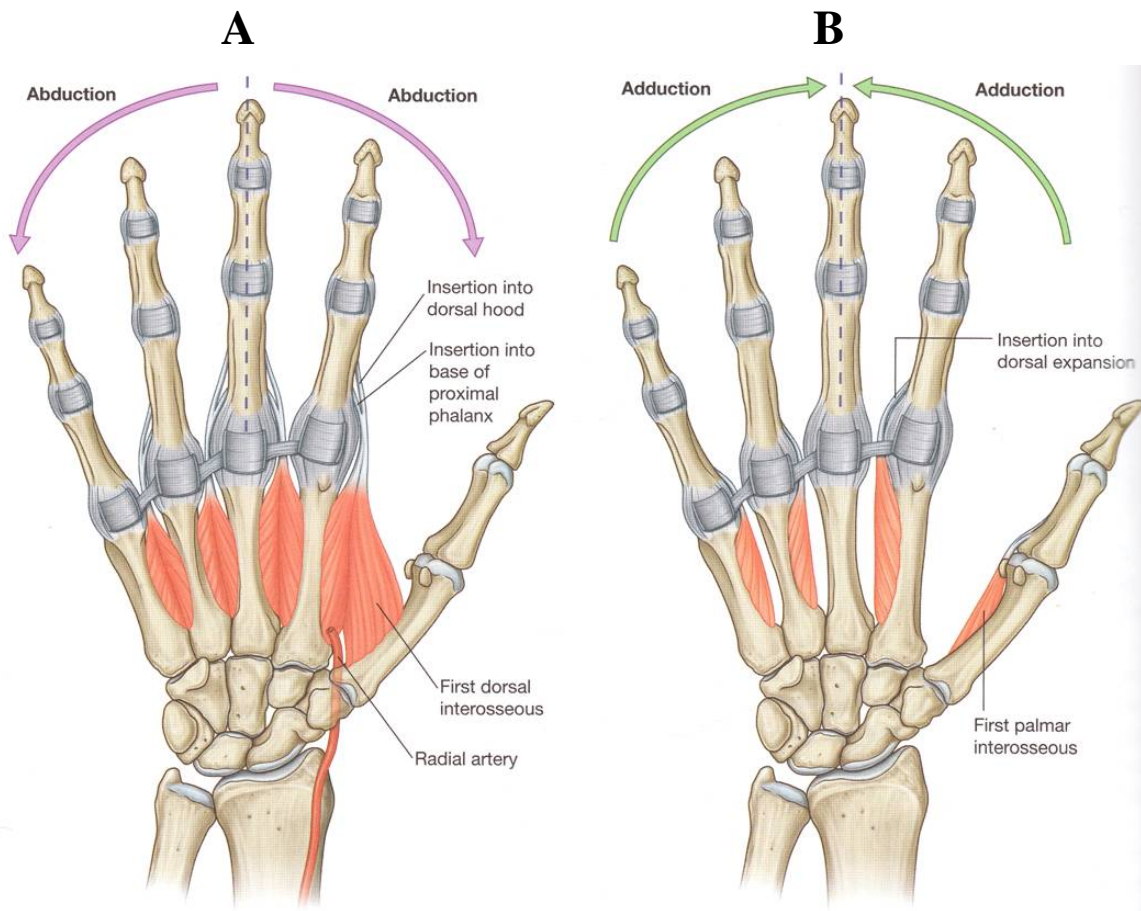


Figure 2.5 Intrinsic hand muscles of the right hand, A) Dorsal interossei; B) Dorsal interossei (Drake et al. 2005)

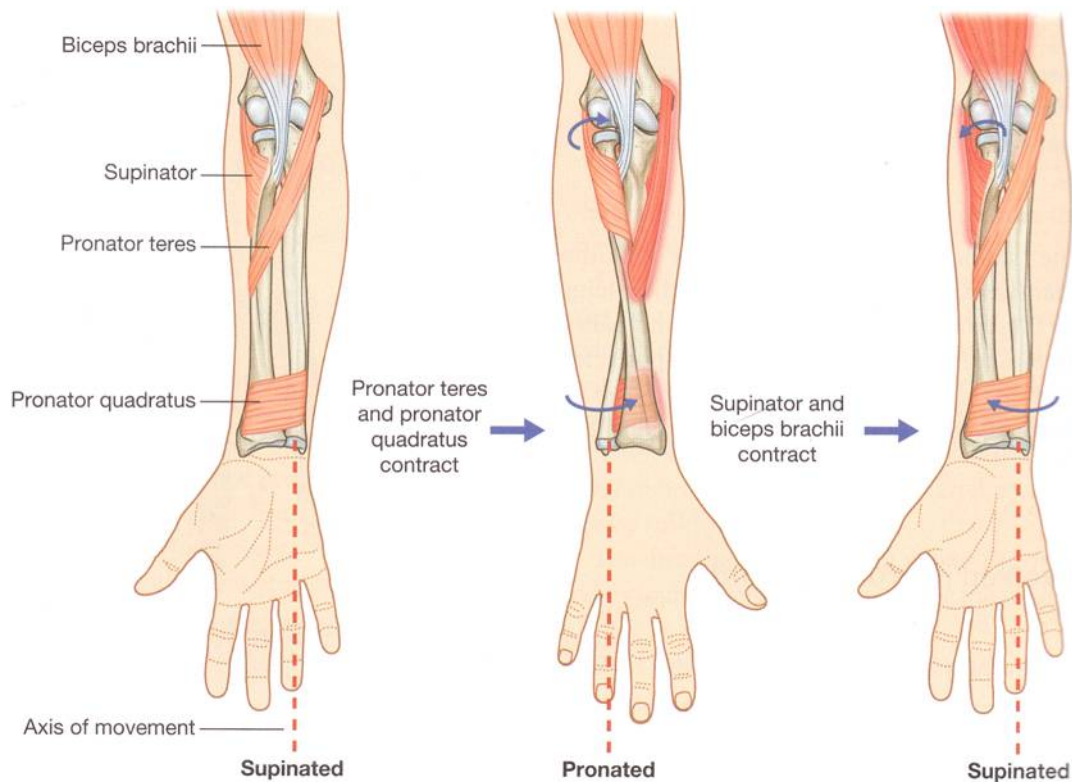


Figure 2.6 Pronation and Supination (Van De Graaff, 2000)

The mechanism of finger extension is slightly more complicated. EDC has the sole function of extending the fingers but is aided by the lumbricales and interossei. The EDC can actuate only the DIP joint or only the PIP joints. The extensor hood, the ligament structure on top of the proximal phalanges that connects the opposing interossei, moves in the direction of the MCP joint, shifting the action of the lumbricals from the extension of the MCP joints to the flexion of the same joints. Since the interossei are directly connected to the tendon of the extensor digitorum, rather than to the bone, they assist also in the extension of the fingers. Figure 2.7 illustrates the extensor mechanism of the fingers. The EDC extends the MP joint and contributes the extension of the PIP and DIP joints (Tubiana 1981).

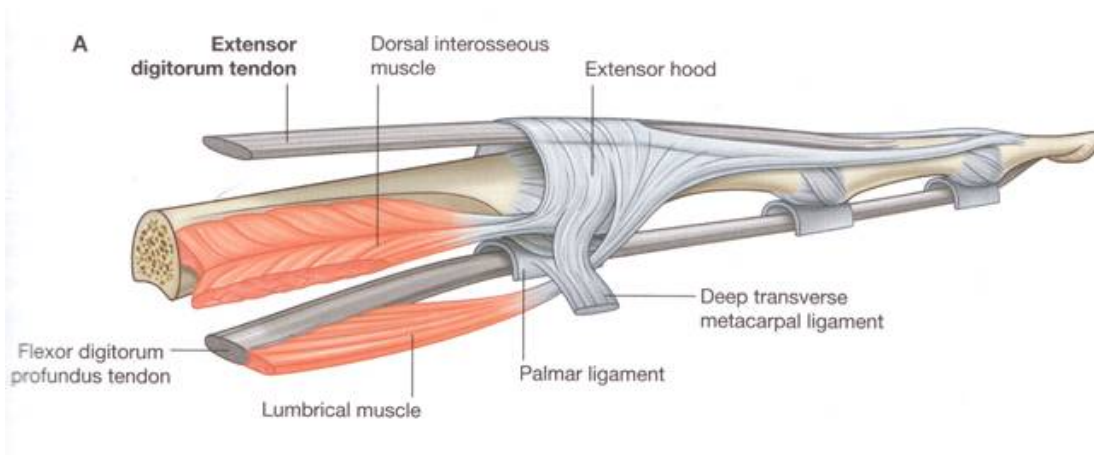


Figure 2.7 Finger extensor mechanisms (Drake et al. 2005).

Intrinsic muscles control adduction/abduction movements of the fingers, the flexion of metacarpophalangeal joints, and the extension of the interphalangeal joints (Jones, 2006). These muscles are functionally and structurally divided into four groups of muscles: the thenar, hypothenar, midpalmar, and lumbricals muscle groups. The thenar group acts on the thumb; the hypothenar group acts on the little finger; the midpalmar muscles act on all of the phalanges except the thumb.

The two main types of intrinsic muscles are the interossei and the lumbricals that control finger movements. The interossei are located between the metacarpals in the palm of the hand and allow for the flexion of the MP joint and the extension of the PIP and DIP joints. These muscles also contribute to abduction and adduction finger movements. The four dorsal interossei are responsible for the abduction of the fingers, while the three palmar interossei are responsible for the adduction of the fingers. The four lumbrical muscles contribute to the extension of the PIP and DIP joints and to the flexion of the MP joints. The lumbrical muscles are unique in the human body in that they originate from tendons and not from bone. Table 2.2 and 2.4 describe the intrinsic muscles of the hand,

the extrinsic muscle of the hand, and the summary of muscles that control the movement of forearm, wrist, and digits (Moore, 1992, Fyloid, 2000; Drake, 2005)

Table 2.2 shows the muscles of intrinsic muscle (Drake 2005)

	Muscle	Origin	Insertion	Function
Metacarpal	Palmar interossei	Metacarpal bones (except the middle)	Bases of proximal phalanges (except of middle finger)	Flexion and adduction of fingers at MCP
	Dorsal interossei	Metacarpal bones	Bases of proximal phalanges and extensor tendons of digits	Abduction and flexion of fingers 2-4 at MCP, extension at IP
	Lumbricales	Tendons of flexor Digitorum profundus	Lateral sides of tendons of extensor digitorum on the proximal phalanx of each finger	Flexion of MCP joints, extension at IP
Thenar	Abductor Pollicis brevis	Scaphoid and trapezium and surrounding area	Base of the 1st proximal phalanx	Abduction of thumb, aids in opposition
	Flexor pollicis brevis	1st metacarpal, trapezium, radial side of carpus	Base of the 1st proximal phalanx	Flexion of thumb, aids in opposition
	Adductor pollicis	Capitate & 2nd & 3rd metacarpals	Base of the 1st proximal phalanx	Adduction and flexion of thumb
	Opponens pollicis	Trapezium & Surrounding area	1st metacarpal	Opposition of thumb, rolls it towards midline
Hypothenar	Abductor digiti minimi	Pisiform & surrounding area	Medial aspect of the 5th proximal phalanx (little)	Abduction and flexion of little finger at MCP
	Flexor digiti minimi brevis	Flexor retinaculum & hamate	Medial side of the proximal phalanx of the little finger	Flexion of little finger at CP and MCP
	Opponens digiti minimi	Hamate & Adjacent region	Medial side of the 5 th proximal phalanx	Opposition of little fingers

Table 2.3 Muscles of Hand and Wrist Motions (April 1997)

	Muscle		Origin	Insertion	Innervation
Hand Supination	Supinator		Lateral epicondyle of humerus	Lateral aspect of midradius	Deep branch of radial n. (C5-C7, posterior)
	Biceps	Long head	Supraglenoid tubercle of scapula	Radial tuberosity of the radius	Musculocutaneous n. (C5-C6, anterior)
		Short head	Coracoid process of scapula		
Hand Pronation	Pronator	Humeral head	Lateral surface of midradius	Lateral surface of midradius	Median n. (C6- C7, anterior)
		Ulnar head	Proximal ulna		
	Pronator quadratus	Anterior surface of ulna		Anterior surface of radius	Median n. (C6- C7, anterior)
Wrist Extension	Extensor digitorum communis		Lateral epicondyle of humerus	Extensor expansion of index, middle & ring fingers	Post. Interosseus branch of radial n.(C7-C8, posterior)
	Extensor carpi radialis brevis		Lateral epicondyle of humerus	Base of 3 rd metacarpal	Post. Interosseus branch of radial n.(C7-C8,posterior)
	Extensor carpi ulnaris		Lateral epicondyle of humerus	Base of 5 th metacarpal	Post. Interosseus branch of radial n. (C7-C8, posterior)
	Extensor carpi radialis longus		Lateral epicondyle of humerus	Base of 2 nd metacarpal	Radial n. (C6-C7, posterior)
Wrist Flexion	Flexor carpi radialis		Medial epicondyle of humerus	Bases of 2 nd & 3 rd metacarpals	Bases of 2 nd & 3 rd metacarpals
	Flexor carpi ulnaris		Medial epicondyle of humerus, and proximal ulna	Pisiform bone & base of 5 th metacarpal	Pisiform bone and base of fifth metacarpal
	Flexor digitorum profundus		Anterior proximal ulna & interosseous membrane	Base of 3 rd phalanx of 2 nd – 5 th digits	Base of third phalanx of second through fifth digits
	Flexor digitorum superficialis		Medial epicondyle of humerus, radius, and ulna	Base of 2 nd phalanx of 2 nd – 5 th digits	Base of second phalanx of second through fifth digits
	Palmaris longus		Medial epicondyle of humerus	Palmar aponeurosis	Palmar aponeurosis

		Muscle	Origin	Insertion	Innervation
Wrist Abduction		Flexor carpi radialis	Medial epicondyle of humerus	Bases of 2 nd and 3 rd metacarpals	Median n. (C6- C7, anterior)
		Extensor carpi radialis brevis	Lateral epicondyle of humerus	Base of 3 rd metacarpal	Superficial or deep radial n. (C6-C7, posterior)
		Extensor carpi radialis longus	Lateral epicondyle of humerus	Base of 2 nd metacarpal	Radial n. (C6-C7, posterior)
		Abductor pollicis longus	Post. Interosseous membrane	Base of 1 st metacarpal and ulna laterally	Post interosseous branch of radial n. (C8-T1, posterior)
		Extensor pollicis longus	Post. Surface Of interosseous Membrane and posterior ulna	Base of 2 nd phalanx of thumb	Post interosseous branch of radial n. (C8-T1, posterior)
		Extensor pollicis brevis	Post. Midshaft of radius & interosseous membrane	Base of 1 st phalanx of thumb	Post interosseous branch of radial n. (C8-T1, posterior)
Wrist Adduction		Flexor carpi ulnaris	Medial epicondyle of humerus, & proximal ulna	Pisiform bone & base of 5 th metacarpal	Ulnar n. (C8-T1, anterior)
		Extensor carpi ulnaris	Medial epicondyle of humerus, and proximal ulna	Pisiform bone & base of 5 th metacarpal	Ulnar n. (C8-T1, anterior)
Finger (2-5) Extension	2-5 Finger Extensors	Extensor digitorum communis	Lateral epicondyle of humerus	Extensor expansion index, middle & ring fingers	Post. Interosseous branch of radial n. (C7 C8, posterior)
	2 nd finger extensor	Extensor indicis	Interosseous membrane and ulna	Extensor hood & proximal phalanx of index finger	Post interosseous branch of radial n. (C8-T1, posterior)
	5 th finger extensor	Extensor digiti minimi	Lateral epicondyle of humerus & tendon of extensor digitorum	Extensor hood & proximal phalanx of little finger	Post interosseous branch of radial n. (C7-C8, posterior)
	IP joints extensor	Lumbricals	1&2 Tendons of the flexor digitorum profundus in the deep palm	Lateral side of dorsal expansion of second and third digits	Median n. (C8-T1, anterior)

	Muscle		Origin		Insertion	Innervation
Finger (2-5) Flexion	MCP joints flexor	Lumbricals	3&4	Tendons of the flexor digitorum profundus in the deep palm	Lateral side of dorsal expansion of fourth and fifth digits	Ulnar n. (C8-T1, anterior)
	PIP joints flexor	Flexor digitorum superficialis	Medial epicondyle of humerus, radius, and ulna		Base of second phalanx of second through fifth digits	Median n. (C7-Finger T1, anterior)
	DIP joints flexor	Flexor digitorum profundus	Anterior proximal ulna and interosseous membrane		Base of third phalanx of 2 nd through 5 th digits	Heads for 2 nd and 3 rd digits: median n. (C7- T1, ant.)Heads for 4 th & 5 th digits; deep br. of ulnar n. (C8-T1, ant.)
Finger (2-5) Abduction & Adduction	Dorsal interossei		Medial side of first metacarpal; both sides of second, third, and fourth metacarpal; and lateral side of fifth metacarpal		Tubercle of Proximalphalanx and Dorsal aponeurosis: laterally on 2 nd & 3 rd digits, medially on 3 rd & 4 th digits	Ulnar n. (C8-T1, anterior)
	Palmar interossei		Medial side of 2 nd and lateral side of 4 th & 5 th metacarpals		Tubercle of Proximalphalanx and Dorsal aponeurosis: medially on 2 nd digit; laterally on 4 th & 5 th digits	Ulnar n. (C8-T1, anterior)
Thumb Extension	Extensor pollicis longus		Post. Surface of interosseous membrane and posterior ulna		Base of second phalanx of thumb	Post interosseous branch of radial n. (C8-T1, posterior)
	Extensor pollicis brevis		Post. Midshaft of radius and interosseous membrane		Base of first phalanx of thumb	Post interosseous branch of radial n. (C8-T1, posterior)

	Muscle		Origin	Insertion	Innervation
Thumb Flexor	Flexor pollicis longus		Anterior midradius and interosseous membrane	Lateral aspect base of second phalanx of thumb	Median n. (C7-T1, anterior)
	Flexor pollicis brevis	Superficial head	Transverse carpal ligament and trapezium	Lateral side of first phalanx base	Median n. (C8-T1, anterior)
		Deep head	Lateral side of second metacarpal		Ulnar n. (C8-T1, anterior)
Thumb Abduction	Abductor longus pollicis		Post. Interosseous membrane	Base of first metacarpal and ulna laterally	Post interosseous branch of radial n.(C8-T1, Thumb Abductionposterior)
	Abductor pollicis brevis		Anterior surface of trapezium and scaphoid	Lateral aspect of first phalanx base	Median n. (C8-T1, anterior)
Thumb Adduction	Adductor pollicis		Oblique head: Anterior surface of capitate, 2 nd and 3 rd metacarpals; Transverse head: Distal half of 3 rd metacarpal	Medial side of base of first phalanx of thumb	Ulnar n. (C8-T1, anterior)
Thumb Oppositi	Opponens pollicis		Trapezium	Anteriolateral surface of first metacarpal	Median n. (C8-T1, anterior)
Thumb Reposition	Extensor pollicis longus		Post. Surface Of interosseous Membrane and posterior ulna	Base of second phalanx of thumb	Post interosseous branch of radial n. (C8-T1, posterior)
	Extensor pollicis brevis		Post. Midshaft of radius and interosseous membrane	Base of first phalanx of thumb	Post interosseous branch of radial n. (C8-T1, posterior)
	Abductor pollicis longus		Post. Interosseous membrane	Base of first metacarpal and ulna laterally	Post interosseous branch of radial n. (C8-T1, posterior)
	Abductor pollicis brevis		Anterior surface of trapezium and scaphoid	Lateral aspect of first phalanx base	Median n. (C8-T1, anterior)

2.3.1.4 Motor and Sensory Innervation

The muscles and skin of the hand are innervated by the radial, median, and ulnar nerves, which contribute to the cutaneous or general sensory innervation. The ulnar nerve innervates all of the intrinsic muscles of the hand except for the three thenar muscles and the two lateral lumbricals, which are innervated by the median nerve. In addition, the radial nerve only innervates skin in the dorsolateral side of the hand.

The radial nerve only innervates the extensors of the hand and the thumb abductor (APL). The primary motor function of the radial nerve is to innervate the muscles that extend the wrist and the MCP joints and the muscles that abduct and extend the thumb. The median nerve also innervates the flexors of the wrist and digits, the abductors and opponens muscles of the thumb, and the first and second lumbricals. The ulnar nerve innervates all other intrinsic muscles of the hand. The wrist and hand receive their blood supply from the radial and ulnar arteries, which run parallel to the bones and enter the hand through the flexor tunnel (Drake, 2005)

The sensory innervation is also provided by the radial, median, and ulnar nerves. The radial nerve innervates the three radial quarters of the dorsum of the hand and the dorsal surface of the thumb. It also supplies sensibility to the dorsal surfaces of the index and middle fingers and to the radial half of the ring finger, reaching as far as the PIP joint of each finger. The median nerve innervates the volar surfaces of the thumb, index, and middle fingers in addition to the radial side of the ring finger. Dorsal branches of the nerve arise to innervate the dorsal aspect of the index and middle fingers distal to the PIP joint and also the radial half of the ring finger. The ulnar nerve innervates the little finger and the ulnar half of the ring finger on the palmar surface as well as the dorsal aspect of

the hand over the ring and little finger metacarpals, the dorsum of the little finger, and the dorso-ulnar half of the ring finger (Jones et al. 2006).

2.3.5 Mobility of the Finger and Wrist Joints

Twenty-five degrees of freedom (DOF) are used to characterize the joints of the five fingers and wrist. The wrist has three DOFs (F/E, A/A, P/S), and the thumb has six DOFs: IP (one DOF, F/E), MCP (two DOF: F/E, A/A), CMC (three DOF: F/E, A/A, P/S). The MCP joints of the four fingers have two DOFs each (F/E, A/A), and the PIP and DIP joints of the four fingers have one DOF each (F/E). Each joint in the five fingers and wrist enable movement within certain degrees of range.

The range of motion (ROM) of the wrist joint is between 80°-90° of flexion to 70°-90° of extension, as well as 15 ° adduction to 30°-45° abduction. The ROM of II-V DIP joints flexion range from 80°-90° and 110°-115° for PIP joints, while their extension range is 20° for DIP joints with no motion occurring in the PIP joints, respectively. The ROM of II-V MCP joint flexion and extension are approximately 90° and 30°-45° respectively, although individual fingers show different ROM; in particular, the index finger shows the smallest ROM of 70°, and the little finger shows the largest ROM of 95°. The ROM of II-V the fingers of adduction and abduction are about 60° for the index finger, 45° for the middle finger, 45° for the ring finger, and 50° for the little finger. The ROM of thumb is different from the other fingers: its CMC and MCP joints can only flex about 50°, but they cannot extend; the IP joint flexes about 90° and extends only slightly. The ROM of thumb of adduction and abduction are about 30° and 60°-70°. The ROM of MCP joints in the flexion-extension direction decrease with an increase in abduction-

adduction deviation from a neutral position and vice versa due to the bicondylar metacarpal structure (Schultz et al., 1987).

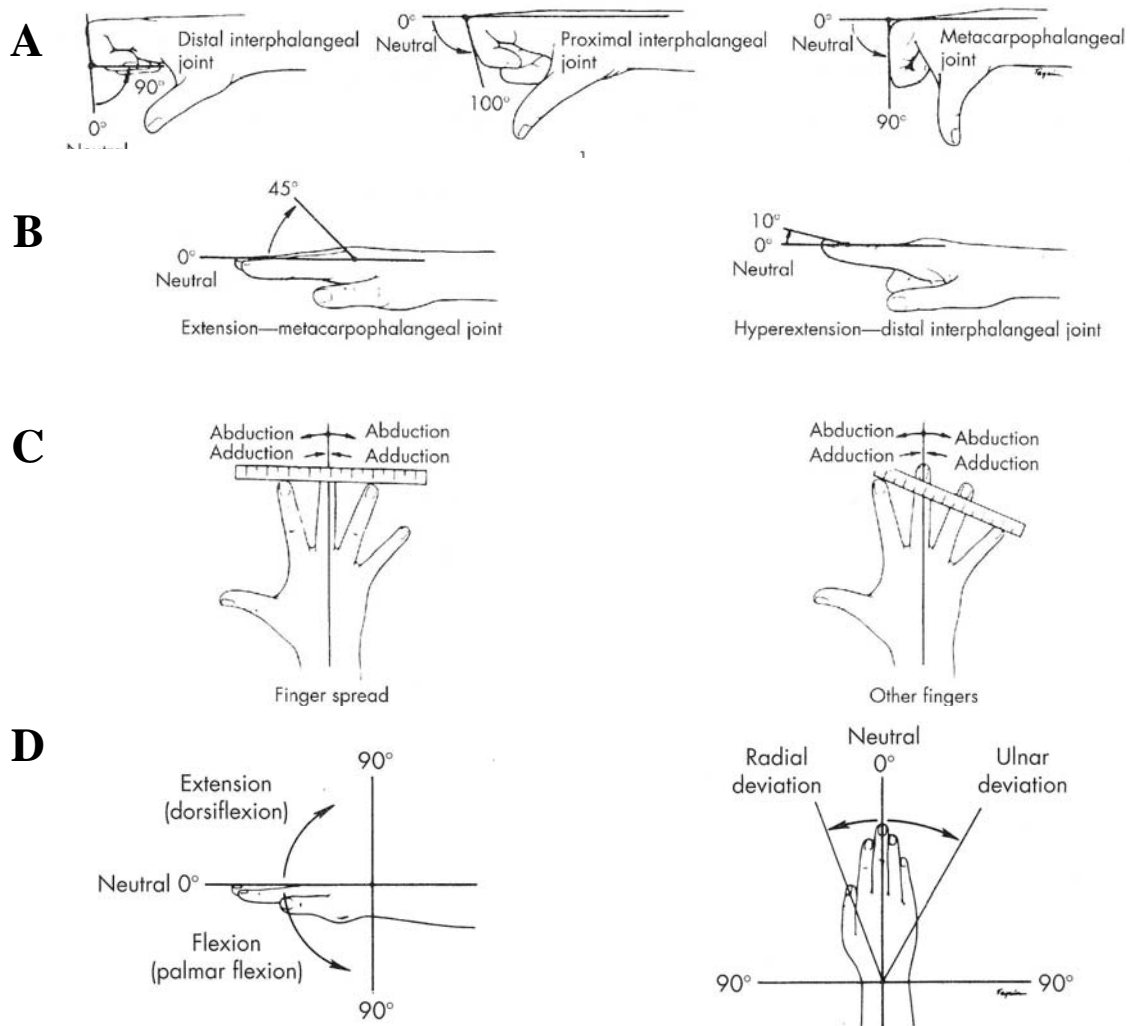


Figure 2.8 ROM of the Wrist, Fingers, and Thumb A) Flexion of DIP, PIP, and MCP joints of finger; B) Extension of MCP and DIP joints of finger; C) Abduction and Adduction of MCP joints; D) Flexion/Extension and radial/ulnar deviation of wrist (Fyloid, 2005)

Table 2.4 Hand Range of Motion (ROM)

Finger II - V			Thumb			Wrist	
Joint	Direction	Degrees	Joint	Direction	Degrees	Direction	Degrees
MP	Flexion	105	CMC	Flexion	45	Flexion	80
	Extension	-30		Extension	0	Extension	-70
	Abduction	25		Abduction	60		
	Adduction	-25		Adduction	0		
PIP	Flexion	110	MP	Flexion	56	Radial Deviation	20
	Extension	-10		Extension	0		
DIP	Flexion	80	IP	Flexion	73	Ulnar Deviation	-30
	Extension	-20		Extension	-5		

2.4 Coordination of Fingers in Kinetic and Kinematic Tasks

Individual fingers do not move entirely independently of each other. When a single finger is flexed or presses down, the other fingers of the hand move or generate force as well. This coupling is a result of both the specific peripheral design of the hand and the neural organization of finger force control (Leijnse et al. 1993; Kilbreath and Gandevia, 1994; Roullier, 1996; Latash et al. 2002b). Peripheral factors are common biomechanical constraints, such as tendons and muscles in the fingers and central factors involve, among other possible factors, the overlapping cortical representations (Schieber et al. 2001).

Studies of finger interaction during finger pressing tasks have been described with three major indices: sharing, enslaving, and force deficit (Li et al. 1998a, b; Zatsiorsky et al. 1998, 2000). Sharing (S) reflects a phenomenon that individual fingers typically produce certain stable percentages of the total force over a wide range of total force magnitudes during multi-finger tasks. Enslaving (E) describes the involuntary force produced by unintended fingers when another finger of the hand is required to produce a

force (Kilbreath and Gandevia, 1994; Schieber, 2001). Force deficit (FD) is a phenomenon that a finger produces less peak force during a multi-finger task than during a single-finger maximal voluntary contraction (MVC) task (Kinoshita et al. 1995; Ohtsuki, 1981; Li et al. 1998). Quantitatively these indices have been characterized as:

$$S_i = 100\% \frac{F_{i,task}}{F_{Tot,task}}$$

$$E_{i,j} = 100\% \frac{F_{i,j}}{F_{i,i}}$$

$$DF_{i,task} = 100\% \frac{(F_{i,i} - F_{i,task})}{F_{i,i}}$$


where, S , E , and FD refer to sharing, enslaving, and force deficit; subscripts i and j refer to fingers (index: I, middle: M, ring: R, little: L); Tot stands for total; and $task$ indicates a multi-finger task.


The relationship between the number of digits used and the force sharing between the fingers has also been studied; it was observed that the force contributions of the middle and ring fingers are affected by the number of digits used, but that of the index finger is not (Kinoshita et al. 1995). During multi-finger pressing tasks, the force produced by a set of fingers is characterized by a sharing pattern. In practically all four-finger tasks, the index and middle fingers produce about 30% of the total force each, while the ring finger produces 25%, and the little finger produces about 15% (Li et al. 1998a; Li et al. 2000; Zatsiorsky et al. 1998). However, the sharing pattern can change if external mechanical conditions are altered (Zatsiorsky et al. 1998). When action is produced by a set of fingers on a mechanically fixed handle, the force sharing among the fingers varies with the direction of the action (Shim et al., 2004). If the thumb is included

in a multi-finger pressing task, the resulting sharing pattern depends on its position relative to the fingers. When the thumb acts in opposition, its share doubles as compared to when it is parallel to the fingers (Olafsdottir et al., 2005).

Enslaving effects are stronger between adjacent fingers (referred to as “proximity rule”), and the index finger is the most independent finger; that is, it induces the least amount of enslaving in other fingers and is the least enslaved. The ring and little fingers, on the other hand, are both highly enslaved (Zatsiorsky et al. 2000). Force enslaving effects have been reported to be large, nearly symmetrical, and dependent on the distance between fingers (Zatsiorsky et al. 1998). Enslaving effects are generally less strong in the fingers of the dominant hand (Li et al., 2000) and in persons who practice individual finger control for a long time, such as pianists (Slobounov et al. 2002). Enslaving is, on average, 2.1 times greater when the thumb opposes the fingers than when it is parallel to them; however, enslaving is not dependent on whether the thumb is a task finger or not (Olafsdottir et al. 2005). Force deficit increases with the number of explicitly involved fingers and is, on average, 38% in two-finger tasks, 48% in three-finger tasks, and 54% in four-finger tasks (Li et al., 1998a). In addition, force deficit increases with fatigue but decreases when the thumb is included (Olafsdottir et al. 2005)

Finger	I	M	R	L
Test				
I	30	10	8	3
M	8	32	11	5
R	5	9	25	8
L	2	5	10	18
IMRL	26	28	18	14

Enslaving (5N) 

Single-Finger Force Deficit (4N) 


Sharing (% of MVC) 

Figure 2.9 The enslaving matrix. For each test, the force of each finger is reported at the time of MVC. Numbers in bold represent the forces produced by the master fingers; other numbers are the forces produced by the slave fingers. The figure illustrates the definitions of enslaving, force deficit, and sharing (Danion et al. 2003)

Peripheral factors may play a significant role in the phenomena of finger interdependence. The peripheral muscular design originates from passive connections, such as soft tissue, interconnections between tendons, and multi-tendoned extrinsic muscles acting at more than one digit. During natural actions, both intrinsic and extrinsic muscles are activated, but their relative involvement may differ from task to task (Darling et al., 1994; Maier and Hepp-Reymond, 1995). The extrinsic and intrinsic muscles attach to the fingers at different anatomical sites, which enable their relative involvement in a task to be manipulated by changing the point of force application (Basmajian and DeLuca, 1985; Danion et al. 2000; Z-M Li et al., 2000).

The major extrinsic muscles, FDP, FDS, and EDC, each act on all four fingers and have four tendons each. When pressing with the fingertips in a MVC task, the extrinsic flexor muscles (FDP and FDS) have to be activated to produce the maximal force at the DIP and PIP joints (Landsmeet and Long, 1965; Long, 1965), and other

muscles also have to be involved to balance the mechanical action. In particular, the intrinsic muscles have to produce forces to balance the rotational action of the reactive force at the MCP joint. When a force is generated by pressing at the proximal phalanges, and an intermediate position at DIP and MCP is held, intrinsic muscles have to produce a close to maximal force, while the extrinsic muscles balance that force with an action of the extensor mechanism at the IP joint (An et al., 1985; Chao et al., 1976). In particular, when MVC is produced at the fingertips, the extrinsic flexors produce close to a peak force, while the intrinsic muscles produce only about 10-30% of their maximum (Harding et al., 1993; Li et al., 2000). During maximal effort at the proximal phalanges, the intrinsic muscles generate maximal force, while about 20% of the maximal output comes from two main extrinsic muscles (FDP and FDS) (Chao and An, 1978; Harding et al., 1993; Landsmeer and Long, 1965; Smith, 1974). Studies of the indices of finger coordination at the distal and proximal sites have shown that when young, healthy subjects produce forces at the proximal phalanges, maximal force, enslaving, and force deficit are all larger (Li et al., 2000; Danion et al., 2000; Latash et al., 2002; Shinohara et al., 2003a). Various factors, for example, age, gender, and fatigue, can affect the difference between the two sites in these indices (Li et al., 2000; Danion et al., 2000; Latash et al., 2002; Shinohara et al., 2003). In addition, the interconnections of tendons also contribute to mechanical coupling between digits in the hand. Thin sheets of inelastic tissue (originating in the lumbrical muscle) interconnect tendons in the palm of the hand (Schieber and Santello, 2004). Additionally, strong tendon connections between the middle and little fingers bring about the phenomena of finger interdependence (Tubiana, 1981).

Common neural inputs can cause several muscles to contract when a signal is sent down to motorneurons that control multiple muscles. This may lead to synchronized contractions in one muscle or in the muscles of one finger. Studies on the S, E, and FD of finger interactions have provided evidence in support of the hypothesis that these indices reflect the central organization of control as well as the anatomical design of the hand (Leijnse et al. 1993; Kilbreath and Gandevia, 1994; Roullier, 1996; Latash et al. 1998; reviewed in Schieber and Santello, 2004). If only the peripheral designs of multi-tendons cause finger interdependence, E and FD indices could be expected to be large when one presses his/her fingertips and absent or much smaller when one presses with his/her proximal phalanges. However, results show that both E and FD are slightly larger when a person presses with the proximal phalanges (Latash et al, 2002; Shinohara et al., 2003). When intrinsic muscles produce most of the force, elderly individuals show less enslaving in spite of having both larger amounts of connective tissue and enlarged motor units (Larsson and Ansved, 1995; Zimmerman, 1993). Overall, there seem to be serious arguments against the dominate role of the peripheral muscular design in these phenomena (Li et al., 2000; Danion et al., 2000; Latash et al., 2002a; Shinohara et al., 2003a, b).

Finger independence among digits has also been investigated using kinematic variables. The most common approaches study the movement of individual fingers (Fish and Soechting, 1992; Flanders and Soechting, 1992; Fleckenstein et al., 1992; Hager-Ross and Schieber, 2000; Kimura and Vanderwolf, 1970; Schieber, 1991, 1995). When fine, flexion finger movement occurs at the PIP joint, the dominant hand has better control of individual fingers than the non-dominant hand (Kimura and Vanderwolf, 1970).

During typing on a keyboard, all fingers are in motion when a subject types a single letter (Fish and Soechting, 1992). Schieber and colleagues performed extensive experimental studies on individuated digit movement in humans, monkeys, and cats (Hager-Ross and Schieber, 2000; Schieber, 1991; Schieber et al., 1997). When individual digits are flexed and extended, the simultaneous movement of the remaining digits was evaluated. These results demonstrate that the ability to individuate digit movement was limited and that the movements of instructed digits were accompanied by unintended digit movement. The investigators quantified the degree to which other digits remained still during the instructed movement of a given digit and the degree to which a given digit remained still when it was a non-instructed digit. They demonstrated that individuated finger movements are produced not by independent sets of muscles acting on each digit but by the activity of several muscles, many of which act on more than one digit (Schieber, 1993; Schieber et al. 1997; Serlin and Schieber, 1993).

Moreover, recordings of single neurons in the primary motor cortex revealed that the representations of different digits in the primary motor cortex were not segregated but overlapped extensively (Schieber and Hibbard, 1993). The index finger is the most independent of the fingers, followed by the little, middle, and ring fingers, and the middle and ring fingers are less independent in both flexion and extension (Heger-Ross and Schieber, 2000). The “motion enslaving” characteristics of multiple fingers have also been quantified during isolated flexion of the DIP. This study has demonstrated that enslaving effects are mainly generated in neighboring fingers and among the compartments of the FDP (Li et al., 2004)

Chapter 3: Methodology

3.1 Participants

Ten healthy right-handed volunteers (five males and five females) participated in this study. Their mean (\pm SD) anthropometric characteristics were: age 27.7 ± 5.5 years, weight 68.1 ± 13.1 kg, height 170 ± 8.2 cm, hand width 7.5 ± 0.9 cm, and hand length 17.5 ± 1.2 cm. The hand length was measured between the middle fingertip and the distal crease of the wrist with the hand extended, and the hand width was measured between the lateral aspect of the index and little finger metacarpophalangeal (MCP) joints. All subjects were right-handed according to their preferential use of the hand during daily activities such as writing, drawing, and eating. None of the participants had a history of neurological or peripheral disorders of the hand or professional training that might affect the hand function such as playing musical instruments. All participants gave informed consent according to the procedures approved by the Office for Research Protection of the Pennsylvania State University in compliance with the Helsinki Declaration.

3.2 Apparatus

A flat aluminum panel (Fig. 3.1A) was mounted vertically on a polyvinyl-chloride panel ($16 \times 14 \times 0.9$ cm). Six piezoelectric sensors (Model 208A03, Piezotronic Inc., Depew, NY) were placed on the aluminum panel, oriented in the vertical direction with the distance of 2.5 cm between the adjacent sensors. This distance was selected as comfortable and natural for the participants and compatible with the size of the force sensors. A slot (3×6 cm) was located between the 3-rd and 4-th sensors. The

participant's finger tips could be comfortably placed on the sensors without making contact with each other. The aluminum panel with the sensors could be moved vertically in order to allow alignment of the slot with different fingers such that three fingers of the hand were always placed on force sensors while the remaining finger could move through the slot. The sensor location could be adjusted in the horizontal direction to accommodate hands of different size. Cotton pads were attached on the upper surface of the sensors to increase friction and to prevent the effects of skin temperature on force measurement.

The participant's lower arm was fixed in a forearm brace (Ebonite Inc, Daytona Beach, FL), and the wrist was locked in the hand brace (STAT, Powel, TN) both in flexion-extension and ulnar-radial deviation. This prevented wrist joint rotation. Small customized splints (made of thin wooden sticks and Velcro straps) were used to restrict movements at the interphalangeal joints of all the fingers; only MCP joint movement was allowed (See Procedure). A two-axis goniometer (SGw65, Biometrics Ltd., Ladysmith VA) was used to record motion of the MCP joint of the finger positioned against the slot in the frame (the task finger).

A 17" computer monitor was located about 0.8 m away from the participant; it was used to display the tasks and provide visual feedback on the current MCP joint angle of the task finger. The signals from the goniometer were amplified using an amplifier model LS800 (Biometrics Ltd., Ladysmith, VA), while the signals from the force sensors were amplified by AC/DC conditioners (M482M66, Piezotronics Inc., Depew, NY). Further, all the signals were digitized at 1000 Hz with a 16-bit A/D board (National instruments, Austin, TX). A Dell 450 MHz laptop computer and customized LabVIEW based software (LabVIEW 6.1, National Instruments, Austin, TX) were used for data

collection. MatLab programs (Mathworks, Natick, MA) were written for data processing and analyses.

3.3 Experimental Procedure

The participant sat on a chair facing the experimental setup. The wrist-forearm brace was affixed to the testing table in front of the participant with a set of Velcro straps. The right upper arm was abducted approximately 45° in the frontal plane and flexed 20° in the frontal plane; the elbow was at about 110° of flexion (figure. 3.1B).

One rigid end of the goniometer was affixed onto the dorsal surface of the hand along the third metacarpal, using double-sided adhesive tape. The other end was attached at the level of the middle phalanx to the splint placed over the task finger. Before each trial, the participant was instructed to extend all the fingers with the thumb pointing upward. The vertical position of the aluminum panel and the horizontal position of the sensors were adjusted such that the task finger could move freely through the slot on the aluminum panel while the non-task finger tips were placed on the sensors (figure. 3.1C).

The participants were given a familiarization session to ensure that they were familiar with the setup and able to perform the tasks. During the session they got a detailed description of the procedure and were allowed to perform a few trials (not recorded). During the experiment, the participant was instructed to perform cyclic flexion-extension movements of the task finger through the slot. The MCP joint angle trajectory of the task finger was shown in real time on the screen, and the task was to match the MCP trajectory with the ramp template shown on the same screen (figure. 3.1B). The template consisted of a sequence of straight lines leading from 0°

(corresponding to the fully extended finger position) to 45° (flexion motion) and back from 45° to 0° (extension motion) over time-intervals that varied across trials. There were five 0°-to-45° lines and five 45°-to-0° lines, the lines alternated to form a cyclic task. We will use expressions “flexion segment” and “extension segment” for the flexion and extension half-cycles of the movement.

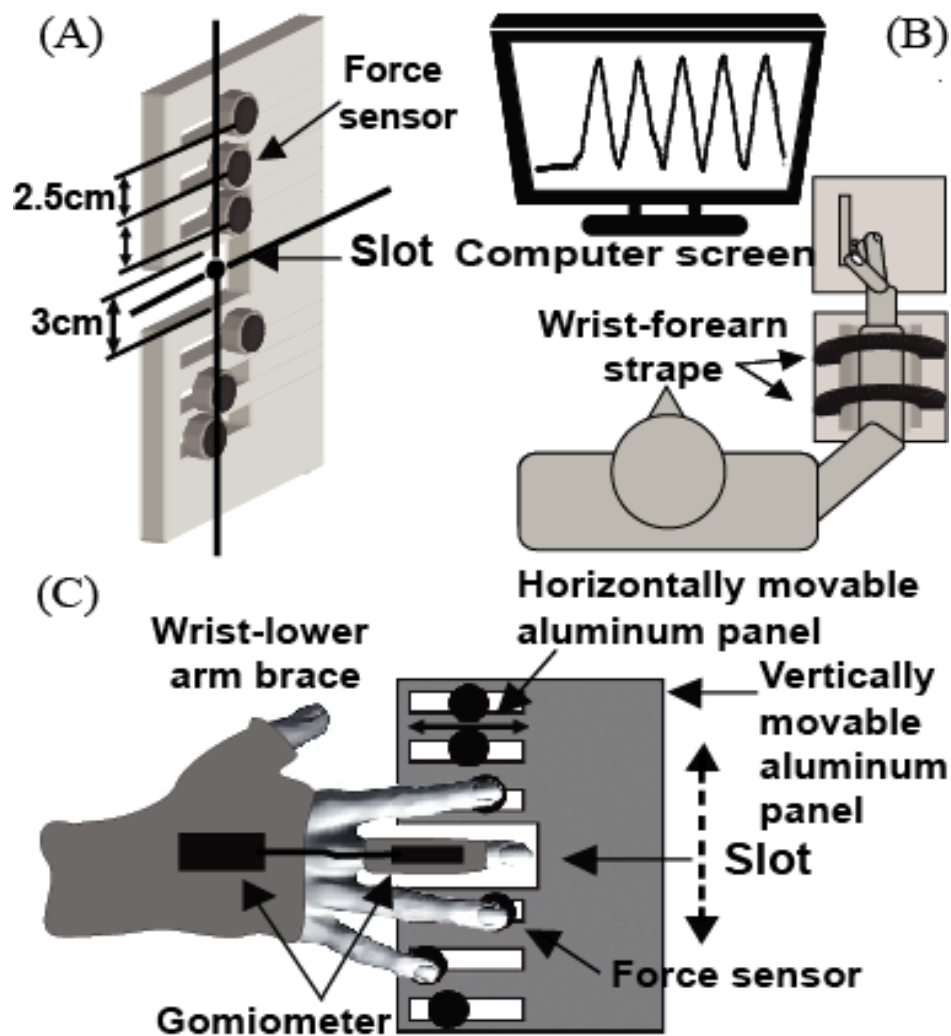


Figure 3.1 An illustration of the experimental setup (A) the vertical plate with force sensors and a slot for finger motion, (B) the position of the participant and the task presentation; and (C) the hand position with the brace and goniometer.

Before each trial, all force signals were zeroed. Each trial started with the computer generating a beep (get ready) and then a yellow cursor showing the current angular position of the MCP joint of the task finger started to move over the screen at a constant speed. The participant was instructed to move the task finger and match the cursor line with the template as accurately as possible. The participants were instructed not to pay attention to possible force production by the other three fingers that rested on the sensors (non-task fingers). This instruction was used to discourage participants from using extension efforts in non-task fingers (see also Li et al., 1998; Zatsiorsky et al., 1998, 2000).

There were four tasks corresponding to different task fingers, the index (I-Task), middle (M-Task), ring (R-Task), and little (L-Task) fingers, and seven durations of the flexion and extension segments forming the template, 3.0, 2.5, 2.0, 1.5, 1.0, 0.75, and 0.5 s. They corresponded to movement periods of 6, 5, 4, 3, 2, 1.5, and 1 s. The duration of trials was adjusted to include five successive complete cycles; it was 30, 25, 20, 15, 10, 7.5, and 5 s, respectively. Three complete cycles in the middle of the trial were always available and used for analysis to avoid possible effects of trial initiation and termination. Two trials were performed for each condition with an 8-s interval between the trials. There were 30-s intervals between conditions. The total of 56 trials were collected, two trials by four task fingers by seven periods. All participants were given two practice, warm-up trials prior to each task. The tasks and periods were presented in a balanced order across the participants.

3.4 Data Analysis

The force and angle data were digitally low-pass filtered with a second-order, zero-lag Butterworth filter at 25 Hz.

The task finger trajectories and force profiles produced by the non task fingers were measured over the three cycles in the middle of each trial. Individual flexion and extension segments of the three accepted cycles were aligned by the onsets of the corresponding segment lines in the template (figure. 4.2). Further, the data were averaged over ramp segments for each task. The duration of each segment was further converted to 100% to allow comparisons across different movement periods.

The root mean square deviation (RMS) of the angular joint trajectory from the template was used as an index of accuracy of the task performance. This index was computed separately over the middle 80% of the flexion and extension segments to avoid possible inconsistencies related to changes in the movement direction. RMS was computed over each segment and then averaged over the six accepted segments.

The unintended force production by the non-task fingers during the movement of the task finger (enslaving) was quantified using the following index:

$$E_{i,j} = \frac{\Delta F_i}{\Delta \alpha_j}$$

where ΔF_i indicates a change in the force of a non-task finger i , and $\Delta \alpha_j$ is a change in the angular position of the task finger j ($i, j = I - \text{index}, M - \text{middle}, R - \text{ring}, \text{ and } L - \text{little}$). Enslaving was quantified within three intervals of equal duration over the flexion and extension segments. The intervals covered the middle 80% of each segment duration. They will be referred to as $FL_1, FL_2,$ and FL_3 (for the flexion segment) and $EX_1, EX_2,$ and

EX₃ (for the extension segment). The subscripts 1, 2, and 3 refer to the intervals 10–36%, 37–63%, and 64–90% of the corresponding segment duration. The enslaving indices (E_{i,j}) were also quantified at the peak flexion position when finger flexion turned into extension (PEAK) as the ratio between the total force produced by an enslaved finger and movement amplitude of the task finger.

3.5 Statistics

The data are presented in the text as means and standard errors of the mean. ANOVAs with and without repeated-measures were run for the following characteristics of performance: Accuracy of the task performance (RMS), non-task finger forces, and the index of enslaving (E). For the RMS index, the factors were *Direction* (two levels: flexion and extension), *Period* (seven levels: 1, 1.5, 2, 3, 4, 5, and 6 s), and *Task-Finger* (four levels: Index, Middle, Ring, and Little). Analysis of non-task finger forces involved factors *Finger* (typically three levels out of four: Index, Middle, Ring, and Little), *Time-interval* (seven levels: FL₁, FL₂, FL₃, PEAK, EX₁, EX₂, and EX₃), *Direction*, and *Period*. Analysis of the index of enslaving E involved factors *Direction*, *Finger*, and *Time-interval*. Appropriate pair-wise contrasts and post-hoc Tukey's Honestly Significant Difference (HSD) tests were used for further analysis of significant effects of the ANOVAs. The level of significance was set at $p < 0.05$.

Chapter 4: Experimental Results

4.1 Movement and force pattern

Motion of the task finger led to force production by all the non-task fingers of the hand. Changes in the flexion force produced by the non-task fingers showed time profiles qualitatively similar to the trajectory of the task finger. Figure 4.1 shows time series of the kinematic and kinetic variables in the M-Task performed by a representative participant.

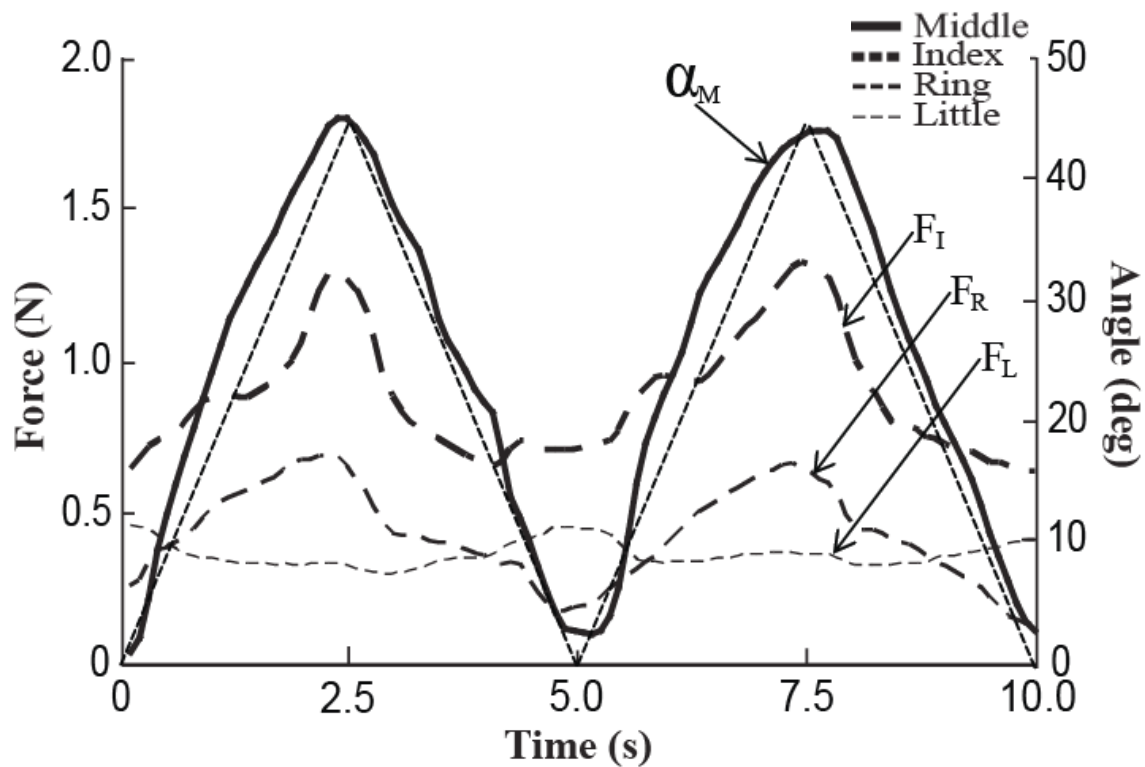


Figure 4.1 An illustration of a typical performance by a representative participant in the middle finger movement task (M-task) over two cycles with the movement period of 5 s. The angular trajectory of the task finger MCP joint is shown with a thick solid line (α_M), and the forces of the non-task fingers are shown with dashed, thin and thick lines (F_I , F_R , and F_L). The thin dashed straight line shows the template. Note the in-phase changes of F_I and F_R , and the task finger trajectory.

Figure 4.2 illustrates relations between the angular trajectory of the task finger and the total force produced by all non-task fingers together (total enslaved force). In this figure, the M-Task is illustrated performed by a representative participant. There is a close to linear relation between the total non-task finger force and the task finger joint angle. Figure 4.2 illustrates an increase in the average level of the total enslaved force (thick bold line) over the three successive cycles (dotted line). For example, the third cycle (FL₃ and EX₃) shows the highest magnitude of force as compared to the first (FL₁ and EX₁) and second (FL₂ and EX₂) cycles. There is a dependence of the angle-force relation shown in Figure 4.2 on the direction of motion, but only close to the most flexed joint position (the rightmost portion of the curves). Within that joint angle range, the enslaved force was higher during flexion motion than during extension motion.

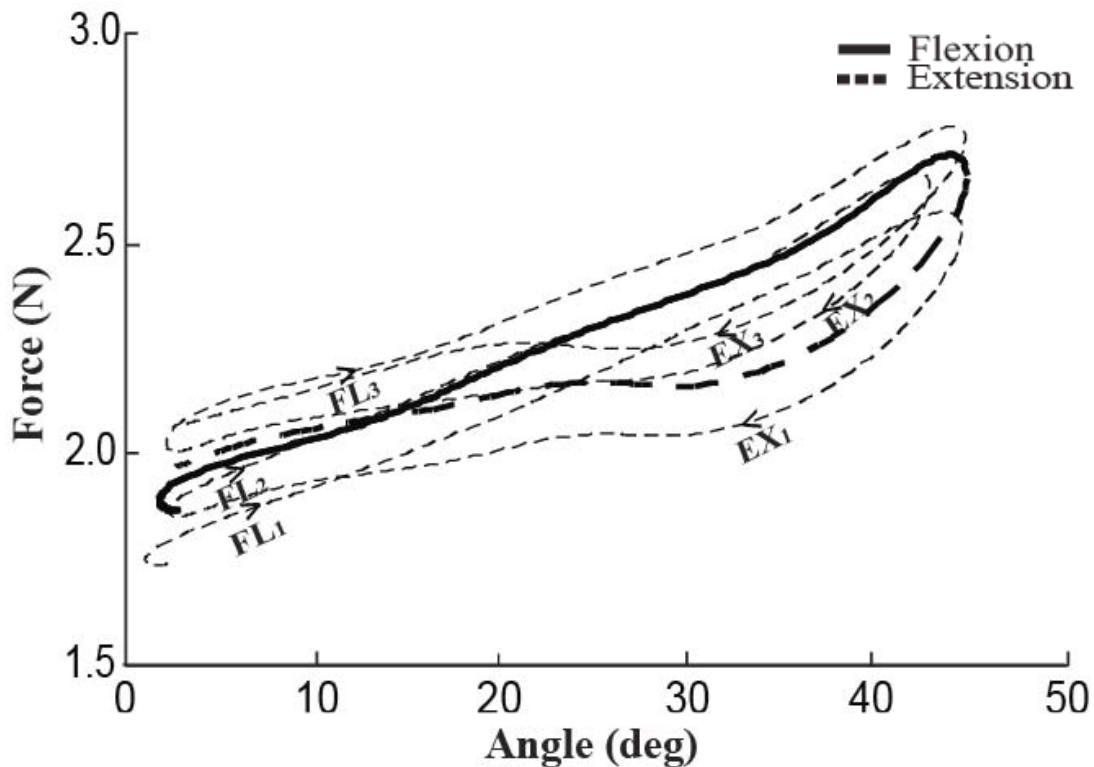


Figure 4.2 Changes in the total enslaved force with task finger motion (middle finger task) over three cycles by a representative participant. Individual cycle data are shown with dashed lines, while the average data are shown with the solid lines. Time direction is shown by arrows. The consecutive flexion and extension segments are shown with labels FL₁, FL₂, FL₃, and EX₁, EX₂, and EX₃, respectively. Note the lower forces produced in the extension segment as compared to the flexion segment. There was also an increase in the average force level from the first cycle to the third cycle.

4.2 Accuracy of the movement task performance

Changes in movement speed led to strong effects on kinematic variability while having little effects on enslaving. Cycle-to-cycle variability of the task finger trajectory was estimated with an index (RMS) computed with respect to the template. The RMS time profiles were close to bell-shaped for every segment of the task finger trajectory with peaks values showing a drop with an increase in the movement period.

Figure 4.3 showed averaged across participants data for all four tasks (subscripts I, M, R, and L correspond to the I-task, M-task, R-task, and L-task, respectively). The four dependences are similar; they were fit with a $1/x$ function. This regression accounted, on average, for 92.7% of the variance in the data. Figure 4.3 illustrates that speeding the movement up (shorter periods) led to higher peak RMS values as compared to slower movements. This was true over all task fingers and both directions, flexion and extension. These findings were tested using repeated-measures ANOVA with three factors, Period, Task-Finger, and Direction. The ANOVA showed a significant main effects of Period, $F(6,54) = 57.7, p < .001$, without other significant effects or interactions. Tukey's HSD tests confirmed significant differences between each of the three fastest tasks and each of the three slowest tasks ($p < .05$).

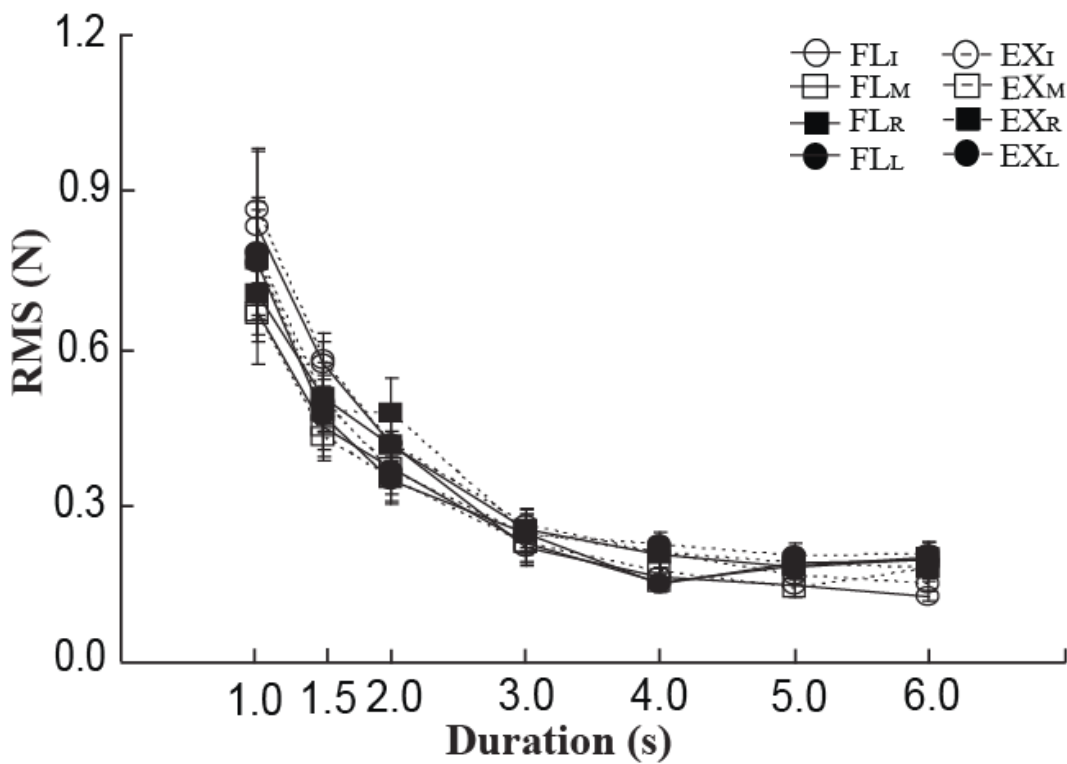


Figure 4.3 Movement accuracy (RMS) depended on the movement period but not on movement direction or the moving finger. Averaged across participants data are shown for the four tasks and two movement directions.

4.3 Characteristics of the forces produced by the non-task fingers

The I-task was characterized by the smallest magnitudes of the enslaved force across all the time-intervals. In all tasks, the most strongly enslaved finger produced force that was strongly modulated over the flexion and extension time-intervals (FL₁, FL₂, FL₃, PEAK, EX₁, EX₂, and EX₃), while the less enslaved fingers showed no or weak force modulation. These results are illustrated in figure 4.4 shows the means and standard errors of individual finger forces of the non-task fingers averaged over the seven intervals. The most strongly enslaved fingers were M for the I- and R-tasks, I for the M-task, and R for the L-task. Note that these are close neighbors of the task finger.

Repeated-measures, *Finger* × *Time-interval* ANOVAs on forces produced by individual slave fingers were run for the four tasks separately. ANOVAs showed significant effects of Finger for the M-, R, and L-tasks, $F(2,18) > 6.10$, $p < .05$, but was under the level of significance for the I-task, $F(2,18) = 3.18$, $p > .05$. These results confirmed the larger enslaving of one of the neighbor fingers in each task. There were also significant effects of Time interval for each of the four tasks, $F(6,54) > 5.0$, $p < .001$, confirming higher enslaving at more flexed positions of the task finger. A *Finger* × *Time-interval* interaction was also significant for all four tasks, $F(12,10) > 4.2$, $p < .001$. Tukey's HSD comparisons revealed that the forces produced by the neighbor fingers of the task finger were more significantly modulated across the time-intervals ($p < .001$).

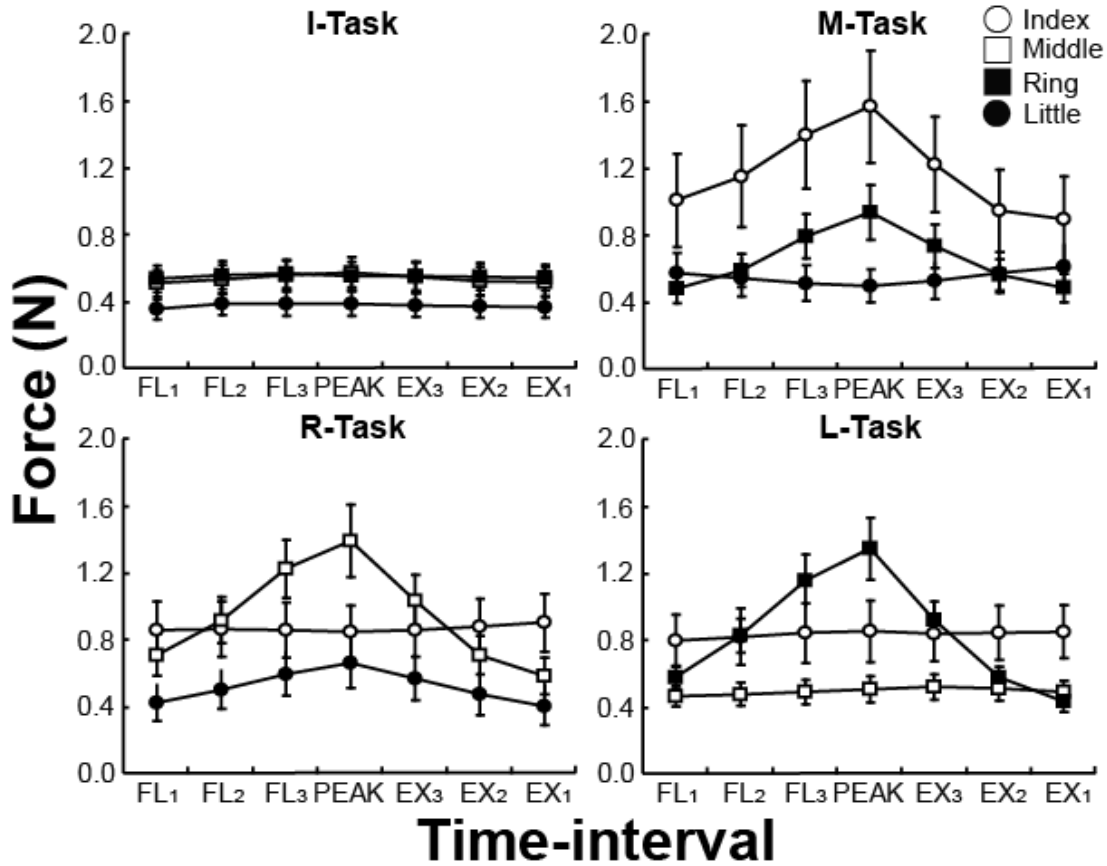


Figure 4.4 Individual finger forces of the non-task fingers averaged across participants with standard error bars: MRL in the I-task, IRL in the M-task, IML in the R-task, and IMR in the L-task. The data are shown for each of the four tasks and all the time-intervals. Note the differences in the profiles of individual finger forces. The closest neighbor tended to produce the highest force.

Figure 4.5 illustrates the average enslaved force with standard error bars produced over the seven time-intervals for all the tasks. The data were averaged across the four tasks and then across participants. There was a statistically significant increase in the total enslaved force with an increase in the movement period; this increase was modest in magnitude. The apparent drop in enslaving from the period of 5–6 s was not significant. The highest enslaved forces were observed at the most flexed task finger position

(PEAK). There was also a trend for the enslaved forces to be higher during the flexion joint motion (FL) as compared to the extension motion (EX).

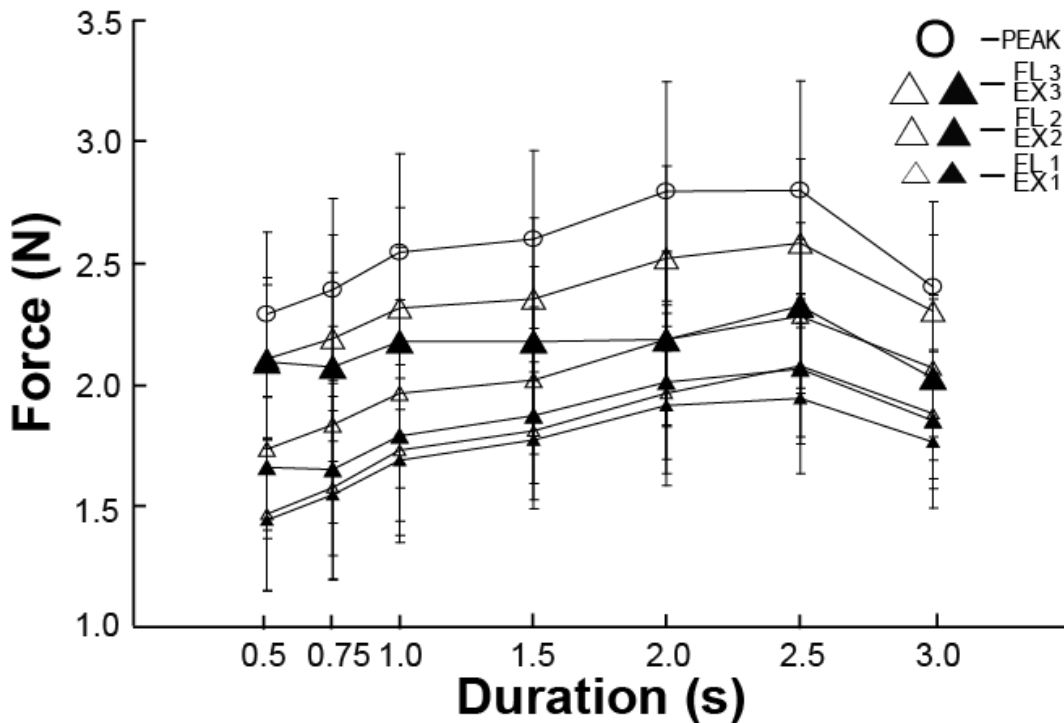


Figure 4.5 The averaged across participants and tasks total enslaved force is shown with standard error bars. Note the trend of an increase in the total enslaved force with an increase in the movement period up to 5 s.

These findings were tested using a three-way repeated-measure ANOVA with the factors Period, Direction, and Time-interval. All three factors showed significant main effects, $F(6,54) = 2.43, p < .05$, $F(1,9) = 19.85, p < .001$, and $F(2,18) = 17.0, p < .001$, respectively. There were also significant two-way interactions *Period* \times *Direction*, *Period* \times *Time-interval*, and *Direction* \times *Time-interval*, $F(6,54) = 6.7, p < .001$, $F(12,108) = 4.38, p < .001$, and $F(2,18) = 50.37, p < .001$, respectively. Pair-wise Tukey's comparisons confirmed higher enslaved forces for flexion movement as compared to

extension movement, and higher enslaved forces at time-intervals corresponding to more flexed finger positions (FL₃ and EX₃) as compared to the other positions (FL₂ and EX₂; FL₁ and EX₁, $p < .05$ for all comparisons).

Interval	Task	Non-task finger (N/rad)			
		I	M	R	L
FL ₁	I	–	0.32 ± 0.09	0.15 ± 0.04	0.06 ± 0.02
	M	0.63 ± 0.19	–	0.39 ± 0.15	–0.08 ± 0.04
	R	–0.01 ± 0.07	0.96 ± 0.17	–	0.47 ± 0.09
	L	0.07 ± 0.06	0.02 ± 0.05	1.10 ± 0.25	–
FL ₂	I	–	0.32 ± 0.05	0.07 ± 0.02	0.03 ± 0.02
	M	0.74 ± 0.15	–	0.36 ± 0.16	–0.14 ± 0.05
	R	0.01 ± 0.05	0.91 ± 0.19	–	0.26 ± 0.08
	L	0.10 ± 0.04	0.06 ± 0.03	1.08 ± 0.24	–
FL ₃	I	–	0.68 ± 0.09	0.04 ± 0.03	0.03 ± 0.01
	M	1.57 ± 0.32	–	1.26 ± 0.28	–0.16 ± 0.08
	R	–0.06 ± 0.05	1.69 ± 0.42	–	0.57 ± 0.18
	L	0.11 ± 0.07	0.07 ± 0.03	1.93 ± 0.44	–
PEAK	I	–	0.46 ± 0.07	0.09 ± 0.03	0.04 ± 0.02
	M	0.95 ± 0.19	–	0.71 ± 0.19	–0.13 ± 0.05
	R	–0.02 ± 0.04	1.16 ± 0.24	–	0.43 ± 0.10
	L	0.09 ± 0.05	0.06 ± 0.03	1.31 ± 0.27	–
EX ₃	I	–	0.97 ± 0.15	0.07 ± 0.03	0.01 ± 0.02
	M	1.76 ± 0.32	–	1.11 ± 0.29	–0.23 ± 0.07
	R	–0.08 ± 0.06	1.83 ± 0.39	–	0.51 ± 0.18
	L	0.02 ± 0.09	–0.01 ± 0.03	2.10 ± 0.42	–
EX ₂	I	–	0.29 ± 0.06	0.04 ± 0.02	0.01 ± 0.02
	M	0.47 ± 0.17	–	0.37 ± 0.16	–0.19 ± 0.07
	R	–0.09 ± 0.05	0.80 ± 0.17	–	0.32 ± 0.07
	L	–0.03 ± 0.02	0.06 ± 0.02	0.83 ± 0.20	–
EX ₁	I	–	0.08 ± 0.04	0.04 ± 0.03	0.05 ± 0.02
	M	0.04 ± 0.17	–	0.37 ± 0.08	–0.12 ± 0.06
	R	–0.09 ± 0.05	0.80 ± 0.17	–	0.32 ± 0.07
	L	–0.02 ± 0.02	0.11 ± 0.03	0.51 ± 0.18	–

Table 4.1. Averages across participants are shown with standard errors for the four tasks (I – Index, M – Middle, R – Ring, and L – Little) and seven intervals (FL₁, FL₂, FL₃, PEAK, EX₁, EX₂, and EX₃).

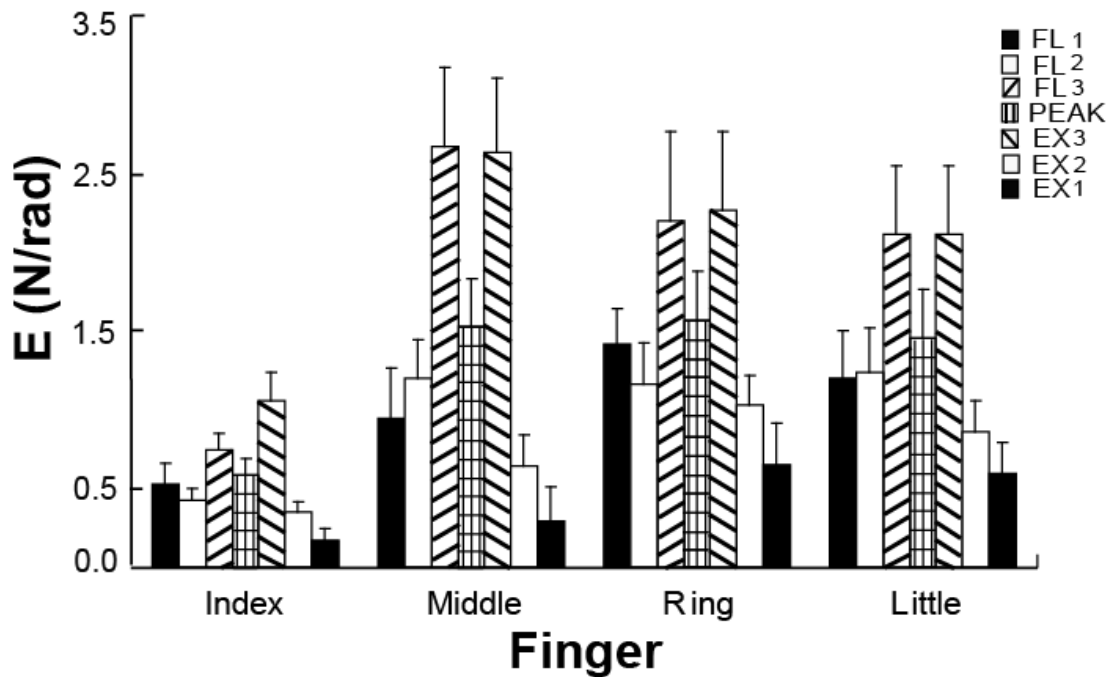


Figure 4.6 Indices of enslaving (E) averaged over all tasks and participants for the seven intervals (FL_1 , FL_2 , FL_3 , EX_3 , EX_2 , EX_1 , and PEAK). The largest enslaving effect was observed when the participants were moving through the most flexed finger interval (hatched bars), whether into flexion or into extension (FL_3 and EX_3).

4.4 Quantitative analysis of the enslaving

The average amount of enslaving across participants (E , in N/rad) is presented in Table 1 for all fingers and across all tasks. The data are shown separately for the three intervals during the flexion motion, during the extension motion, and also at the most flexed position of the task finger (PEAK). Note that the E -index for the PEAK position was computed differently from other intervals and reflected “average enslaving” over the whole range of motion. The I-task showed much weaker enslaving effects on other fingers over both directions. For example, the average E for the M-, R-, and L-tasks was between 2 and 3 times larger than for the I-task. These results are summarized in Figure

4.6, which shows E-indices averaged over all tasks and participants for the seven intervals (FL₁, FL₂, FL₃, EX₃, EX₂, EX₁, and PEAK) separately. The largest enslaving indices were observed when the participants were moving through the more flexed angle interval, whether into flexion or into extension (FL₃ and EX₃). The smallest enslaving was seen in the I-task, and there were no significant differences across the other three tasks. Three-way repeated-measure ANOVA with factors *Time interval*, *Direction*, and *Finger* confirmed these results with significant main effects of each of the factors, $F(2,18) = 27.31$, $p < .001$, $F(1,9) = 12.41$, $p < .01$, and $F(3,27) = 4.51$, $p < .01$, respectively, and a significant interaction *Direction* \times *Time-interval*, $F(2,18) = 6.73$, $p < .01$. Pair-wise Tukey's comparisons confirmed higher E for the flexion movement as compared to the extension movement ($p < .01$, also see figures 4.3 and 4.6), and higher E over the more flexed intervals (FL₃ and EX₃) as compared to the less flexed intervals (FL₁ and EX₁; and FL₂ and EX₂) ($p < .001$).

Chapter 5: Discussion and Conclusion

Two specific questions were formulated in the Introduction: “Does the motion of a finger in flexion and in extension bring about symmetrical changes in forces produced by enslaved fingers?” and “Are quantitative indices of enslaving similar over the range of flexion and extension motion of the instructed finger?” Both questions received negative answers in the experiments. In particular, enslaved forces were larger when the task finger moved into flexion than when it moved into extension. These findings look opposite to those reported recently in a study of isometric tasks in children (Shim et al. 2007). However, note that the cited study by Shim and colleagues used maximal isometric force production into flexion and extension, while in our study the task finger never moved into extension beyond the straight position (0°) and no maximal exertion was required. Another important finding is that the index of enslaving was not constant over the range of finger motion; it increased towards more flexed positions. These findings were confirmed over a wide range of task finger speeds.

5.1 Central and peripheral mechanisms of finger inter-dependence

There have been arguments in favor of both peripheral and central (neural) origins of the lack of finger independence. The anatomical design of the extrinsic flexors and the presence of passive connective tissue links between fingers have been invoked as peripheral factors that potentially contribute to enslaving (Kilbreath & Gandevia, 1994; Leijnse et al. 1993). An important role of neural factors has been supported in experimental studies that showed substantial overlaps of finger projections in the primary motor cortex of primates (Schieber, 1991; Schieber & Hibbard, 1993), effects similar to

enslaving observed in experiments with motor imagery (Li, Latash, & Zatsiorsky, 2004), studies of slow brain potentials (Slobounov, Johnston, Chiang, & Ray, 2002a, 2002b), and by neural network modeling works (Gao et al., 2003; Goodman, Latash, Li, & Zatsiorsky, 2003). Some of the observations of our study are more compatible with a dominant role of neural factors in enslaving. In particular, both muscle and connective tissues are known to have viscoelastic properties. Such connections between the task finger and other fingers (Leijnse, 1997; Leijnse, Walbeehm, Sonneveld, Hovius, & Kauer, 1997) may be expected to lead to velocity-dependence of forces transmitted to the slave fingers. In our experiments, such dependence was not observed (figure 4.5). The indirect observation tentatively points at another important factor that defines the magnitude of enslaving effects, likely a factor at the level of neural signals to muscles and muscle compartments serving different fingers. Data in figure 4.2 suggest a hysteresis-like effect. Such curves usually manifest viscous properties of the system, which seem to contradict a conclusion drawn in the previous paragraph that the system does not show viscous properties (see Zatsiorsky, 1997). However, this contradiction is seeming since figure 4.2 shows dependences between motion of one finger and forces produced by the remaining fingers of the hand.

5.2 Differences among the fingers

In line with a number of earlier reports (Kinoshita et al., 1996; Lang & Schieber, 2004; Li et al., 1998; Zatsiorsky et al., 2000), action by the index finger was associated with the lowest indices of enslaving (table 1 and figures 4.6 and 4.7). In addition, motion of this finger was associated with the smallest modulation of the enslaved force. This

may be causally related to the well documented better independent action of the index finger across a variety of tasks (Hager-Ross & Schieber, 2000; Lang & Schieber, 2004; Reilly & Hammond, 2000; Shinohara, Latash, & Zatsiorsky, 2003; Zatsiorsky et al., 2000). The highest indices of enslaving were observed in the neighboring fingers corroborating the so-called proximity hypothesis (Zatsiorsky et al., 2000). According to this hypothesis, the strongest lack of individuation is observed in immediate neighbors of a task finger. We would also like to note that in our experiments the immediate neighbors were much more likely to show substantial modulation of the enslaved force over the range of motion of the task finger. Variations in the amount of enslaving across conditions apparently had no major effect on the ability of the participants to perform the explicit kinematic task accurately. At least, changes in the speed of movement were associated with substantial changes in the index of kinematic accuracy (figure 4.3) while there were no comparable changes in enslaved forces (figure 4.4). In contrast, enslaving effects differed significantly across task fingers while the index of kinematic variability did not (figures 4.3 and 4.4).

5.3 Implications for studies of multi-digit coordination

The results of this study have potential implication for studies of finger coordination. In particular, the phenomenon of enslaving has frequently been assumed to lead to positive covariation among finger forces independently of the task. This assumption has been based on observations of close to linear changes in finger forces in one finger tasks during both maximal (Li et al., 1998) and submaximal force production (Latash et al., 2001). This assumption has led to analysis of finger coordination using a

different set of variables, finger modes that are assumed to be manipulated by the central nervous system independently of each other (Danion et al., 2003). A number of studies used the method of uncontrolled manifold (UCM) analysis (Scholz & Schöner, 1999; reviewed in Latash et al., 2002) in the space of finger modes to discover and quantify multi-finger synergies stabilizing such variables as the total force and the total moment of force (Scholz et al. 2002; Zhang, Zatsiorsky, & Latash, 2006). This analysis assumes that the controller organizes in the space of finger modes subspaces (UCMs) corresponding to desired magnitudes of potentially important performance variables and then allows relatively large variability across trials to these subspaces while restricting variability orthogonal to these subspaces.

Our current results cast doubt on the assumption that finger modes corresponding to linear dependences among finger forces can indeed be used over a range of dynamic tasks, i.e., the tasks involving not only force production but also finger movements, since enslaving seems to be both range and direction of motion dependent. Interaction among the fingers seems to be much more complex and less linear (Goodman, Latash, & Zatsiorsky, 2004) than it has been commonly assumed. In particular, some of the differences described for indices of multi-finger synergies during flexion force increase and decrease (Shim, Olafsdottir, Zatsiorsky, & Latash, 2005) as well as over different force ranges (Shim, Park, Zatsiorsky, & Latash, 2006) may be due to the differences in the enslaving effects demonstrated in the current study. Studies of multi-digit synergies involving fast movements and force production should consider the complex relations between indices of finger interdependence and action characteristics.

5.4 General Conclusions

- 1) The index of enslaving expressed in (N/rad) depended on the movement speed and was higher when the task finger moved through the more flexed postures. Therefore, this velocity dependence of enslaving suggests an important role of central, neural mechanisms in the patterns of finger interdependence.
- 2) Larger forces are produced by the neighbors of the task finger; these forces showed strong modulation over the range of motion of the task finger. Therefore, the earlier proximity hypothesis was supported.
- 3) The dependence of enslaving on both range and direction of task finger motion poses problems for methods of analysis of finger coordination based on an assumption of universal matrices of finger interdependence. Therefore, the analysis of finger interactions (such as in recent studies of multi-finger synergies) should consider dependence of enslaving on direction, range, and rate of force (movement) by the task finger.

REFERENCES

An KN, Chao EY, Cooney WP, and Linscheid RL. Forces in the normal and abnormal hand. *J Orthop Res* 3: 202-211, 1985.

April E. W. (1997). *Clinical anatomy*, 3rd ed. New York, Williams & Wilkins.

Atkeson CG (1989) Learning arm kinematics and dynamics. *Annu Rev Neurosci* 12:157-183.

Babinski F. De l'asynergie cerebelleuse. *Revue Neurologique* 7: 806-816, 1899.

Baud-Bovy G and Soechting JF. Factors influencing variability in load forces in a tripod grasp. *Exp Brain Res* 143: 57-66, 2002.

Baud-Bovy G and Soechting JF. Two virtual fingers in the control of the tripod grasp. *J Neurophysiol* 86: 604-615, 2001.

Ben Hamed S, Schieber MH, and Pouget A. Decoding M1 neuron activity during multiple finger movements. *Society for Neuroscience abstracts* 27: 289, 2001.

Bernstein NA. *The co-ordination and regulation of movements*. Oxford: Pergamon Press, 1967.

Bernstein NA. *On the construction of movements*. Moscow: Medgiz, 1947.

Chao EY and An KN. Graphical interpretation of the solution to the redundant problem in biomechanics. *J Biomech Eng* 100: 159-167, 1978.

Danion F, Descoins M, and Bootsma RJ. Aging affects the predictive control of grip force during object manipulation. *Exp Brain Res*, 2007.

Danion F, Latash ML, Li ZM, and Zatsiorsky VM. The effect of a fatiguing exercise by the index finger on single- and multi-finger force production tasks. *Exp Brain Res* 138: 322-329, 2001.

Danion F, Latash ML, Li ZM, and Zatsiorsky VM. The effect of fatigue on multifinger co-ordination in force production tasks in humans. *J Physiol* 523 Pt 2: 523-532, 2000.

Danion F, Schoner G, Latash ML, Li S, Scholz JP, and Zatsiorsky VM. (2003) A mode hypothesis for finger interaction during multi-finger force-production tasks. *Biol Cybern* 88: 91-98, 2003.

Darling WG, Cole KJ, and Miller GF. Coordination of index finger movements. *J Biomech* 27: 479-491, 1994.

Drake R, Wayne V, and Mitchell A. *Gray's anatomy for students*: Churchill Livingstone, 2005.

Enoka RM. Muscle strength and its development: New perspectives. *Sports Med* 6: 146-168, 1988.

Enoka RM. Neural strategies in the control of muscle force. *Muscle Nerve Suppl* 5, S66
Fahrer, M. (1981). Interdependent and independent actions of the fingers. In: R. Tubiana (Ed.), *The hand* (pp. 399-401). Philadelphia: Saunders.

Fish, J., & Soechting, J.F. (1992). Synergistic finger movements in a skilled motor task. *Experimental Brain Research*, **91**, 327-334.

Flanders, M., & Soechting, J.F. (1992). Kinematics of typing: Parallel control of the two hands. *Journal of Neurophysiology*, **67**, 1264-1274.

Fleckenstein, J.L., Watumull, D., Bertocci, L.A., Parkey, R.W., & Peshock, R.M. (1992). Finger-specific flexor recruitment in humans: Depiction by exercise-enhanced MRI. *Journal of Applied Physiology*, **72**, 1974-1977.

Freivalds A. (2004) *Biomechanics of the upper limbs: mechanics, modeling and musculoskeletal injuries*. Boca Raton: CRC Press.

Fyloid, RT, *Manual of structural kinesiology*: McGraw-Hill Higher Education, 2007

Gao, F., Li, S., Li, Z. M., Latash, M. L., & Zatsiorsky, V. M. (2003). Matrix analyses of interaction among fingers in static force production tasks. *Biological Cybernetics*, **89**, 407-414.

Goodman, S. R., Latash, M. L., Li, S., & Zatsiorsky, V. M. (2003). Analysis of a network for finger interaction during two-hand multi-finger force production tasks. *Journal of Applied Biomechanics*, **19**, 295-309.

Gelfand IM and Latash ML. On the problem of adequate language in biology. In: *Progress in Motor Control 2, Structure-Function Relations in Voluntary Movements*, edited by Latash ML. Champagne, IL: Human Kinetics, 2002, p. 209-227.

Gelfand IM and Latash ML. On the problem of adequate language in motor control. *Motor Control 2*: 306-313, 1998.

Gelfand IM and Tsetlin ML. On Mathematical modeling of the mechanisms of the central nervous system [In Russian]. In: *Models of the structural-functional organization of certain biological systems*, edited by Gelfand IM, Gurfinkel VS, Fornin SV and Tsetlin ML. Moscow: Nauka, 1966, p. 9-26.

Goodman, S. R., Latash, M. L., & Zatsiorsky, V. M. (2004). Indices of non-linearity in finger force interaction. *Biological Cybernetics*, 90, 264–271.

Gray H. *Gray's Anatomy*, edited by Lewis WH. New York: bartleby.com, 2000.

Hager-Ross, C., & Schieber, M. H. (2000). Quantifying the independence of human finger movement: Comparisons of digits, hands, and movement frequencies. *Journal of Neuroscience*, 22, 8542–8550.

Harding D, Brandt K, and Hillberry B. Finger joint force minimization in pianists using optimization techniques. *J Biomech* 26: 1403-1412, 1993.

Hepp-Reymond MC. *Functional organization of motor cortex and its participation in voluntary movements*. New York: Liss, 1988.

Hughlings Jackson J. On the anatomical and physiological localisation of movements in the brain. In: *Selected writings of John Hughlings Jackson. On Epilepsy and Epileptiform convulsions*, edited by Taylor J, Holmes G and Walshe F. New York: Basic Books, 1958, p. 37-76.

Jones L. A. and Lederman S. J. (2006). *Human hand function*. New York, Oxford university press.

Kilbreath, S. L., & Gandevia, S. C. (1994). Limited independent flexion of the thumb and fingers in human subjects. *Journal of Physiology*, 479, 487–497.

Kimura, D., & Vanderwolf, C.H. (1970). The relation between hand preference and the performance of individual finger movements by left and right hands. *Brain*, **93**, 769-774.

Kim, S. W., Shim, J. K., Zatsiorsky, V. M., & Latash, M. L. (2008) Finger interdependence: Linking the kinetic and kinematic variables. *Human Movement Science*, 27, 408–422.

Kinoshita H, Kawai S, and Ikuta K. Contributions and co-ordination of individual fingers in multiple finger prehension. *Ergonomics* 38: 1212-1230, 1995.

Kinoshita, H., Murase, T., & Bandou, T. (1996). Grip posture and forces during holding cylindrical objects with circular grips. *Ergonomics*, 39, 1163–1176.

Kleinschmidt A, Nitschke MF, and Frahm J. Somatotopy in the human motor cortex hand area. A high-resolution functional MRI study. *Eur J Neurosci* 9: 2178-2186, 1997.

Landsmeer JM and Long C. The mechanism of finger control, based on electromyograms and location analysis. *Acta Anat (Basel)* 60: 330-347, 1965.

Lang, C. E., & Schieber, M. H. (2003). Reduced muscle selectivity during individuated finger movements in humans after damage to the motor cortex or corticospinal tract. *Journal of Neurophysiology*, 91, 1722–1733.

Larsson L and Ansved T. Effects of ageing on the motor unit. *Prog Neurobiol* 45: 397-458, 1995.

Lang, C. E., & Schieber, M. H. (2004). Human finger independence: limitations due to passive mechanical coupling versus active neuromuscular control. *Journal of Neurophysiology*, 92, 2802–2810.

Latash, M. L. (1996). How does the brain make choices? In *Dexterity and Its Development* (pp. 277-304), edited by M. L. Latash and M. T. Turvey. Mahwah, NJ: Erlbaum Publishers.

Latash M. L. (2000). "There is no motor redundancy in human movements. There is motor abundance." *Motor Control* 4(3): 259-60. Latash M. L. (2008). *Synergy*. New York, Oxford university press.

Latash M. L., Kang N, Patterson D. Finger coordination in persons with Down syndrome: atypical patterns of coordination and the effects of practice. *Exp Brain Res* 146: 345-355, 2002a.

Latash M. L., Kang N, Patterson D. Finger coordination in persons with Down syndrome: atypical patterns of coordination and the effects of practice. *Exp Brain Res* 146: 345-355, 2002a.

Latash, M. L., Li, S., Danion, F., & Zatsiorsky, V. M. (2002). Central mechanisms of finger interaction during one- and two-hand force production at distal and proximal phalanges. *Brain Research*, 924, 198–208.

Latash, M. L., Scholz, J. F., Danion, F., & Schöner, G. (2001). Structure of motor variability in marginally redundant multi-finger force production tasks. *Experimental Brain Research*, 141, 153–165.

Latash, M. L., Scholz, J. F., Danion, F., & Schöner, G. (2002). Finger coordination during discrete and oscillatory force production tasks. *Experimental Brain Research*, 146, 419–432.

Latash, M. L., Scholz, J. P., & Schöner, G. (2002). Motor control strategies revealed in the structure of motor variability. *Exercise and Sport Science Reviews*, 30, 26–31.

Latash, M. L., Scholz, J. P., & Schöner, G. (2007). Toward a new theory of motor synergies. *Motor Control*, 11, 275–307.

Leijnse, J. N. (1997). Measuring anatomic connections in the deep flexor of the musician's hand: Theoretical analysis, clinical examples. *Journal of Biomechanics*, 30, 873–882.

- Leijnse, J. N., Snijders, C. J., Bonte, J. E., Landsmeer, J. M., Kalker, J. J., van der Meulen, J. C., et al. (1993). The hand of the musician: The kinematics of the bidigital finger system with anatomical restrictions. *Journal of Biomechanics*, 10, 1169–1179.
- Leijnse, J. N., Walbeehm, E. T., Sonneveld, G. J., Hovius, S. E., & Kauer, J. M. (1997). Connections between the tendons of the musculus flexor digitorum profundus involving the synovial sheaths in the carpal tunnel. *Acta Anatomica (Basel)*, 160, 112–122.
- Li, S., Latash, M. L., & Zatsiorsky, V. M. (2004). Effects of motor imagery on finger force responses to transcranial magnetic stimulation. *Cognitive Brain Research*, 20, 273–280.
- Li S., latish M.L., Yue G.H., Siemionow V., Sahgal V (2003).The effects of stroke and age on finger interaction in multi-finger force production tasks. *Clinical Neurophysiology* 114: 1646-1655.
- Li, Z. M., Dun, S., Harkness, D. A., & Brininger, T. L. (2004). Motion enslaving among multiple fingers of human hand. *Motor Control*, 8, 1–15.
- Li, Z. M., Latash, M. L., & Zatsiorsky, V. M. (1998). Force sharing among finger as a model of the redundancy problem. *Experimental Brain Research*, 119, 276–286.
- Li, Z.M., Zatsiorsky, V.M., & Latash, M.L. (2000). Contribution of the extrinsic and intrinsic hand muscles to the moments in finger joints. *Clinical Biomechanics (Bristol, Avon)*, 15, 203-211.
- Moore. *Clinically oriented anatomy*. Baltimore: Williams & Wilkins, 1992.
- Mussa Ivaldi FA, Morasso P, Zaccaria R (1988) Kinematic networks. A distributed model for representing and regularizing motor redundancy. *Biol Cybern* 60:1-16.
- Ohtsuki T. Inhibition of individual fingers during grip strength exertion. *Ergonomics* 24: 21-36, 1981.
- Olafsdottir H, Zatsiorsky VM, and Latash ML. Is the thumb a fifth finger? A study of digit interaction during force production tasks. *Exp Brain Res* 160: 203-213, 2005a.
- Olafsdottir H. *Is the thumb a fifth finger? Studies of digit interaction during force production tasks* (Masters thesis). State College: Pennsylvania State University, 2004.
- Reilly, K. T., & Hammond, G. R. (2000). Independence of force production by digits of the human hand. *Neuroscience Letters*, 290, 53–56.
- Rosenbaum D. A., Loukopoulos, L.D., Meulenbroek, R.G.M., Vaughan, J., Engelbrecht, S.E. (1995). "Planning reaches by evaluating stored postures." *Psychological Reviews* 102: 28-67.

Schieber M. Constraints on Somatotopic Organization in the Primary Motor Cortex. *J Neurophysiol* 86: 2125-2143, 2001.

Schieber, M. H. (1991). Individuated finger movements of rhesus monkeys: A means of quantifying the independence of the digits. *Journal of Neurophysiology*, 65, 1381–1391.

Schieber, M. H. (1993). Electromyographic evidence of two functional subdivisions in the rhesus monkey's flexor digitorum profundus. *Experimental Brain Research*, **95**, 251-260.

Schieber, M. H. (1999). Somatotopic gradients in the distributed organization of the human primary motor cortex hand area: Evidence from small infarcts. *Experimental Brain Research*, 128, 139–148.

Schieber M. Constraints on Somatotopic Organization in the Primary Motor Cortex. *J Neurophysiol* 86: 2125-2143, 2001.

Schieber, M. H. (1995). Muscular production of individuated finger movements: The roles of extrinsic finger muscles. *Journal of Neuroscience*, **15**, 284-297.

Schieber, M. H., & Hibbard, L. S. (1993). How somatotopic is the motor cortex hand area? *Science*, 261, 489–492.

Schieber, M. H., & Santello, M. (2004). Hand function: Peripheral and central constraints on performance. *Journal of Applied Physiology*, 96, 2293–2300.

Scholz, J. P., Danion, F., Latash, M. L., & Schöner, G. (2002). Understanding finger coordination through analysis of the structure of force variability. *Biological Cybernetics*, 86, 29–39.

Scholz, J. P., & Schöner, G. (1999). The uncontrolled manifold concept: Identifying control variables for a functional task. *Experimental Brain Research*, 126, 289–306.

Schultz RB, Stroave A, Krishnamurthy S (1987) Metacarpophalangeal joint motion and the role of the collateral ligaments. *International Orthopedics* 11:149-155.

Serlin, D.M., & Schieber, M.H. (1993). Morphologic regions of the multitendoned extrinsic finger muscles in the monkey forearm. *Acta Anatomica*, **146**, 255-266.

Sherrington CS. Flexion-reflex of the limb, crossed extension-reflex, and reflex stepping and standing. *J Physiol* 40: 28-121, 1910.

Shim, J. K., Oliveira, M. A., Hsu, J., Huang, J., Park, J., & Clark, J. E. (2007). Hand digit control in children: Age-related changes in hand digit force interactions during maximum flexion and extension force production tasks. *Experimental Brain Research*, 176, 374–386.

Shim, J. K., Olafsdottir, H., Zatsiorsky, V. M., & Latash, M. L. (2005). The emergence and disappearance of multi-digit synergies during force production tasks. *Experimental Brain Research*, 164, 260–270.

Shim, J. K., Park, J., Zatsiorsky, V. M., & Latash, M. L. (2006). Adjustments of prehension synergies in response to self-triggered and experimenter-triggered load and torque perturbations. *Experimental Brain Research*, 175, 641–653.

Shinohara, M., Latash, M. L., & Zatsiorsky, V. M. (2003). Age effects on force production by the intrinsic and extrinsic hand muscles and finger interaction during maximal contraction tasks. *Journal of Applied Physiology*, 95, 1361–1369.

Slobounov, S., Johnston, J., Chiang, H., & Ray, W. J. (2002a). Motor-related cortical potentials accompanying enslaving effect in single versus combination of fingers force production tasks. *Clinical Neurophysiology*, 113, 1444–1453.

Slobounov, S., Johnston, J., Chiang, H., & Ray, W. J. (2002b). The role of submaximal force production in the enslaving phenomenon. *Brain Research*, 954, 212–219.

Smith R. Balance and kinetics of the fingers under normal and pathological conditions. *Clin Orthop* 104: 92-111, 1974.

Tubiana R (1981) Architecture and functions of the hand. In: *The Hand* (Tubiana R, ed), pp 19-93. Philadelphia, PA: W. B. Saunders.

Turvey MT (1990) Coordination. *Amer Psychol* 45:938-953.

Zatsiorsky, V. M. (1997). On muscle and joint viscosity. *Motor Control*, 1, 299–309.

Zatsiorsky, V. M., Li, Z. M., & Latash, M. L. (1998). Coordinated force production in multi-finger tasks: Finger interaction and neural network modeling. *Biological Cybernetics*, 79, 139–150.

Zatsiorsky, V. M., Li, Z. M., & Latash, M. L. (2000). Enslaving effects in multi-finger force production. *Experimental Brain Research*, 131, 187–195.

Zhang W, Scholz JP, Zatsiorsky VM, Latash ML. What do synergies do? Effects of secondary constraints on multi-digit synergies in accurate force-production tasks. *J Neurophysiol* (2008, in press).

Zhang W, Scholz JP, Zatsiorsky VM, Latash ML. What do synergies do? Effects of secondary constraints on multi-digit synergies in accurate force-production tasks. *J Neurophysiol* (2008, in press).

Zhang, W., Zatsiorsky, V. M., & Latash, M. L. (2006). Accurate production of time-varying patterns of the moment of force in multi-finger tasks. *Experimental Brain Research*, 175, 68–82.

Zimmerman SD, McCormick RJ, Vadlamudi RK, and Thomas DP. Age and training alter collagen characteristics in fast and slow twitch rat limb muscle. *J Appl Physiol* 75: 1670-1674, 1993.