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ABSTRACT

One of the central issues in the field of motor control is how movements are controlled, or more specifically, what is controlled by the central nervous system (CNS). Typically, movements involve the interaction of multiple effectors to produce a desired output. An attractive approach to addressing this problem is studying the interaction of fingers in multi-finger tasks. One issue that arises when studying finger interaction is that single finger force production cannot be performed independently of the other fingers. A behavior known as enslaving occurs when one tries to press with a single finger – the other fingers also produce force. The dissertation was divided into two parts. The purpose of the first part of the dissertation was to use single- and multi-finger pressing paradigms to investigate: 1) anatomical changes induced in fingers due to changes in configuration and force production of a single finger; 2) force changes of fingers due to an involuntary perturbation of a single finger during a four-finger pressing task; and 3) force changes of fingers due to voluntary pressing of a single finger which followed a task that required establishing a total force stabilizing synergy among the four fingers. The main findings from the first part of the dissertation were: 1) the changes in configuration and force production of a single finger resulted in no significant anatomical changes in the other fingers; 2) an involuntary perturbation of a single finger resulted in the non-perturbed fingers displaying changes in force that acted to stabilize task performance; and 3) following the establishment of a force stabilizing synergy the CNS was able to quickly abolish that synergy such that typical finger enslaving was observed during voluntary pressing with a single finger. The second part of the dissertation investigated whether it is plausible the CNS uses hypothetical control variables (called neural commands) instead of the mechanical variables (force in our case) to control and regulate movements. The neural commands are essentially free of the enslaving effects. Estimating neural commands is non-trivial and a methodological study was performed to determine the best procedure for computing neural commands. It was determined that a neural network model provided the most accurate estimation of neural commands. Analytical inverse optimization (ANIO) and uncontrolled manifold analysis (UCM) were used to compare performance of neural commands to finger forces in a multi-finger pressing task. Based on the experimental results it appears plausible that the CNS may operate in the space of neural commands. The neural commands performed equally as well to the forces in terms of optimality and outperformed forces in terms of the structure of variance. These findings agree with the notion that the CNS controls patterns of muscle activity, not individual muscles and the findings also support a synergistic hierarchical organization of the elemental variables.
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CHAPTER 1

Introduction

1.1 Problem Background

Finger interaction during multi-finger tasks is an attractive approach to studying the motor redundancy problem (Bernstein 1967). Recently, the referent configuration (RC) hypothesis (Feldman & Levin 1995) has been merged with the concept of a hierarchical control of multi-element systems (Latash 2010; Latash et al. 2010), such as multi-finger pressing. A synergistic relationship exists among the fingers such that they co-vary to stabilize specified performance variable(s). The problem has been formulated within the framework of the uncontrolled manifold hypothesis (UCM; Scholz & Schoner 1999; reviewed in Latash et al. 2007). In the case of multi-finger pressing the finger forces are referred to as elemental variables (EVs) and the desired performance output (i.e. total force, total moment, or a combination of both) are the performance variable (PV). The finger forces exhibit “good” and “bad” variance. Good variance does not result in changes in the performance variable while bad variance does.

Motor synergies feature two key components: sharing and flexibility/stability (Latash et al. 2007). Sharing is the average distribution patterns of elemental variables across trials. The shape of these distributions describes the synergy. Flexibility is necessary to deal with multiple PVs, as well as, unexpected perturbations. Recently, two research methods have been developed which allow for analysis of each synergy component based on experimental data. Analytical inverse optimization (ANIO; Terekhov et al. 2010) reconstructs an additive cost-function from experimental data collected from a sub-space of a given task. The task is specified by linear constraints. It is likely that average sharing patterns are chosen based on optimization criteria selected by the CNS. The relative flexibility, or strength of the synergy, can be estimated by decomposing the good and bad variance of the EVs.

Finger force output during multi-finger pressing is a complex interaction of anatomy and neurophysiological mechanisms. Finger forces are not independent of one another and the behaviors of enslaving (Zatsiorsky et al. 1998; Zatsiorsky 2000; Yu et al. 2010) and force deficit (Ohtsuki 1981; Li et al. 1998; Yu et al. 2010). These behaviors are assumed to be due to: i) mechanical connections among the fingers (Fahrer 1981); ii) multi-digit motor units in the
extrinsic flexor and extensor muscles (Kilbreath & Gandevia 1994; Schieber 1995); and iii) overlapping cortical areas controlling individual finger movements (Schieber 1993).

Ideally the elemental variables, used in both ANIO and UCM analysis, should be independent of one another. Finger forces do not meet this requirement. As a result, a method has been proposed that transforms finger forces into hypothetical neural commands (NCs). The NCs are related to finger forces via the following relationship: 

\[
[F] = [IFC][NC],
\]

where \([F]\) is a \((4 \times 1)\) vector of finger forces, \([IFC]\) is the \((4 \times 4)\) inter-finger connection matrix, and \([NC]\) is a \((4 \times 1)\) vector of the NCs. The \([IFC]\) accounts for the enslaving and force deficit behaviors.

1.2 Problem Statement & Dissertation Objectives

The purpose of this dissertation was to study finger interaction, with respect to forces and NCs, during tasks in which a specified PV results in a synergistic relationship among the EVs. Often during everyday tasks involving multi-finger interaction perturbations, which may be involuntary or voluntary, occur. The effects of voluntary pressing and involuntary perturbations were addressed in the first three studies (Chapters 3-5). Based on the results of the first three studies the question of whether force or NC data lead to more desirable performance of tasks based on certain performance criteria were further evaluated. The best method of computing NCs was examined in the fourth study (Chapter 6). The ANIO and UCM analysis tools were used to describe the synergies in the last study (Chapter 7). The results were formulated within the context of the RC hypothesis (Feldman & Levin 1995). The specific purposes of the studies were to:

1. examine how changes in position and activation level of one finger affects the moment arm of the FDS tendon about the MCP joint of that finger, as well as, the other fingers;
2. study the force changes of fingers in response to different involuntary perturbations to a single finger during a multi-finger force production task;
3. analyze the changes in force and NCs due to involuntary perturbations and voluntary pressing;
4. determine the most accurate method of computing NCs;
5. perform ANIO on NC data then compare ANIO performance of NC data to force data;
6. perform UCM analysis on NC data then compare results to UCM analysis of force data.
1.3 Research Studies Comprising Dissertation
This dissertation consists of five research papers (Chapters 3-7) that addressed each of the specific purposes listed above. All of the research papers have been published, submitted, or soon to be submitted for publication. In addition, there is a literature review (Chapter 2) and a conclusion (Chapter 8) that discusses the overall findings of the five studies. The research papers comprising Chapters 3 – 7 are:


1.4 Overview of Individual Research Studies
Mechanical connections among the fingers contribute to the lack of independence of the fingers. The goal of the first study (described in Chapter 3 of the dissertation; Martin et al. 2012a) was to examine how changes in position and activation level of one finger affects the moment arm of the FDS tendon about the MCP joint of that finger and the other fingers. *We hypothesized that the index finger FDS moment arm would show systematic changes with MCP joint position and force production level. No formal hypothesis was formulated for changes in the moment arms of
the FDS of the other fingers. MRI was used to scan the hands of subjects with the index finger in a flexed, neutral, and extended MCP joint position. In each position there as an active force production condition and a passive force production condition (i.e. no force intentionally produced).

The second study (Chapter 4; Martin et al. 2011a) investigated the force response of fingers to an involuntary perturbation of a single finger. The study required subjects to produce a certain level of total force by pressing with all four-fingers. After a total force stabilizing synergy was established one of the fingers was randomly raised. It was expected that the raised finger would increase its force production due to peripheral spring-like properties of the muscles and the stretch reflex. A previously published study had used a similar paradigm, except that the perturbation was voluntarily produced by the subject (Latash et al. 1998). Synergistic reactions to stabilize force were observed in that study. The goal of the Chapter 4 study was to examine the force changes of fingers in response to an involuntary perturbation applied to a single finger. We hypothesized that similar synergistic reactions would be observed in response to the involuntary perturbation, or in other words the non-raised fingers would show a force decrease to stabilize the total force.

Following the second study (Chapter 4) the notion of NCs (referred to as modes in the published paper) was introduced to the dissertation work. The third study (Chapter 5; Martin et al. 2011b) examined changes in forces and NCs in response to perturbations. An involuntary perturbation, qualitatively the same as in the second study was used. The involuntary perturbation was then followed by a voluntary pressing in which subjects were asked to produce a quick, hard force pulse with the perturbed finger. The goal of the third study was to analyze the changes in finger forces and NCs due to the perturbations. Two hypotheses were formulated. The first hypothesis was that due to the involuntary perturbation the force and NCs of other fingers will decrease. The second hypothesis was that due to the voluntary pressing of a single finger the force and NC of the pressing finger will increase, the forces of the non-pressing fingers will increase and the NCs of the non-perturbed fingers will not change. The results were formulated in the context of the referent configuration hypothesis.

The next study (Chapter 6; Martin et al. 2012b) addressed the question of which of the previously used methods is best for computing NCs. The two methods compared were the one using only single-finger MVC trials (proposed by Danion et al. 2003) and the neural network
method (Zatsiorsky et al. 1998) using all fifteen combinations of MVC trials. The formal hypothesis was that the neural network model will outperform the single-finger MVC method because it will better predict enslaving and force deficit in multi-finger trials. The error of each method’s predicted values versus experimental values for the fifteen MVC trials and mathematical properties of the inter-finger connection matrices were compared.

The final study (Chapter 7; Martin et al. 2012c) had four main goals: 1) to perform ANIO on NC data; 2) to compare ANIO results on NC and force data; 3) analyze NC data variability within the framework of UCM analysis then compare to the variability of force data; and 4) to use statistical modeling techniques to check the probability of the results. Whether or not ANIO could be performed on NC data was unknown. Two hypotheses were formulated. The first hypothesis was that ANIO will work in the space of finger forces but not in the space of NCs. The second hypothesis was that the UCM results will favor the NCs due to the enslaving behavior. Subjects were asked to press to match specified combinations of total force and total moment with four-fingers. A neural network model was used to compute finger inter-connection matrices. Using the inter-connection matrices the force data from the experimental trials were transformed to neural commands. ANIO and UCM analysis was performed on both types of data (force and NC) then the results were compared.

1.5 Study Limitations
There were limitations encountered during each of the studies. The specific limitations of each study are detailed in the discussion sections of those respective studies. The following is a list of general limitations for the dissertation work:

1. Only young, healthy male subjects were used in the experiments. Thus, effects of age, sex, injury, and disease on the results were not investigated.
2. The sample population was limited to the surrounding community which may not be an accurate representation of larger populations.
3. Only the right hands of right hand dominant subjects were tested. Testing the non-dominant hands may have yielded interesting results.
4. Only normal forces were recorded. Subjects may have produced substantial forces in the tangential directions.
5. Subjects were only tested on a single day and a limited number of trials for each condition were performed during each testing session. Collecting more trials may have resulted in more accurate depictions of finger interaction in the various studies.

1.6 Future Research
The future research performed should attempt to address the limitations mentioned above, as well as, limitations outlined in the discussion sections of each of the five studies (Chapters 3-7). More importantly, future work should focus on identifying differences in populations that have “poor” finger interaction due to injury or disease. Loss of the ability to properly coordinate fingers can severely limit one’s ability to perform common everyday tasks (i.e. eating, cooking, writing, typing, brushing teeth, etc). Improving our current knowledge of the motor control mechanisms of finger interaction should lead to improved rehabilitation methods to aid these individuals, which is ultimately the goal of our line of research.

1.7 Glossary of Terms
Analytical Inverse Optimization – optimization procedure in which a cost function is computed from experimental data.

Bad Variance - variance of elemental variables that does cause undesired changes in the task performance. Bad variance is orthogonal to the uncontrolled manifold.

Elemental Variable – a variable that is controlled by a central controller during a task. Finger forces and neural commands are the selected elemental variables in this dissertation.

Enslaving – the behavior of unintentionally producing force with a finger when other finger(s) intentionally produce force.

Force Deficit – the behavior that a single finger produces less force in a multi-finger maximum voluntary contraction than in a single finger maximum voluntary contraction.

Good Variance – variance of elemental variables that does not cause undesired changes in the task performance, variance parallel to the uncontrolled manifold.
Inter-Finger Connection Matrix – a $4 \times 4$ matrix that contains diagonal and off-diagonal elements that model the enslaving behavior. The diagonal elements are forces produced intentionally by fingers. The off-diagonal elements are forces produced unintentionally. The matrix may be multiplied by a gain factor that varies with the number of fingers involved in the task.

Inverse Piano – a device consisting of force sensors mounted on top of actuators that produce movement in the vertical direction. The device is used to produce perturbations during multi-finger pressing tasks.

Involuntary – a behavior that cannot be modified at the will of the performer.

Mode Command – see Neural Command.

Motor Synergy – an organization of effectors to stabilize a certain value, or output of the effectors. A synergy is characterized by a co-variation of elemental variables to achieve this goal. Synergies allow for flexible sharing patterns among the effectors.

Neural Command – hypothetical command to a finger that is scaled from 0 to 1. A command of 0 represents no intentional force production while a command of 1 represents maximal force production. A neural command accounts for the enslaving behavior; thus a neural command to one finger results in force production of other fingers as well.

Neural Network – a form of artificial intelligence that attempts to model how the brain works. A neural network consists of connections between input units and output units, which are the equivalent of neurons. Neural network models are based on a database and are commonly used to predict events.

Performance Variable – the goal, or output, that the central controller attempts to achieve through the organization of elemental variables. In this dissertation the performance variables were assumed to be total force or total moment.

Perturbation – an event that induces a sudden change in the current behavior of the system. The perturbation may be induced voluntarily by the performer or by an external mechanism (involuntary).
*Uncontrolled Manifold* – the space of elemental variables that results in no change in the desired value of the performance variable. In mathematical terms, this is the null space of the jacobian relating changes in elemental variables to changes in the performance variable(s).

*Virtual Finger* – an imaginary finger that has the same mechanical action as the index, middle, ring, and little fingers combined.

*Voluntary* - a behavior that can be modified at the will of the performer.
CHAPTER 2

Literature Review

2.1 Introduction
Finger interaction is incredibly complex yet dexterous manipulations of objects are performed hundreds of times a day with ease. Most people take for granted how much easier everyday life is with healthy finger and hand function. However, many diseases and injuries severely limit how one can use their hands. For this reason, the study of finger interaction is an area of biomechanics and motor control that deserves a great deal of focus. Although much is known about finger interaction there are still many unanswered questions. The following review will provide a basic understanding of what is already known. The review starts with basic anatomy and neurophysiology of the hand. Next, basic characteristics of finger interaction will be discussed. One of the most commonly performed tasks requiring proper finger interaction –prehension – will be covered. The last portion of the review will focus on control theories as to how the central nervous system controls fingers. Several popular analysis methods relating to control of the fingers are presented as well.

2.2 Finger/Hand Anatomy & Physiology

2.2.1 Bones & Joints
There are twenty-seven bones in the human hand. These bones are divided into three groups: phalanges, metacarpals, and carpals (Appendix A -Figure A.1). The fourteen phalanges are located in the fingers, distal to the metacarpals. Each finger has a distal, middle, and proximal phalanx, while the thumb only has distal and proximal phalanges. The joints between the phalanges are called interphalangeal joints. The proximal interphalangeal (PIP) joints are between the proximal and middle phalanges. The distal interphalangeal (DIP) joints are between the middle and distal phalanges. Interphalangeal joints only allow one degree of freedom, which is flexion/extension. There are five metacarpal bones in the palm of the hand. Metacarpals articulate with the base of proximal phalanges and the distal row of carpals. The articulation between the head of a metacarpal and base of proximal phalanx is appropriately termed a metacarpophalangeal (MCP) joint. MCP joints allow both flexion/extension and
abduction/adduction. The base of a metacarpal bone articulates with a distal carpal bone to form a carpometacarpal (CMC) joint. The proximal region of the hand consists of eight carpal bones, arranged in two rows. The proximal row, from lateral to medial, is contains the scaphoid, lunate, triquetrum, and pisiform. The distal row, from lateral to medial, contains the trapezium, trapezoid, capitate, and hamate. The articulations between carpal bones are called intercarpal joints. The radius and ulna bones of the forearm articulate with the proximal row of carpals to form the wrist.

2.2.2 Muscles
The muscles of the hand are divided into two categories: extrinsic and intrinsic. Extrinsic muscles originate from the forearm and insert within the hand, while intrinsic muscles originate and insert within the hand. The major extrinsic muscles are flexor pollicus longus (FPL), flexor digitorum profundus (FDP), flexor digitorum superficialis (FDS), extensor pollicus brevis (EPB), extensor pollicus longus (EPL), extensor digitorum communis (EDC), and extensor digiti minimi (EDM). The insertions, origins, and actions of these extrinsic hand muscles are illustrated in Appendix A - Figure A.2 and described in Appendix A - Table A.1.

The intrinsic muscles of the hand are subdivided into three groups: thenar, hypothenar, and intermediate. The thenar muscles makeup the lateral muscle bulge on the palm of the hand, the hypothenar muscles are located in the medial palm of hand, and the intermediate muscles are located in the palm, between the thenar and hypothenar muscles (Appendix A - Figure A.3). The insertions, origins, and actions of these intrinsic hand muscles are described in Appendix A - Table A.2.

2.2.3 Innervation
The hand is innervated by three nerves that branch off from the brachial plexus which originates from the cervical vertebrate C5-C7 and T1. The median nerve innervates the radial two-thirds palmar side of hand and the majority of finger flexor muscles. Muscles that perform fine precision and pinch function of the hand are typically innervated by the median nerve. The radial nerve innervates the lateral two-thirds, dorsal side, of the hand, which includes most finger extensor muscles. The third nerve, the ulnar nerve, innervates the rest of the muscles of the
hand. Most muscles activated during power grasping are innervated by the ulnar nerve. The muscles innervated by each nerve are described in Appendix A-Table A.3.

2.2.4 Skin, Cutaneous Receptors, & Sensation

The characteristics of the skin on the dorsal and palmar sides of the hand differ in several regards. Skin on the palmar side of hand is characterized by a thicker epidermis, papillary ridges that increase contact friction, and a denser concentration of sensory receptors. The dorsal skin of hand has a thinner epidermis, contains hair follicles, fewer sweat glands, and is more pliable.

One of the more important features of the skin of the hand is the high density of cutaneous receptors on the palmar side. The cutaneous receptors sense various stimuli that make the hand an asset for gaining tactile information about objects and the surrounding environment. The three categories of receptors are mechanoreceptors, thermoceptors, and nociceptors. Mechanoreceptors sense mechanical stimuli, thermoceptors sense temperature, and nociceptors sense pain or damaging stimuli. Mechanoreceptors are especially important in human movement because they detect tactile stimuli that may elicit responses.

There are four types of mechanoreceptors: Meissner corpuscles, Merkel disks, Ruffini endings, and Pacinian corpuscles. Vallbo and Johansson (1984) performed a study to examine various properties of mechanoreceptors in the human hand. Distinct differences between the mechanoreceptors in terms of receptive field size, types of stimuli that provoked a response, and density distribution in the hand were reported. Some distinguishing qualitative properties of each type of mechanoreceptor, from the study are shown in Appendix A - Table A.4. Not surprisingly, they found that mechanoreceptors are very densely distributed in the fingertips and estimated that the hand contains roughly 17,000 tactile sensing units.

2.3 Neurophysiology of Hand & Finger Control

2.3.1 Cortical Control of the Hand

The area of the brain that is responsible for producing commands to activate muscles is the primary motor cortex (M1). The more control required for a given body part the greater the percentage of M1 that is devoted to that part. M1 is characterized by a disproportionately large representation of the hand with no clear borders between anatomical structures (Schieber 1993; Schieber 2001; Schieber & Santello 2004). The general scheme of the neural control of finger
muscles involves a control loop in which commands are sent from neurons in the motor cortex down descending pathways to motoneurons in the spinal column. These motoneurons send action potentials to muscle fibers, which cause the muscle fibers to contract. The motoneuron and the muscle fibers innervated are called a motor unit (MU). Feedback information, which may be position, velocity or force, is then sent from muscle spindles to ascending pathways to the brain that then regulates the commands based on the feedback it has received. The major pathways are the pyramidal and extrapyramidal tracts. Afferent information travels back to the spinal cord and provides feedback to the central nervous system (CNS) via the extrapyramidal tract. Individual neurons in the corticospinal tract produce both excitatory and inhibitory effects on α-motoneurons of hand muscles on the contralateral side of the body. The excitatory effects can be direct, resulting from a single excitatory synapse of a corticospinal fiber on the α-motoneuron. The inhibitory effects are always mediated by at least one interneuron (Latash 2008a).

Another important structure for performing voluntary movements is the cerebellum. The cerebellum has been speculated to be responsible for a number functions such as: timing of muscle activation, learning device for acquiring new motor skills, coordinating multi-joint movements, and comparator for detecting movement errors. The cerebellum receives inputs from the mossy fibers and the climbing fibers. The mossy fibers carry information from the vestibular, somatosensory, visual, auditory, and proprioceptive systems, as well as from the cerebral cortex. The climbing fibers originate in the medulla and synapse on Purkinje cells. Their inputs are excitatory and strong. The Purkinje cells are responsible for the only outputs of the cerebellum. The axons of the Purkinje cells make inhibitory synapses on neurons within the cerebellar and vestibular nuclei, which then project to the thalamus and then onto the cerebral cortex. It should be noted that neurons in the cerebellum do not connect with neurons in the spinal column. A number of studies have investigated if cerebellar activity is related to movement parameters, such as muscle force or EMG. A weak correlation with movement direction (Fortier et al. 1989) has been shown; however, the overall findings have been inconclusive. In terms of control of movements the cerebellum has been the structure that stores internal models (Bastian et al. 1996) and assembling motor synergies (Houk et al. 1996). Internal models and synergies are discussed later.
The basal ganglia are involved in voluntary movements. Like the cerebellum the exact function of the basal ganglia is not known; however, people suffering from basal ganglia disorders exhibit excessive involuntary movements and slow voluntary movements. The main input to the basal ganglia is from the cerebral cortex and the main output is back to the cerebral cortex. Although the exact function of basal ganglia is not known it appears that some of the functions are to disinhibit areas of the motor system, such as turning off postural activity which in turn allows voluntary movement to occur, and preventing unwanted movements. The basal ganglia function also appears to be related to learning, memory, and cognition.

The major pathways of the CNS can be divided into afferent and efferent pathways. Afferent pathways carry information from the periphery to the CNS, while efferent pathways carry information in the opposite direction. The dorsal columns of the spinal cord carry afferent information from sensory information from the periphery. The major afferent pathways in the dorsal column of the spinal cord are the dorsal, ventral and rostral spinocerebellar tracts, as well as, the cuneocerebellar and spino-olivary-cerebellar tract. The major efferent pathway that carries information from the cortex to the rest of the body is the pyramidal tract. The pyramidal tract is further divided into the corticospinal tract and the corticobulbar tract. The corticospinal tract fibers go down to the spinal cord and the corticobulbar tract fibers lead into motor nuclei of the cranial nerves. Several pathways carry information from the cerebellum to other structures. These pathways are the rubrospinal, lateral vestibulospinal, and medial vestibulospinal tracts.

2.3.2 Studies of Motor Unit Firing Patterns of Fingers

The neural control of the muscles in the hand is an area that has been actively researched for the past thirty years. Advancements in technology have allowed for new and improved research techniques over the past several decades. Research techniques typically involve recording of neural activity in the motor cortex or electromyography (EMG) activity in the muscles during tasks involving the fingers and correlating the MU firing (synchronization; for review see Farmer et al. 1997; Semmler 2001) or analyzing MU firing in the frequency domain (coherence). For a more comprehensive review of the literature on neural control mechanisms of finger function see Johnston et al. (2009). Additionally, MU structure and physiology is extremely complex. The relationship between cortical, or muscular EMG, activity and forces produced by muscles are not a direct one to one relation. Reasons for this statement are reviewed in Monti et al. (2001).
following text will review several of the key studies, in chronological order, from the past twenty years that relate to the hand and fingers.

A number of studies were performed in the 1970’s and 1980’s by the researchers EJ Buys, RN Lemon, PD Cheney, and EE Fetz (Lemon et al. 1976; Fetz & Cheney 1980; Lemon 1981; Fetz & Sawyer 1983; Buys et al. 1984; Lemon et al. 1984; Buys et al. 1986; Lemon et al. 1986) that investigated cortical control of forearm muscles in monkeys. These studies provided much insight on the cortical control of muscles involved in finger movements. They also paved the way for later studies that are more applicable to this dissertation. Several of these later studies are described in the following text.

A study by Schieber and Hibbard (1993) provided evidence that there is considerable overlap in the motor cortex of areas controlling different fingers. Two rhesus monkeys were trained to perform flexion and extension movements with each digit, as well as, the wrist. Neuronal activity was recorded from both monkeys during the movements. The main findings were: 1) many of the individual neurons were related to two or more finger movements, 2) the neurons related to the instructed movement were distributed throughout the hand area of M1, 3) the areas responsible for finger movements overlapped with areas responsible for wrist movements, and 4) the M1 neurons related to finger movements were found in the anterior bank and lip of the central sulcus.

Kilbreath and Gandevia (1994) performed one of the first studies that used intramuscular EMG recordings to attempt to quantify co-activation of finger flexors (FDP) during finger flexion tasks. Subjects were asked to lift weights ranging from 2.5% to 50% of their maximum voluntary contraction (MVC) by performing flexion of the DIP joint. EMG was recorded from each digital portion of the FDP while the flexion task was performed. The major findings were that: 1) at forces levels as low as 2.5% of MVC other non-lifting fingers displayed EMG activity, 2) a proximity effect was observed – fingers closer to the lifting finger showed more EMG activity than fingers further away, 3) co-activation depended on the angular velocity of lifting finger and angular range lifting finger went through. Another finding that was reported relates to finger independence, which will be discussed later. Cadaver arms were dissected and the separation of the digital tendons from the FDP muscle belly was measured. The index portion of FDP extended much more proximally than the tendons of the other digits.
The following year (1995) Schieber published a study that supported the findings of Kilbreath and Gandevia (1994). However, his subjects were rhesus monkeys not humans. Three rhesus monkeys were trained to perform finger flexion and extension movements. Intramuscular EMG was recorded from the FDP, FDS, FCR, PL, FCU, EPL, EDC, ECU and ECRB. The findings showed simultaneous muscle activity in several muscles that acted as agonists, antagonists, or stabilizers for the non-instructed digits. The study provided further evidence that finger muscles are unable to contract independently and that this lack of independence has strong neural origin (i.e. not due to passive connections).

More recently Dr. Marco Santello and colleagues have performed a number of studies analyzing EMG activity using more advanced coherence and correlation analysis techniques during common tasks, such as prehension. A 2004 study (Santello and Fuglevand) used a motor unit model to simulate force produced by two muscles. Three physiological levels of motor unit synchrony across the muscles were simulated. The results demonstrated a tendency for forces to be exerted in a synchronous manner and provided evidence that motor unit synchronization may play an important role in coordinate finger forces, especially during grasping. Several studies were performed that measured motor unit synchrony (Winges & Santello, 2004) and further quantified motor unit firing properties (Johnston et al. 2005) during a static prehension task performed by eight human subjects. Subjects were asked to statically hold an instrumented handle for three minutes. The handle was equipped with force sensors for each digit. Intramuscular EMG activity was recorded from the individual digit compartments of FDP and FDL muscles. The first study focused on the strength of motor unit synchrony between FDP compartments and FDL. Strong synchrony was observed between the index FDP compartment and FDL, as well as between individual FDP compartments. Weak synchrony was observed between the FDL and middle-, ring-, and little-finger compartments of the FDP. The results indicated that the motor unit synchrony was related to the functional (force) requirements of the task. The second study (Johnston et al. 2005) analyzed the data to further characterize neural control mechanisms. The firing of motor units was analyzed in the frequency domain by computing coherence. The major findings were: 1) motor units belonging to different muscles and compartments of FDP showed significant coherence in the low frequency range (<10 Hz), 2) the strength and incidence of coherence was different among pairs of digits, and 3) across muscle coherence can be stronger than within muscle coherence. Some other relevant findings are
discussed in the following text. The study also measured pooled coherence across motor unit pairs. Significant pooled coherence was assumed to indicate common periodic input to the motor unit pairs. The greatest amount of pooled coherence occurred in the lower frequency range (<10 Hz). Linear correlation analysis was performed between motor unit synchrony strength and coherence. Significant correlations would indicate common periodic input. Results showed that 9% of the motor unit pairs had significant correlations while the other 91% did not. This finding shows that there is a heterogeneous distribution of periodic and non-periodic inputs to extrinsic hand muscles. It was suggested that there may be functional reasons explaining many of the results. The FPL and index portion of FDP produce the largest normal forces during prehension, thus the strength of motor unit synchrony between these muscles may reflect this. Likewise, the index and little fingers have the greatest effect on the moment produced about the center of mass of the handle, so it is very likely that the strength of motor unit synchrony between these pairs results from the functional roles of these fingers.

The studies mentioned above illustrate how complex neural control of the fingers is. Representation of the fingers in the motor cortex has no clear boundaries, which for motor control researchers makes studying the cortical control of fingers more difficult, but undoubtedly makes controlling fingers easier for the CNS. It promotes neural plasticity which decreases the loss of function that may occur due to an injury to a region of the motor cortex if other neurons, not in the injured area, are also capable of controlling the same fingers as the injured neurons. Analysis of EMG activity shows that the CNS is not able to activate individual digits of extrinsic muscles independently. Descending control of extrinsic muscles appears to be organized in a way that facilitates synergistic control of fingers in a task relevant manner. One thing is clear, much more work needs to be performed to understand neural control mechanisms of the fingers.

2.4 Characteristics of Finger Interaction

The number of studies investigating various aspects of finger interaction is quite numerous and continues to be a lively area of research. The following section will focus on basic qualities of finger interaction that have important functional implications on various tasks. The characteristics that will be reviewed are: enslaving, force deficit and force sharing. Neural network models, which incorporate all these characteristics, will also be reviewed.
2.4.1 Enslaving

When a person is asked to voluntarily produce force with one finger other fingers involuntarily produce force as well. This behavior is referred to as enslaving in the literature (Zatsiorsky et al. 1998; Zatsiorsky et al. 2000; Slobounov et al. 2002a,b; Yu et al. 2010). Enslaving occurs in both flexion and extension (Yu et al. 2010), as well as in isometric and non-isometric tasks (Hager-Ross and Schieber 2000; Kim et al. 2008). Enslaving may be due to three factors: 1) passive connections among the digits (Fahrer 1981; Kilbreath & Gandevia 1994; Leijnse 1997); 2) multi-digit motor units of the extrinsic muscles (Kilbreath & Gandevia 1994; Schieber 1995); and 3) overlapping cortical representation of the digits (Schieber & Hibbard 1993; Sanes et al. 1995; Rathelot & Strick 2006). A number of studies have documented enslaving characteristics of the digits. The following text reviews some of the major studies that focused on quantifying the enslaving behavior. The studies referenced as reasons for enslaving are discussed in other sections of this literature review.

One of the first studies to quantify the independence of finger movements was performed using rhesus monkeys trained to perform flexion and extension movements of the digits (Schieber 1991). Two monkeys performed flexion and extension of all the digits individually. Motion of all the digits was recorded. They found that during instructed movements of the thumb and wrist there was little movement of the digits. However, during instructed movement of the I-, M-, R-, and L-fingers other, non-instructed, fingers tended to move in the same direction, but to a lesser degree. In a few instances non-instructed fingers moved in the opposite direction as the instructed. An individuation measure was computed to numerically rate the independence of each digit. According to the individuation measure the thumb was the most independent, followed by the I-finger. The M-, R-, and L-fingers all had low individuation measures. Flexion was found to have a higher individuation measure than extension for most fingers. It was also found that one monkey was able to perform finger movements more independently than the other monkey. The author concluded that mechanically connections among the fingers were not the sole reason for lack of independence. A limitation of the study was that monkeys are known to have less independent finger movements than humans.

Zatsiorsky et al. (1998) studied enslaving using human subjects. Ten subjects were asked to press with all fifteen finger combinations to achieve MVC in an isometric contraction. Forces were recorded. Subjects were asked to keep all fingers on the force sensors. Four main findings
were reported: 1) the enslaving effects were large – uninstructed fingers produced forces as large as 54.7% of their MVC; 2) the enslaving effects were symmetrical – finger A enslaved finger B approximately the same as finger B enslaved finger A; 3) the enslaving effects were larger for fingers in closer proximity to the instructed finger(s); and 4) the enslaving effects were non-additive. The authors listed several reasons why the observed enslaving effects were not due to passive mechanical effects alone. Several of the reasons listed were the fact that the task was isometric made it difficult to assess how internal forces were transmitted between the fingers and the unintentional force production by finger(s) several fingers away from the instructed finger(s) was likely not to be purely due to mechanical connections. Fingers are also unable to be selectively activated, even at low force levels (Kilbreath & Gandevia 1994).

In a follow up to the 1998 study Zatsiorsky et al. (2000) investigated whether the enslaving effects were the same if the point of force application was at different locations along the finger. The locations for point of force application used were at the middle of the distal phalanx, at the DIP joint and at the PIP joint. This method changed the contribution of muscles to the force produced at the point of application due to different insertions of the muscles. Similar to the previous study subjects pressed with MVC for all fifteen finger combinations at each of the points of force application. The main result was that the enslaving effects were similar for all three points of force application conditions. The four properties of enslaving reported in the 1998 study were also observed. This study provided further support for a strong neural origin of the enslaving behavior.

The previously mention Yu et al. (2010) study documented enslaving during finger extension. The authors found that enslaving was greater in extension than flexion. All of the previous properties of enslaving in finger flexion were similar in finger extension. It was suggested that enslaving was greater in extension than flexion because in everyday tasks independent flexion movements are more common, or desirable, than extension movements.

2.4.2 Force Deficit
When a person is asked to produce a MVC contraction with multiple fingers the maximum forces produced by the individual fingers in the multi-finger MVC task is not as great as the maximum force produced by any of the fingers in a single-finger MVC task. This behavior is
referred to as force deficit (Ohtsuki 1981; Li et al. 1998). Force deficit is exhibited in both finger flexion and extension (Yu et al. 2010).

Li et al. (1998) studied force deficit of the fingers using a MVC isometric pressing task for all one-, two-, three-, and four-finger combinations of I-, M-, R-, and L-fingers on one hand (fifteen combinations total). A force deficit was observed in the multi-finger pressing combinations. They found that as the number of fingers in the task increase so too did the force deficit. Additionally, it was found that increasing the number of fingers from three to four did not significantly increase the total force produced. They also found that the force deficit was different for different fingers. Several hypotheses were offered to explain the observed force deficit. One of the hypotheses offered was based on the idea that a central neural drive gets distributed among all the fingers involved in a given task. There is a limit to how much central neural drive can be delivered and thus the more fingers involved in a task the more the neural drive has to be divided among the fingers, resulting in a force deficit compared to tasks involving fewer fingers.

A decade later another study was performed that studied force deficit during finger extension (Yu et al. 2010). The study had eleven subjects perform MVC contractions with all fifteen combinations of single- and multi-finger flexion and extension tasks. In terms of force deficit, they found that the force deficit was smaller in extension than flexion, but still present. There was also an effect of the number of non-instructed fingers between the fingers instructed to produce MVC – tasks with non-instructed fingers between instructed fingers had a high force deficit. The authors also reported a negative relationship between enslaving and force deficit for the three finger tasks. A variety of neural factors were listed as potential reasons for the observed force deficit and enslaving behaviors of fingers.

2.4.3 Sharing
During multi-finger force production tasks, which may be pressing or prehension, the forces are typically shared among the fingers in a reproducible manner (Flanagan et al. 1999; Kinoshita et al. 1995; Zatsiorsky & Latash 2008). Observed force sharing patterns are task-dependent and thus change significantly from task to task. The sharing pattern may reflect force production capabilities of fingers, mechanical advantages of fingers or task constraints. The I- and M-fingers have the greatest force producing capabilities. The I- and L-fingers have the greatest
moment producing capabilities about the midline of the hand. Generally, force sharing patterns are established at the onset of the task and do not deviate much from the initial pattern of sharing. Force sharing patterns are fairly repeatable for repeated trials performed by the same subject and across subjects. Force sharing among the fingers is commonly studied as a means of addressing the motor redundancy problem (Li et al. 1998). Enslaving and force deficit effects can also affect force sharing patterns.

The minimum secondary moment hypothesis was offered to explain sharing patterns in multi-finger pressing tasks (Li et al. 1998). The hypothesis states that the forces produced by fingers are shared in a way to minimize the moment produced about the longitudinal axis of the hand. It may be more plausible that this is a secondary goal of many finger pressing tasks, in which the main goal is to produce an MVC force level (Li et al. 1998; Zatsiorsky et al. 2000), as the neutral line of the forces shifts depending on the number of fingers involved.

It is assumed that the control of fingers involves a hierarchical process. The higher level reflects the overall tasks requirements and the lower level reflects a synergy among the finger to achieve the goals of the higher level. Supporting evidence is that has been observed that in total force production tasks the variance of the total force is less than the sum of the variance of the individual finger forces (Li et al. 1998). The fact that most people perform tasks in a similar fashion suggests that some sort of optimization is used by the CNS in deciding how movements are performed.

2.4.4 Neural Network Modeling

Neural network (NN) models have been used to relate hypothetical neural commands (NCs) to forces produced by fingers (Zatsiorsky et al. 1998; Li et al. 2002; Zatsiorsky et al. 2002b; Zatsiorsky et al. 2004). NN models are able to account for enslaving, force deficit, and force sharing which make them an attractive approach to modeling finger interaction. The previous NN models have been comprised of three layers: 1) an input layer that models a central neural drive; 2) a hidden layer that models extrinsic muscles; and 3) an output layer that models the force output of fingers. The NN models used previously incorporated the following ideas:

1) The extrinsic muscle groups serve multiple fingers. These are represented by the hidden layer and its multiple connections. The intrinsic muscles are represented by direct connections from the input to output layer.
2) Force deficit is modeled by multiplying the output of the hidden layer by a gain that is inversely proportional to the number of fingers explicitly involved in the task. The force deficit is assumed to only affect the output of the hidden layer (i.e. extrinsic muscles).

3) Enslaving is modeled through the connection weights that affect the output from the hidden to the output layer.

The first experimental study to use a NN model of finger interaction was Zatsiorsky et al. (1998). The network was trained using a back-propagation algorithm (Bose & Liang 1996) on fifteen MVC tasks. Satisfactory results were obtained after 500 epochs of the algorithm with a learning rate of 0.01. The RMSE between the experimental data and model data was 1.14 N. Overall, the results of the NN model were very close to the experimental data in all conditions. It was concluded that the NN supported the idea that there is no direct correspondence between the intensity of neural commands to an individual finger’s force output. The idea of neural commands is discussed in a later section.

Three other studies reported findings of NN models of finger interaction (Danion et al. 2003; Zatsiorsky et al. 2002b; Zatsiorsky et al. 2004). All of these studies reported favorable findings in the ability of NN models to predict finger forces in multi-finger tasks. Compared to other methods the NN model was the only one to predict positive forces of antagonist fingers, with respect to moment production during a prehension task (Zatsiorsky et al. 2002, 2004). Using NN models to predict finger forces is proven to be an effective modeling technique.

### 2.4.5 Muscle Mechanics & Models

The biomechanics of the fingers is more complicated than other joints due to the complex anatomy within the hand and fingers. The majority of research has focused on the effects of FDS and FDP muscle-tendon units (MTUs) on finger flexion of the DIP, PIP, and MCP joints. The FDP has been shown to perform most of the flexion during low force tasks (Long et al. 1970) and the FDS is recruited when more strength is needed. For a more complete review of the biomechanics of the finger flexors see Gonzalez et al. (2005), Goodman & Choueka (2005), and Freivalds (2004).

One of the factors complicating analysis of finger flexor tendon is the pulley system (also called the flexor sheath) that holds the tendons against the finger bones to prevent bowstringing and maintain relatively constant moment arms. The pulley system consists of five
annular pulleys and three cruciate pulleys. A consequence of the pulley system is relatively large tendon excursions are needed to produce rotation of the finger joints.

Landsmeer (1960) constructed three static tendon-pulley models that establish the tendon-joint displacement relationships under different assumptions. The first model assumes that the tendon is held securely around the curved surface of the proximal bone of the joint. The equation describing this relationship is:

\[ x = r \theta \]  \hspace{1cm} (2.1)

where \( x \) represents the tendon displacement, \( r \) is the distance from the joint center to the tendon, and \( \theta \) is the joint rotation angle. The second model assumes that the tendon is not held securely and can be displaced from the joint when it is flexed. Modeled by the equation:

\[ x = 2r \sin \left( \frac{\theta}{2} \right) \]  \hspace{1cm} (2.2)

The third model assumes that the tendon runs through a tendon sheath that holds it securely against the bone, allowing the tendon to curve around the joint. Tendon displaced is described by:

\[ x = 2 \left[ y + \left( \frac{1}{2} \right) \theta \left( d - \frac{y}{\tan \left( \frac{\theta}{2} \right)} \right) \right] \]  \hspace{1cm} (2.3)

where \( y \) is the tendon length to joint axis measured along the long axis of bone and \( d \) is the distance of tendon to the long axis of bone.

2.4.6 Mechanics of Multi-Link Bodies

The mechanics of pressing with the fingers can be modeled as a three-link chain (distal, middle, and proximal phalanges) with an endpoint force at the distal link (Figure 2.1). For a complete review see Zatsiorsky 1998 & 2002. The chain may be open or closed. An open chain is one that the end is free to move. A closed chain is one in which the end is constrained from movement by a mechanical stop. An example of a closed chain would be isometric finger pressing against a force sensor. The total number of degrees of freedom (DOF) in a multi-link chain is called the mobility of the chain. The mobility of a chain can be computed using Gruebler’s formula:

\[ F = 6(N - k) + \sum_{i=1}^{k} f_i \]  \hspace{1cm} (2.4)

where \( F \) is the mobility of the chain, \( N \) is the number of links, \( k \) is the number of joints and \( f_i \) is the number of DOF of the \( i \)th joint. For a finger the mobility, \( F \), is 4 \((F = 6 \times (3-3) + (2 + 1 + 1))\).
This is assuming there are three joints (MCP, PIP, DIP) with the MCP, PIP, DIP have two, one, and one DOF, respectively.

**Figure 2.1**: Schematic of three-link chain with external force, F, and couple, C, applied to the distal link. This is representative of pressing with a finger.

The motion of the endpoint of a three-link chain is affected by motion at all of the joints and can be described with the following equation:

\[ v = J \dot{\theta} \]  

(2.5)

where \( v \) is the velocity of the end-point \([\dot{x}, \dot{y}]^T\), \( J \) is the jacobian that relates displacements of the endpoint to displacements of the individual joints, and \( \dot{\alpha} \) is a vector of joint angular velocities \([\dot{\theta}_1, \dot{\theta}_2, \dot{\theta}_3]^T\). The end-point acceleration is found by differentiating equation 2.5:

\[ a = J \dot{\theta} + \ddot{J} \]  

(2.6)

where \( a \) is the acceleration vector \([\ddot{x}, \ddot{y}]^T\), and \( \ddot{J} \) is obtained by differentiating \( J \).

The motion of the joints and/or the end-point force result from torques produced about the joints by muscles. From a mechanical viewpoint muscles are torque actuators that produce a moment about a joint due to either passive or active force production. One factor complicating the computation of the joint torques a muscle produces is that some muscles cross more than one
joint, thus producing a moment about multiple joints. The FDS inserts on the middle phalange, crossing both the MCP and PIP joints. The FDP inserts on the distal phalange, crossing the MCP, PIP and DIP joints. In studies of finger force production often the end-point (force produced at fingertip) is recorded. The general equation relating the end-point force to joint torques is:

$$ T = J^T F $$

(2.7)

where $T$ is the vector of joint torques, $J^T$ is the transpose of the jacobian relating joint displacement to end-point displacement and $F$ is a vector of forces at the end-point. For a planar three-link chain, as shown in Figure 2.1, the transpose of the jacobian is:

$$ J^T = \begin{bmatrix} -L_1 S_1 - L_2 S_{12} - L_3 S_{123} & L_1 C_1 + L_2 C_{12} + L_3 C_{123} & 1 \\ -L_2 S_{12} - L_3 S_{123} & L_2 C_{12} + L_3 C_{123} & 1 \\ -L_3 S_{123} & L_3 C_{123} & 1 \end{bmatrix} $$

(2.8)

where $L_1$, $L_2$, and $L_3$ represent the lengths of the links, $C$ and $S$ stand for cosine and sine. The subscripts 1, 12, and 123 following $C$ and $S$ represent $\theta_1$, $(\theta_1 + \theta_2)$, and $(\theta_1 + \theta_2 + \theta_3)$, respectively. For the three-link chain with an external couple the force vector becomes:

$$ F = \begin{bmatrix} F_x \\ F_y \\ C \end{bmatrix} $$

(2.9)

where $F_x$ and $F_y$ are the x- and y-components of the external force. $C$ is the external couple.

The magnitude of the end-point force is determined by the magnitudes of the joint torques while the direction of the end-point force is determined by the difference between the joint torques. Often the forces and moments acting on the joints are of interest in biomechanics. These values can be estimated using the inverse dynamics approach. Inverse dynamics is an iterative approach that uses measured values of external forces acting on links and measured motion of the links to compute internal moments and forces at the joints using Newton’s 2nd law equations of motion:

$$ \sum F = ma $$

(2.10a)

$$ \sum M = I \ddot{\theta} $$

(2.10b)

For a multi-link chain that is static the joint torques and reaction forces are only due to the external contact forces and the weight of the links. However, if the link is moving (i.e. any of the joint angles are changing) then there are additional forces due to the angular velocities.
and accelerations of the joints. These forces are assumed to act at the center of mass (COM) of the link. There is a normal (centripetal) force, \( F_n \), directed along the link that is equal to:

\[
F_n = mL\ddot{\theta}^2
\]  
(2.11)

There is also a tangential force due to the angular acceleration of the link:

\[
F_t = mL\dot{\theta}
\]  
(2.12)

The weight of the link is also assumed to act at the COM. In multi-link chains there are Coriolis forces that are due to the rotating reference frames experienced by distal links relative to proximal links. The most proximal link does not experience a Coriolis force. The Coriolis force is given by:

\[
F_{\text{cor}} = ma_{\text{cor}}
\]  
(2.13)

where \( a_{\text{cor}} \) is:

\[
a_{\text{cor}} = 2L_2\dot{\theta}_1\dot{\theta}_2
\]  
(2.14)

where the subscripts 1 and 2 represent the proximal and distal links, respectively. For a three-link planar chain there are eight inertial forces acting on the third link, five on the second link, and two on the first link. All of the forces acting on one link cause reaction forces on the other links, which makes the computation of joint reaction forces quite complex for multi-link chains. The equations are often simplified and written in state-space form. The state-space form for a three-link chain is:

\[
\begin{bmatrix}
T_1 \\
T_2 \\
T_3
\end{bmatrix} =
\begin{bmatrix}
I_{1,1} & I_{1,2} & I_{1,3} \\
I_{2,1} & I_{2,2} & I_{2,3} \\
I_{3,1} & I_{3,2} & I_{3,3}
\end{bmatrix}
\begin{bmatrix}
\dot{\theta}_1 \\
\dot{\theta}_2 \\
\dot{\theta}_3
\end{bmatrix} +
\begin{bmatrix}
v(\theta, \dot{\theta})_1 \\
v(\theta, \dot{\theta})_2 \\
v(\theta, \dot{\theta})_3
\end{bmatrix} +
\begin{bmatrix}
G(\theta)_1 \\
G(\theta)_2 \\
G(\theta)_3
\end{bmatrix}
\]  
(2.15)

where \([T]\) is the vector of joint torques, \([I]\) is the inertia matrix of the chain, \([v]\) is the vector of centrifugal and Coriolis terms, and \([G]\) is the vector of gravity terms. For a more detailed description of the terms see Zatsiorsky (2002).

### 2.4.7 Moment Arms of Finger Muscles

There are a number of muscle properties that are important to know in order to understand the function of a muscle. In order to perform a biomechanical analysis on the fingers the main parameters of the FDS and FDP that need to be known are the force and moment arms about each joint. A number of studies have been performed to measure the moment arms of these tendons in different joint positions. Magnetic resonance imaging (MRI; Wilson et al. 1999;
Fowler et al. 2001), as well as cadaver based methods (Brand et al. 1975; Armstrong & Chaffin 1978; Youm et al. 1978; An et al. 1983) have previously been used to measure moment arms (MAs) of the flexor digitorum superficialis (FDS) and flexor digitorum profundus (FDP) muscles about the metacarpophalangeal (MCP) finger joint. The Wilson et al. (1999) study used 3D MRI imaging to compute the moment arm of the FDP with the I-finger positioned in various flexion positions. MAs were computed using: (a) a 3D tendon excursion method, (b) a 3D geometric method, and (c) a 2D geometric method. All three methods were found to produce approximately the same mean MA values per position; however, the variance between repeated trials was lowest for the 3D tendon excursion method and highest for the 2D geometric method. In the Fowler et al. (2001) study 3D MRI imaging was applied on a single female subject to compute 3D MAs of multiple muscles that cross the distal interphalangeal (DIP), proximal interphalangeal (PIP), and MCP joints. Again, only passive force production was investigated. Both studies found an increase in the MA at greater flexion angles.

In the cadaver studies tension was applied to the extrinsic flexor tendons to artificially simulate active force production (Brand et al. 1975; Armstrong & Chaffin 1978; Youm et al. 1978; An et al. 1983). This may not be an accurate depiction of what occurs in vivo as muscular force development may be different in vivo than in vitro. Co-contraction of other muscles crossing the MCP joint is neglected and the cadaver hand data may not be an accurate representation of a young, healthy hand. These studies all found that as the flexion angle of the MCP joint increased the MAs of the FDS and FDP also increased. Another significant finding was that the center of rotation of the MCP was located at the geometric center of the MCP head (Youm et al. 1978).

2.5 Prehension
The coordination of digit forces during prehension has been extensively studied over the past several decades. This review will focus on a select few of the studies that describe basic patterns of finger interaction during a five finger prismatic grasp (ZM Li 2002; Zatsiorsky et al. 2002a; Zatsiorsky & Latash 2008; Latash & Zatsiorsky 2009). It should be mentioned that several researchers made significant contributions to this area of research prior to the studies referenced above. They are JR Flanagan, RS Johansson, MKO Burstedt, KJ Cole, H Kinoshita, and G Westling. The lab group of Dr. Marco Santello has recently made significant contributions to
knowledge of the neural control of prehension (reviewed in Johnston et al. 2009). A more
detailed review of the findings related to multi-finger prehension was performed by Zatsiorsky &
Latash (2008).

Grasping, manipulating, and transporting an object is a task that is performed numerous
times every day without much thought by the performer. Although, easy to perform, the task is
mechanically complex since there are infinite combinations of finger forces that can be used to
achieve the same net output. In fact, even the best robotic graspers are unable to match the
dexterity of the human hand. During static prehension of an object there are mechanical task
constraints that need to be met such that the object doesn’t move, nor dropped by the performer.
For a prismatic grasp with all four fingers opposing the thumb the following three constraints
must be met. First, the sum of the tangential forces of the fingers has to equal the weight of the
grasped object:

\[ W = F^t_i + F^t_m + F^t_r + F^t_l + F^t_{TH} \]  \hspace{1cm} (2.16)

Where \( W \) is the weight of the grasped object and \( F^t_j \) is the tangential force of the \( j \)th finger.

Secondly, the normal forces of the fingers must equal the normal forces of the thumb:

\[ F^n_{TH} = F^n_i + F^n_m + F^n_r + F^n_l \]  \hspace{1cm} (2.17)

Where \( F^n_j \) is the normal force of the \( j \)th finger. The third condition that must be met is the
external moment must equal the net moment produced by the normal and tangential forces of the
fingers:

\[ M = F^n_{TH}d_{TH} + F^n_id_i + F^n_md_m + F^n_rd_r + F^n ld_l + F^t_{TH}r_{TH} + F^t_lr_l + F^t_mr_m + F^t_r r_r + F^t_lr_l \]  \hspace{1cm} (2.18)

where \( M \) is the external moment, \( d_j \) is the moment arm of the normal force of the \( j \)th finger, and \( r_j \)
is the moment arm of the tangential force, \( F^t_j \), of the \( j \)th finger. From the equations it is observed
that grasping an object with a prismatic grasp is a redundant system (more unknowns than
equations). Thus, studying such a system is also interesting from a motor control perspective, as
it may shed light on how the CNS coordinates multi-elements to perform redundant tasks. The
following studies report results on the coordination of finger forces when things such as the
objects weight (\( W \)) and external moment (\( M \)) are varied.

One of the most comprehensive studies to document finger forces during prehension of
an object was performed by Zatsiorsky et al. (2002b). Subjects were asked to statically grasp an
instrumented handle in which the load and external moment was systematically varied. Four
different load conditions and nine different external moment conditions (four requiring a pronation effort, four requiring a supination effort, and a zero moment condition) were used. Only the normal forces of the fingers were recorded; however, both the normal and tangential forces of the thumb were recorded. The following results were reported: 1) the total moment of the normal finger forces showed a linear relation with external torque, 2) the total normal force of the fingers increased with increasing torque, 3) the total normal force of the fingers increased with load at each level of external torque, 4) the peripheral fingers (I- and L-fingers) forces varied mainly with external torque, 5) the central fingers (M- and R-fingers) forces varied with both external torque and load, and 6) fingers exerted moments in the antagonist direction, which meant that the agonist moment producing fingers had to produce more force. The authors concluded that the CNS selects finger forces during prehension based on both mechanical and neural factors.

The same year ZM Li (2002) published a study in which subjects grasped a handle that was equipped with six-component force/moment sensors for all of the fingers. The goal was to investigate force sharing patterns among the fingers. However, load and external moment was not varied in this experiment. It was reported that the vertical load of the handle was shared 39.4, 9.9, 19.3, 14.0, and 17.5 % by the thumb, I-, M-, R-, and L-fingers. The normal forces were shared 50.0, 15.4, 14.6, 11.7, and 7.3 % by the thumb, I-, M- R-, and L-fingers. The coefficient of variation of the normal forces of fingers was approximately 9 % (averaged across fingers).

The forces exerted on a grasped object can be divided into manipulation and internal forces (Kerr & Roth 1986; Yoshikawa & Nagai 1991). Manipulation forces result in motion of the object while internal forces effectively cancel each other out and there is no motion of the object. People adjust internal forces during manipulation of objects even though they are not mechanically necessitated (Gao et al. 2005a; Gao et al. 2005b; Smith & Soechting 2005; Zatsiorsky et al. 2005).

Prehension tasks have been used to study how the CNS varies individual elements (finger forces) in a synergistic way to perform a task (Baud-Bovy & Soechting 2001; Pataky et al. 2004a,b; Rearick & Santello 2002; Santello & Soechting 2000; Shim et al. 2003, 2005a,b; Zatsiorsky et al. 2003; Zatsiorsky & Latash 2004). The analysis of grasping is sometimes simplified so that the net output of the fingers opposing the thumb is summed and said to be a virtual finger (VF; Arbib et al. 1985; Iberall 1987). The VF has the same effect as the fingers...
together but allows for analysis to be performed on two levels. The highest level of analysis is at the thumb and VF level. The lower level is at the individual finger level. In general, it has been discovered from these studies that all of the finger forces are interrelated such that a change in one finger’s force results in changes in all the others to stabilize the output of the VF. Latash and Zatsiorsky (2009) reviewed the findings in the context of motor synergies. A synergy, in the context of motor control, has been defined as an organization of variables (elements) in a task-specific way that acts to stabilize task-specific performance variables (Gelfand & Tsetlin 1966). This disagrees with the notion that the CNS eliminates redundant degrees of freedom (Bernstein 1967), but rather prefers to use the degrees of freedom to stabilize performance with respect to the performance variables. This has been called the principle of abundance (Gelfand and Latash 1998). Prehension synergies are generally analyzed at two levels: 1) thumb & VF, and 2) individual finger. The normal forces of the thumb and virtual finger exhibit positive co-variation to maintain constant grasping force, as well as moment. However, the variation of forces to stabilize force and moment are performed separately, such that control of these is decoupled (principle of superposition, Zatsiorsky et al. 2004). Individual finger forces display a pattern of negative co-variation during static prehension tasks. Forces produced by fingers during prehension depend on several factors, including: 1) enslaving, 2) force deficit, and 3) mechanical advantage of individual fingers.

2.6 Control Theories
How the CNS controls movements has been the focus of much research over the past 100 years. Some of the pioneers in the field of motor control theory are Nikolai Bernstein, Michael Tsetlin, and Israel Gelfand. The famous motor redundancy problem is also commonly known as the “Bernstein Problem”, since Bernstein was the first researcher to study and formulate the basic issues underlying how the CNS controls redundant degrees of freedom (1967). Tsetlin and Gelfand took the ideas of Bernstein and developed some basic principles the CNS may use to control movements. Tsetlin and Gelfand proposed that the CNS organizes elements into structural units based on three axioms (1966):

1) The internal structure of a structural unit is always more complex than its interaction with the environment.
2) Part of a structural unit cannot itself be a structural unit with respect to the same group of tasks.

3) Elements of a structural unit that do not work with respect to the task:
   a) are eliminated and a new structural unit is formed or
   b) find their own places within the task.

The idea of structural units assumes hierarchical organization of tasks in which the functional outcome of the task is at the highest level. Elements at the lower levels of the hierarchy are organized such that their output leads to achievement of sub-tasks necessary to achieve the overall outcome or goal. A principle of minimal interaction among the elements at the lower level of the hierarchy was suggested by Gelfand and Tsetlin (1966). The underlying idea was that the elements at the lower level interacted in a way that minimized the external control needed to coordinate their activities. Elements within a structural unit were assumed to exhibit flexibility and/or stability with regards to their output. In other words the elements could change their sharing patterns in a way that errors of the total output were compensated for by other elements in the structural unit. This is also referred to as error compensation in the literature (Latash et al. 1998).

Currently, there are several basic schools of thought on how the CNS controls movements. In general, these are based on basic concepts of control systems used in classic mechanics. Control systems consist of closed-loop and open-loop types of control. Closed-loop control receives an input and continuously monitors the output, using feedback mechanisms. If the output deviates from the desired output, within a certain tolerance, the system uses the feedback to adjust the output in the correct fashion. Open-loop systems receive an input and produce an output with no feedback. These systems are sometimes called feed-forward systems. It seems evident that the CNS utilizes feedback control since structures such as muscle spindles and golgi-tendon organs exist. However, some key differences between artificial robots and humans should be noted (Latash 2008a). First, muscles are not ideal force actuators. They are elastic bodies whose force producing properties change with length and velocity. Secondly, compared to machine actuators muscles are much slower. They take time to build up force and the feedback loops involving muscle spindles and golgi-tendon organs can take several hundred milliseconds before a force response is seen in the muscle. Last, muscles are non-linear
actuators with non-constant moment arms. Another aspect of control loops is that systems often operate in a manner that optimizes some important value (cost function) and operates under a set of constraints. Optimization in regards to motor control will be addressed in a later section.

2.6.1 Internal Models
One school of thought on the control of movements is that the CNS uses stored models, internal models, of movements to send feed-forward commands to the muscles. The idea of internal models that control movement originally came from control functions, called engrams (Bernstein 1935), and then were further developed into a generalized motor program theory (Schmidt 1975, Schmidt 1980). The concept behind these ideas is that the brain stores commands that produces certain movements. The feed-forward commands account for the torques necessary to produce the desired movement (Wolpert et al. 1998; Kawato 1999; Shadmehr & Wise 2005). The joint torques needed to produce a movement are very complex due to the interaction torques and reaction forces among body segments involved in the movement (Zatsiorsky 2002 – Kinetics of Human Motion). The commands must also account for physiological factors (i.e. muscle force-length & force-velocity properties). One of the arguments for internal models is based on studies in which reaching movements are performed in a force field environment (Shadmehr & Mussa-Ivaldi 1994). After the force field was removed the reaching movements were performed as if the force field was still present. The cerebellum has been the structure that supposedly stores internal models of movements (Wolpert et al. 1998; Kawato 1999; Grush 2004).

A major argument against internal models is related to the concept of equifinality. Equifinality is the idea that an end position can be realized in different ways. The fact that during reaching movements with an unexpected perturbation during the movement still lead to the correct final position of the arm does not seem possible if the CNS does control movements using internal models. For a fast reaching movement (<500 ms) in which a perturbation occurs during the movement it would not be possible for the CNS to sense the perturbation, resend a command to correct for the perturbation, and still reach the same final position within this short time duration. However, some research has shown that reaching movements are able to correct for unexpected perturbations and still reach the same endpoint position (Bizzi et al. 1978) while other research has shown this is not true (Hinder & Milner 2003). An alternative control theory
has been proposed that does not require computing complex mechanical variables and is based on physiology of the neuromuscular system.

2.6.2 Equilibrium Point Hypothesis
The ability of people to relax muscles in different postures by modifying spring-like properties of muscles is the foundation of the equilibrium-point (EP) hypothesis (also called referent configuration, threshold control theory in recent literature). The underlying idea behind the EP hypothesis is that the CNS changes the threshold of the tonic stretch reflex (λ) in muscles (Feldman 1966). The threshold of λ varies with muscle length. If the length of the muscle is below the threshold then it is silent and if the length is over the threshold it is activated. At any joint there is at least one agonist and one antagonist muscle. If you assume zero net torque and would like to the joint to be in a certain configuration the lengths of the muscles and the activation of the muscles need to be set (note: zero net torque does not mean muscles are not actively producing force). There have been two commands associated with these parameters in the framework of the EP hypothesis (Feldman 1980). The r-command controls the muscle lengths and the c-command controls the co-activation. Movements can be produced by changing these commands.

The observation by Kurt Wachholder in the early 1900’s that muscles could relax at different lengths was the first experimental evidence supporting the EP hypothesis, and formed the basis of the posture-movement paradox (Von Holst & Mittelstaedt 1973). The response of the stretch reflex versus muscle length in decerebrate cats (Matthews 1959) provided further knowledge that helped to form the EP hypothesis. The EP hypothesis resulted from a series of experiments that involved unloading of the elbow joint that was isometrically contracting against an external load (Asatryan & Feldman 1965; Feldman 1966). Subjects were asked to “not interfere voluntarily” when the load was removed by the experimenter. It was observed that after the load was removed the elbow moved to a new position that depended on the load and muscle length. In terms of the EP hypothesis the length and force defined the initial EP and after removal of the load the muscles moved to a new EP. Certain combinations of EPs (force & length combinations) share the same threshold of tonic reflex. These points can be connected and form a smooth line called the invariant characteristic (Figure 2.2).
These ideas can easily be applied to a joint served by an agonist and antagonist muscle. Each muscle has its own invariant characteristic. Movement can occur by shifting the invariant characteristics of both muscles. This is known as the $r$-command, defined as:

$$r = (\lambda_{\text{flexor}} + \lambda_{\text{extensor}}) / 2$$

(2.19)

The joint can stiffen by activating both muscles at the same time. This is the $c$-command, defined as:

$$c = (\lambda_{\text{flexor}} - \lambda_{\text{extensor}}) / 2$$

(2.20)

The value of $\lambda$ is dependent on several factors. These factors are the central contribution, velocity sensitivity of muscle spindles, history of muscle activation and signals from other muscles (Latash 2008b). In terms of producing movements it has been suggested that this can be accomplished by changing the EP with time (Latash 2008b).

Two attractive features of the EP hypothesis are that can resolve the posture-movement paradox (Von Holst & Mittelstaedt 1973) and predicts equifinality. Additionally, the EP hypothesis can be combined with the dynamic systems approach to controlling movements.
(Kugler & Turvey 1987; Kelso 1995). The EP hypothesis requires state variables (muscle length) and system parameters ($\lambda$) to produce movements (Latash 2008).

2.7 Motor Variability & Analysis Techniques

Variability is one of the main features of motor tasks. Quantifying and explaining this variability is one of the central problems in motor control. Some researchers believe that variability is due to neuromotor noise (Harris & Wolpert 1998) caused by various intrinsic and extrinsic variables that cause deviation from the optimal behavior the CNS is trying to perform. However, most researchers believe that variability observed in repeated trials of a task is more than neuromotor noise (Schmidt et al. 1979; Newell & Carlton 1988). In fact, much of the variability may be desirable in that it allows the CNS to perform movements using an abundant combination of solutions (principle of abundance, Gelfand & Latash 1998; Latash 2012). Bernstein observed that blacksmiths display a higher amount of variability in their joints than the endpoint (hammer). It seems reasonable that this variability is actually good and allows better performance of a task since it is a movement they performed hundreds of times a day for many, many years. An analysis method was developed that allows for analysis of variance and division of the variance into “good” ($V_{\text{Good}}$) and “bad” ($V_{\text{Bad}}$) variance (uncontrolled manifold hypothesis – UCM; Scholz & Schoner 1999; reviewed in Latash et al. 2002).

2.7.1 Uncontrolled Manifold (UCM) Hypothesis

The UCM hypothesis is based on two key assumptions. The first is that control is organized in a hierarchy of multi-level structures. The second is that there is not a unique solution to solve a given problem, rather a family of solutions exists (principle of abundance). The UCM hypothesis requires two types of variables: elemental and performance variables. Elemental variables (EVs) are variables that the controller manipulates to perform a task. They may be forces, moments, joint motion, etc. Performance variables (PVs) are features of the output of the system that the controller tries to achieve through the organization of the EVs. For example, if the task is to produce 10 N of force using the I- and M-fingers the force of the individual fingers would be the EVs and the total force produced would be the PV. The force could be shared between the fingers in an infinite number of ways and the controller would not care as long as the total force was equal to 10 N ($F_I + F_M = 10$ N). If you were to ask a person to perform fifty
trials of this task and plot the average force of each finger on a graph you would get something that looked like Figure 2.3.

![Figure 2.3](image)

**Figure 2.3**: Clouds of data points from a task that requires the total force produced by the I- and M-fingers to be 10 N. The data points, which are fictitious data, are distributed in an ellipse along a line that is represented by the equation $F_I + F_M = 10$ N. The line is the principal axis of the ellipse. Variance along the principal axis is called “good variance” ($V_{\text{Good}}$) as it results in no change in the performance variable, total force. Variance along the minor axis is called “bad variance” ($V_{\text{Bad}}$) which results in the maximum change in the performance variable per change in elemental variables.

It is assumed that a synergy exists among the EVs if $V_{\text{Good}} > V_{\text{Bad}}$. The term uncontrolled manifold is somewhat misleading as it implies the controller does not need to control the variables within the UCM subspace. The uncontrolled manifold is the null space of the jacobian relating changes in elemental variables to changes in the PV. As long as the EVs are operating within the UCM (null space) the controller does not need to intervene to correct for mistakes in the output. This is in line with the principle of minimal intervention (Todorov & Jordan 2002). The strength of the synergy is measured by how much of the variance is confined to the UCM. An attractive feature of UCM analysis is it allows for different control hypotheses to be tested using the same, or different, EVs. The strength of different synergies related to the
different control hypotheses can then be compared. One drawback of UCM analysis is that the method is linear and if the relationship between EVs and PVs is highly non-linear the UCM approach can fail. UCM analysis is performed with the following steps (reviewed in Latash 2007):

1. EVs are selected.
2. PV is selected.
3. A linear model of the system is created. This involves creating a jacobian that relates changes in EVs to changes in the PV. After the jacobian is established the null space is computed.
4. Variances within the UCM ($V_{\text{Good}}$ or $V_{\text{UCM}}$) and orthogonal to the UCM ($V_{\text{Bad}}$ or $V_{\text{ORT}}$) are computed. First, the data is demeaned by subtracting the mean value of the EVs across all trials. The resulting data is deviations of the EVs about their mean. These deviations are then projected onto the null space of the jacobian and onto the orthogonal component. The variance across all the data points is then computed per dimension within the UCM and orthogonal to the UCM. The normalized difference between the two variance components is sometimes computed. This value indicates the strength of the synergy among EVs.

2.7.2 Principal Component Analysis (PCA)

Perhaps the most difficult step in the UCM analysis is the first step. Selecting the EVs is a non-trivial task. The EVs should ideally be free of task-independent co-variations (Latash 2007). An example of this is the enslaving behavior of fingers such that the fingers forces are not independent of each other. It is important to not include EVs that have no effect on performance. One method that can provide insight as to what the EVs are is principal component analysis (PCA). PCA analyzes the correlation matrix between variables and defines eigenvectors in the space of EVs. The first PC is in the direction of maximum variance; the second PC is orthogonal to the first one and is in the direction of maximum remaining variance, and so on. The number of PCs is equal to the number of EVs. The PCA is similar to UCM in that it compares variance in different directions in the space of EVs except for one key difference: PCA is unbiased in that no PV need be selected.
PCA and UCM are complimentary techniques in analyzing multi-element synergies. The two basic features of synergies are sharing and error compensation. PCA can be used to identify stable relationships among the EVs (sharing). UCM quantifies the co-variation (error compensation) of EVs to stabilize task performance. Both of these methods focus on the variance of EVs. Another characteristic, that is equally important, is the average values of EVs. Optimization methods may be used to study this facet of tasks.

2.7.3 Mode control of Fingers
The concept of EVs within the framework of the UCM hypothesis has led to the idea of modes (Latash et al. 2001; Latash et al. 2002; Scholz et al. 2002; Danion et al. 2003). The assumption that the EVs are independent of one another imposes a problem when selecting finger forces as the EVs. Due to enslaving and force deficit behaviors fingers forces are not independently able to change their output. UCM analysis was first performed in the space of modes as EVs by Scholz et al. (2002). Modes are hypothetical neural commands (NCs) sent to fingers or other muscles (Krishnamoorthy V, Goodman SR, Latash ML, Zatsiorsky 2003a,b) that vary between 0 and 1. A NC of 1 signifies an MVC while a NC of 0 signifies zero intentional force production. In the case of the fingers a NC sent to one finger will also result in unintentional force production of other fingers due to enslaving. In order to relate NCs and force output of fingers a jacobian needs to be computed that relates force changes in one finger to force changes in other fingers. This jacobian is referred to as an enslaving matrix or finger interaction matrix ($E$). The relationship between finger force production and NCs is represented by the following:

$$[F] = [E][NC]$$  \hspace{1cm} (2.21)

where $[E]$ is the enslaving matrix, $[F]$ is a ($4 \times 1$) vector of finger forces and $[NC]$ is a ($4 \times 1$) vector of NCs. NCs can be computed by rearranging the equation:

$$[NC] = [E]^{-1}[F]$$  \hspace{1cm} (2.22)

The mode approach was further developed by Danion et al. (2003). The model was of the form of equation 2.21 above with the addition of a gain factor that accounted for force deficit. The gain factor ($G$) is inversely proportional to the number of fingers explicitly involved in the task ($N$). Based on experimental data $G$ was approximated to be equal to:

$$G = 1 / N^{0.712}$$  \hspace{1cm} (2.23)

Giving the general relationship between forces and NCs as:
\[ [F] = G [E][NC] \] 

It should be noted that, like enslaving, force deficit is different for different subjects so the assumption that \( G \) is the same for everyone is incorrect but based on comparison to experimental data offers a good approximation (Danion et al. 2003). Danion et al. tested their model on five previously published data sets and found excellent agreement between experimental and predicted data in nearly all cases (Zatsiorsky et al. 1998; Danion et al. 2000a,b; Li et al. 2000a,b). The mode approach (Danion et al. 2003) was compared to the NN model of Zatsiorsky et al. (1998) and it was found that overall the NN model slightly outperformed the mode approach. However, one advantage is that the mode approach only requires the four single finger MVC trials while the NN model requires all fifteen combinations of finger MVC trials. Overall, the studies performed using modes as EVs suggest that it is feasible the CNS controls hypothetical variables resembling NCs as opposed to other variables that are more easily measured and thus more commonly used as variables in motor control studies.

2.8 Optimization

The problem of motor redundancy is one of the central problems of motor control (Bernstein 1967). The problem arises because for any given motor task the number of controlled variables (unknowns) is greater than the number of constraints (equations) and thus an infinite number of solutions can exist. Despite the option of performing movements in a variety of ways the coordination of movement patterns are quite repeatable from trial to trial. The variability across people is also low, as most people perform movements in more or less the same general manner. It is generally accepted that people perform movements by optimizing the way in which they perform movements by minimizing some cost function. One approach to solving the problem of motor redundancy is based on search for possible cost functions that the central nervous system (CNS) might be optimizing (reviewed in Nelson 1983; Prilutsky 2000). Such an optimization could be based on mechanical (i.e. energy, jerk), physiological (i.e. fatigue), or psychological (i.e. effort) variables (Seif-Naraghi et al. 1990; Tsirakos et al. 1997; Rosenbaum et al. 2004; Raikova et al. 2001; Prilutsky et al. 2002; Ait-Haddou et al. 2004) criteria or on some other not known measures. Various tasks have been studied to examine what people may be optimizing. These include reaching movements (Biess et al. 2007); Cruse et al. 1990; Engelbrecht 2001; Flash & Hogan 1985; Plamondon et al. 1993; Tsirakos et al. 1997), walking (Anderson & Pandy
A newly developed method, called analytical inverse optimization (ANIO; Terekhov et al. 2010; Terekhov, Zatsiorsky, 2011; Park et al. 2010, Niu et al. 2011, Park et al. 2011), allows for identifying unknown cost functions based on experimental data (certain constraints are applied). A detailed description of the ANIO approach is available in Terekhov et al. (2010) and Terekhov, Zatsiorsky (2011). The following is a brief background of the basic premises. The ANIO method allows for the determination of an unknown objective (cost) function based on an experimental data set, finger forces in the case of finger pressing or prehension tasks. ANIO requires knowledge of the surface that contains the experimental data. The objective function is assumed to be additive with linear constraints. The constraints must also have a dimension greater than or equal to two. It is also assumed that constraints of the inverse optimization problem are non-splittable. These conditions must be met to guarantee that the solution to the inverse optimization problem is unique. The previous studies have assumed that the finger forces are confined to a two-dimensional hyperplane in the four-dimensional force space (Park et al. 2010; Terekhov et al. 2010). To test this assumption PCA has been performed on the finger force data sets. The amount of variance explained by the first two PCs was used to test whether or not the data were confined to two-dimensional hyperplane. The Kaiser Criterion was used to extract the significant PCs (Kaiser 1960). The data were considered to be confined to a two-dimensional hyperplane if greater than 90% of the total variance was represented by the first two PCs. To check the performance of the reconstructed cost function several criteria are used, e.g. the root mean square difference between the actual measurements and the values predicted from the reconstructed cost function, the dihedral angle between the plane of optimal solutions and the plane of experimental observations, etc.

The ANIO method has been tested for four-finger pressing (Park et al. 2010; Park et al. 2011) and prehension tasks (Terekhov et al. 2010; Niu et al. 2011). The four-finger pressing task tested has been to press with all four fingers to match a target force and moment. For this task there are two constraints \( F_{TOT} \) and \( M_{TOT} \) and four elemental variables (finger forces). The cost function is assumed to be of the form given in equation 2.25 with the linear constraints of
The cost function contains finger force terms \( F_i \) multiplied by the first-order \((w_i)\) and second-order \((k_i)\) coefficients. The constraints \((C)\) reflect the total force \((F_{TOT})\) and total moment \((M_{TOT})\) task constraints that must be produced by the finger forces \((F_i)\).

\[
\text{Cost Function: } J = \frac{1}{2} \sum_i k_i (F_i)^2 + \sum_i (w_i) F_i
\]  

\[
\text{Constraints:}
\]

\[
CF = B
\]  

\[
F = [F_i \ F_m \ F_r \ F_l]
\]  

\[
C = \begin{bmatrix}
1 & 1 & 1 & d_l
\end{bmatrix}
\]  

\[
B = \begin{bmatrix}
F_{TOT} \\
M_{TOT}
\end{bmatrix}
\]  

Park et al. (2010) asked subjects to press to match five levels of total force (20, 30, 40, 50, and 60% of four-finger MVC) and five levels of moment (two supination efforts, two pronation efforts, and a zero total moment effort). The average forces during a selected time interval of each trial were computed. Each of the twenty-five combinations of force and moment was repeated three times giving a total of seventy-five data points. The PCA of the data revealed that the first two PCs accounted for at least 90% of the total variance in finger force space, in most cases (Table 2.1). The second-order finger force coefficients \((k_i)\) were all positive. The index and little first-order finger force coefficients \((w_i)\) were negative while the middle and ring coefficients were positive. The dihedral angle (D-angle) between the optimal plane and experimental plane was \(2.05 \pm 0.59^\circ\) (mean ± standard error). The 2011 study by Park et al. used the same task with the exception of increasing the number of total force levels (20, 25, 30, 35, 40, 45, 50, 55, and 60% of four-finger MVC) and total moment levels (four supination efforts, four pronation efforts, and a zero total moment effort) from five to nine. The subject pool consisted of seven young healthy subjects and seven healthy, elderly subjects. For the elderly subjects the first two principal components accounted for only 75% of the total force variance while for the young subjects it was above 90% of the total variance. They found a significant difference in the second-order coefficients of the young group compared to elderly (young were larger); however, no significant difference was found between the first-order coefficients of the two age groups. There was a significant difference in the angle between the optimal and experimental data set planes between the young \((1.38^\circ \pm 0.80)\) and elderly \((5.10^\circ \pm 1.07)\).
The first experimental study using the ANIO method was performed using a prehension task (Terekhov et al. 2010). Three subjects were asked to grasp a handle instrument with five six-dimensional force-torque sensors. The load, external moment and grasping force were varied. The average normal forces from each trial were analyzed using the ANIO method. The D-angle between optimal and experimental data set planes was $2.7^\circ \pm 0.5$. The values of the second- and first-order finger force coefficients were qualitatively similar to those obtained in the pressing task. Table 2.2 shows a comparison of the main results from previous studies using the ANIO method.

\begin{table}[h]
\centering
\caption{Principle Component Analysis results from Park et al. 2010.}
\begin{tabular}{lcccc}
\hline
 & PC1 & & PC2 & \\
 & Mean & Range & Mean & Range \\
 & (min, max) & (min, max) & (min, max) & (min, max) \\
\hline
Session-1 & & & & \\
 20\% MVC & 65.43 & (61.56, 71.72) & 25.15 & (18.63, 33.12) \\
 2PR  & 68.04 & (54.19, 79.99) & 25.77 & (13.54, 36.99) \\
 2SU & 66.48 & (57.35, 82.43) & 26.04 & (13.74, 33.43) \\
\hline
Session-2 & & & & \\
 20\% MVC & & & 90.59 & (84.07, 94.66) \\
 2PR & & & 93.80 & (91.18, 98.14) \\
 2SU & & & 92.52 & (91.18, 98.14) \\
\hline
40\% MVC & & & & \\
 2PR & 69.20 & (58.53, 82.43) & 28.73 & (20.17, 39.77) \\
 2SU & 67.52 & (54.57, 89.77) & 30.76 & (8.81, 44.11) \\
\hline
\end{tabular}
\end{table}
**Table 2.2**: Comparison of Previous ANIO Studies. Values in brackets are standard errors.

Finger coefficients were normalized relative to the second-order index finger coefficient.

<table>
<thead>
<tr>
<th>Study</th>
<th>Task</th>
<th>% Variance in PC 1 + PC 2</th>
<th>Dihedral Angle (Deg)</th>
<th>Finger Second-Order ($k_i$) and First-Order Coefficients</th>
</tr>
</thead>
<tbody>
<tr>
<td>Park et al. 2010</td>
<td>4-Finger Pressing</td>
<td>90.59</td>
<td>2.05</td>
<td>1.00 0.82 0.98 1.79 -1.16 1.31 0.85 -1.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.59)</td>
<td>(0.22)</td>
<td>(0.35) (0.74) (0.19) (0.25) (0.12) (0.14)</td>
</tr>
<tr>
<td>Park et al. 2011</td>
<td>4-Finger Pressing (Young)</td>
<td>91.16</td>
<td>1.38</td>
<td>1.00 0.36 0.43 0.58 -0.48 0.63 0.18 -0.33</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.80)</td>
<td>(0.06)</td>
<td>(0.09) (0.12) (0.10) (0.12) (0.10) (0.10)</td>
</tr>
<tr>
<td></td>
<td>4-Finger Pressing (Old)</td>
<td>76.75</td>
<td>5.10</td>
<td>1.00 0.03 0.13 0.23 -0.49 0.60 0.27 -0.38</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1.07)</td>
<td>(0.01)</td>
<td>(0.09) (0.08) (0.07) (0.08) (0.05) (0.06)</td>
</tr>
<tr>
<td>Terekhov et al. 2010</td>
<td>Prehension</td>
<td>N/A</td>
<td>2.7</td>
<td>1.00 2.07 2.39 5.45 -1.16 0.99 1.50 -1.33</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.5)</td>
<td>(0.27)</td>
<td>(0.22) (1.18) (0.47) (0.30) (0.85) (0.66)</td>
</tr>
</tbody>
</table>

Terekhov and Zatsiorsky (2011) used simulations to test some of the assumptions underlying the ANIO method. It was concluded that the cost function must be additive otherwise there exists an infinite number of essentially different non-additive cost functions. The cost function approximation becomes significant worse when the data lie on a curve as opposed to a surface. It was shown that if the number of constraints in the inverse optimization problem equals one then there exists in infinite number of cost functions that explain the data. Lastly, if the constraints of the optimization problem are splittable then not all of the terms of the cost function can be identified.
CHAPTER 3

Study #1: Effects of the Index Finger Position and Force Production on the FDS Moment Arms at the MCP Joints- an MRI Study

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3.1 Introduction

Precise coordination of the fingers is necessary in order to perform numerous everyday tasks. The contact forces produced by fingertips result from the interaction of numerous architectural and physiological properties of the hand, forearm, and central nervous system (CNS). A better understanding of these properties is crucial for advancing many fields concerned with hand function such as motor control, biomechanics, motor disorders, rehabilitation and finger related surgeries (i.e. tendon transfers, joint replacements, etc.). It is well known that altering the angles of finger joints significantly affects the maximal fingertip force and the moments about the joints (Kamper et al. 2006). The effects of one finger activation and/or position changes on other fingers are much less understood.

Individual finger movements are not independent of other fingers (reviewed by Schieber and Santello 1994) due to: 1) mechanical links provided by connective tissue (Fahrer 1981; Kilbreath and Gandevia 1994; Leijnse 1997), 2) multi-finger motor units in the extrinsic finger muscles (Kilbreath and Gandevia 1994; Schieber 1995), and 3) overlapping cortical representations of the finger muscles (Schieber and Hibbard 1993; Sanes et al. 1995; Rathelot and Strick 2006). The result of these constraints is a behavior referred to as enslaving (Zatsiorsky et al. 1998, 2000): When a single finger intentionally moves or produces force, other fingers also unintentionally move or produce force. It is generally accepted that enslaving is due to a combination of the three previously mentioned constraints on individuated finger movements;
however, the relative contribution of each is unknown. It is unknown whether the activation of the finger flexors of one finger and/or change of the finger position will change the moment arms of the flexors of other fingers.

Magnetic resonance imaging (MRI; Wilson et al. 1999; Fowler et al. 2001), as well as cadaver based methods (Brand et al. 1975; Armstrong & Chaffin 1978; Youm et al. 1978; An et al. 1983) has previously been used to measure moment arms (MAs) of the flexor digitorum superficialis (FDS) and flexor digitorum profundus (FDP) muscles about the metacarpophalangeal (MCP) finger joint. The Wilson et al. (1999) study used 3D MRI imaging to compute the moment arm of the FDP with the index finger positioned in various flexion postures. Moment arms were computed using: (a) a 3D tendon excursion method, (b) a 3D geometric method, and (c) a 2D geometric method. All three methods were found to produce approximately the same mean moment arm values per posture; however, the variance between repeated measurements was lowest for the 3D tendon excursion method and highest for the 2D geometric method. In the Fowler et al. (2001) study 3D MRI imaging was applied on a single female subject to compute 3D moment arms of multiple muscles that cross the distal interphalangeal (DIP), proximal interphalangeal (PIP), and MCP joints. Again, only passive force production was investigated. Both studies found an increase in the moment arm at greater flexion angles.

In the cadaver studies tension was applied to the extrinsic flexor tendons to artificially simulate active force production (Brand et al. 1975; Armstrong & Chaffin 1978; Youm et al. 1978; An et al. 1983). This may not be an accurate depiction of what occurs in vivo as in vivo muscular force development may be different. Co-contraction of other muscles crossing the MCP joint is neglected and the cadaver hand data may not be an accurate representation of a young, healthy hand. These studies all found that as the flexion angle of the MCP joint increased the moment arms of the FDS and FDP also increased. Another significant finding was that the center of rotation of the MCP was located at the geometric center of the MCP head (Youm et al. 1978).

To the best of our knowledge, the effects of the muscle force levels on the moment arms of the fingers have not addressed in the literature. With regard to other joints, the data are scarce and controversial. Zatsiorsky et al. (1985) and Aruin et al (1987) applied a pulling force to the m. triceps surae of a cadaver leg and did not find substantial changes in the magnitude of the
moment arms while Maganaris et al. (1998, 1999) and Maganaris (2004) found large changes in moment arms of the tibialis anterior and Achilles tendon during maximum voluntary contractions (MVC) at the ankle compared to rest. At the wrist level, a change in tension of one of the extrinsic flexor tendons has been shown to change the moment arm of that tendon and transmit force to neighboring tendons (Agee et al. 1998).

Unfortunately, many of the previous studies are limited in that they have: (1) been performed on cadavers, and/or (2) only looked at passive conditions in which no active contraction of the muscle was occurring. The purpose of this study was to measure in vivo changes in moment arms of the flexor digitorum superficialis (FDS) about the metacarpophalangeal (MCP) joints of the 2-5 fingers due to: (1) changes in joint posture of the index finger MCP joint and 2) changes in muscle force production levels (passive vs. active flexion force). A secondary goal was to create regression models using anthropometric data to predict moment arms of the FDS about the MCP joint of each finger.

3.2 Methods

3.2.1 Subjects
Ten male subjects volunteered to be in the study. The subjects were all young, healthy and had no history of musculoskeletal injury or disease of the upper limbs. Subjects provided informed consent and the experiment followed a protocol that was approved by the Institutional Review Board of the Pennsylvania State University.

3.2.2 Experimental Procedure
Prior to the MRI scan a number of anthropometric measures were taken from the subjects (Supplementary Material Table B.1; Appendix B). Supplementary Figure B.1 provides an illustration of the boundary points of specific measurements. Hand length was measured from the most distal crease at the wrist to the tip of the longest finger. Hand breadth was measured on the palmar surface at the level of the MCP joints of fingers 2-5 with the fingers in a relaxed state of ab/adduction. Measurements of the fingers were taken on the dorsal surface. Phalange distances were measured from the approximate joint centers, based on visual inspection. Phalange circumferences were measured around the approximate midpoint of each phalange. Individual and four-finger flexion (MVCs) were recorded. Subjects placed their four fingers on
uni-dimensional force transducers (208C02, PCB Piezotronics, Depew, NY, USA) and were instructed to press as hard as they could for five seconds. Two trials of each MVC were recorded and the average computed.

3.2.3 MRI Equipment and Scans
The MRI scans were performed using a 3.0 Tesla MRI scanner (Siemens Magnetom Trio 3T, Siemens Corporation, Germany) at the Social, Life, and Engineering Imaging Center (SLEIC) facility of the Pennsylvania State University by a trained MRI technician. Subjects were required to lay prone on the scanning table with their right arm extended, above their head, inside of the head coil and positioned in the custom made finger positioning apparatus (Figure 3.1). The index finger was in three MCP joint postures: 1) Neutral (0 degrees), 2) Flexed (30 degrees of flexion), and 3) Extended (15 degrees of extension). The middle, ring, and little fingers were lightly taped together so that their posture did not change during the scans. The distal interphalangeal, proximal interphalangeal, and MCP joint postures of the non-index fingers was 180° for all scans. For each index finger MCP posture two sets of scans were obtained: 1) passive force and 2) active flexion force. The passive scans were always performed first. The subjects were then removed from the scanner and a 400 g mass was hung from the apparatus then looped around their index fingertip. The suspended load generated an extension moment about the MCP joint. To resist the load, subjects had to produce a small active flexion force with their index finger. It was necessary to use a low amount of resistive force since subjects were required to maintain the contraction for several minutes. For most subjects the suspended load required them to exert 10-15% of their index MVC during the active flexion force scans. After the scan was completed subjects were removed from the scanner, the index finger was repositioned and the passive and active scans were obtained for the next posture. The index finger MCP joint was positioned in neutral posture first, followed by flexion and then extension. Two minutes of rest were given after completion of the active flexion force scans. The entire time to collect all of the scans was less than an hour.
For each combination of force level and index finger posture, a localization and a T1 weighted 2D sagittal scans were taken. The time required for the localization and 2D sagittal was 0:51 and 1:53 min, respectively. The voxel size of these images was 0.7 x 0.7 x 3.0 mm (width x height x depth). The localization scan was aligned along the long axis of the index finger. The other fingers were positioned as parallel as possible to the index finger. Using this slice thickness (3.0 mm), 35 slices were sufficient to scan entirely through the 2-5 fingers of all subjects. The TR (repetition time) and TE (echo time) values were 1380 ms and 11 ms, respectively. The flip angle was 120°. Multiple pilot tests were performed to optimize the scan quality while minimizing the scan time. Reduction of scan time was important as longer times caused subjects to become fatigued during the active pressing scans, as well as, experience discomfort from lying with the arm extended overhead. Fatigue and discomfort both led to movements by the subjects that decreased the scan image quality.

3.2.4 Data Processing and Analysis
Processing and analysis of the images was performed using Syngo Viewer (Siemens Corporation, Germany) and Matlab (Mathworks, Massachusetts, USA). For each index finger position and force production level single images of the sagittal scan slice passing closest to the
center of the metacarpal head, of each finger, in the medial-lateral direction were identified. These images were saved and exported for further analysis. For each subject a total of 24 images comprised the data set (3 index finger postures x 2 activation levels x 4 fingers = 24). Only the FDS tendon was analyzed because its boundaries were most clearly identifiable in all of the images. Moment arms were computed using a 2D geometric method in which the moment arm was taken as the perpendicular distance from the line of action of the FDS tendon to the center of rotation at the MCP joint. Based on previous research we assumed that the center of rotation of the MCP joint was located at the center of curvature of the distal surface of the carpal head that articulates with the proximal phalanx (Youm et al. 1978; Unsworth et al. 1979).

The images were imported into custom Matlab program for digitizing. Five points along the tendon line of action and ten points along the outer contour of the carpal head were digitized. The center of curvature was computed and assumed to be the center of rotation. The perpendicular line from the center of rotation to the tendon of action was then calculated. The length of the perpendicular line was then computed, which was the moment arm. This procedure was repeated five times for every image. The average of the five computations was calculated and was used as the moment arm for the given finger and condition. In nearly all cases the standard deviation of the five measurements was less than 0.2 mm. The actual index MCP angle was measured from the sagittal image slices to ensure subjects maintained the correct hand posture during the scans. Small deviations (± 5°) from the set angles on the positioning apparatus did occur.

3.2.5 Statistics
Moment arms were averaged across subjects and the standard deviation computed. A separate repeated measure ANOVAs were performed to examine the effect of index finger MCP posture (3 levels: flexion, neutral, extension), and force (2 levels: non-zero, zero) on moment arm values of each finger. To examine the effect of force level on change in moment arm (tested response = Δ moment arm = moment arm under passive force condition minus moment arm under active flexion force condition) a separate repeated measure ANOVA was performed for each finger. The factor was index finger MCP posture (3 levels: flexion, neutral, extension). Repeated measure ANOVAs were performed using the statistical software SPSS (SPSS Inc., Chicago, IL, USA). Statistical significance was set to alpha = 0.05.
Stepwise regression models were constructed to predict moment arm values based on anthropometric measurements taken from subjects. The models included the first and second order terms, along with the measured index MCP joint angle. The first order terms were the measurement values and the second order terms were the measurement values squared. The data for all index finger MCP postures during the passive force condition were used to create separate models for each finger. Only the circumference and length measurements of the finger whose moment arm was being modeled were included in the stepwise regression model. The significance level to include a predictor in the model was set to 0.25. Stepwise regression was performed using Minitab software (Minitab Inc., State College, PA, USA).

3.3 Results
The results for the moment arm values of the index finger will be presented first, followed by the moment arm results of the other fingers. Lastly the regression models of moment arms based on various anthropometric measurements will be presented.

3.3.1 Index Finger Moment Arms
The moment arm values for the index finger were largest in the MCP flexed posture and decreased as the finger moved to the MCP neutral posture (Figure 3.2). The average values of the moment arms were similar for the neutral and extended index finger MCP posture. For the flexion index finger MCP posture under the active flexion force condition the moment arm were slightly larger (13.3 (1.3) mm) than for the passive force condition (12.5 (1.0) mm). However, the opposite tendency was seen for both the neutral and extended index finger MCP where the average moment arms were slightly smaller under the active flexion force condition (neutral: 10.8 (1.0) mm; extended: 10.5 (0.7) mm) compared to the passive force condition (neutral: 11.2 (0.7) mm; extended: 10.9 (0.6) mm). The FDS moment arm of index finger was significantly affected by the index finger MCP posture ($F_{2,18} = 68.708, p < 0.001$), but not by force ($F_{1,9} = 0.936, p > 0.9$). The interaction effects of index finger MCP posture × force were also highly significant ($F_{2,18} = 6.679, p < 0.01$). Using pair-wise comparisons, the differences in moment arm for the neutral ($p < 0.05$) and extended ($p < 0.05$) index finger MCP posture were estimated as significant; however, they were not statistically different in the flexed index finger MCP posture ($p > 0.05$). Additionally, the range of moment arm values across
subjects was statistically greater ($p < 0.05$) for the active flexion force condition (mean range = 2.9 (1.2) mm) than for the passive force condition (mean range = 2.5 (1.1) mm).

The percent changes in moment arms for flexion and extension, as compared to the neutral index finger MCP posture, are shown in Figure 3.3. Flexion under active flexion force and passive force conditions both increased the moment arm. The active flexion force condition showed a larger increase than the passive force condition (approx. 24% vs. 12% increase). Extension of the index finger decreased the moment arm by approximately the same amount for both passive force and active flexion force conditions (approximately 3% decrease).

![Figure 3.2: Average index finger FDS moment arm values. Error bars are standard deviations. Single stars indicate a significant difference between passive and active conditions for a given index finger position using a pair-wise comparison test. Double stars indicate a significant difference between positions.](image-url)
3.3.2 Middle, Ring and Little Finger Moment Arms

The average moment arms for the middle, ring, and little fingers under different conditions are shown in Figure 3.4. In general, middle finger moment arms were the largest (range across conditions: 10.8 (1.0) mm to 11.5 (0.6) mm) followed by the ring finger (range across conditions: 10.1 (0.7) mm to 10.5 (0.7) mm), and the little finger (range across conditions: 9.1 (0.6) mm to 9.7 (0.4) mm) had the smallest moment arms (Figure 3.4). The repeated measure ANOVA results indicated that the effect of index finger MCP posture (p > 0.2 for all non-index fingers) and force of index finger (p > 0.1 for all non-index fingers) were not significant on the moment arms of the middle, ring, and little fingers. The effect of the interaction of index finger MCP posture × force was significant for all fingers except the ring finger (F_{2,18} = 0.559, p > 0.5).
(A) Middle finger

![Graph A: Moment Arm (mm) vs. Index Position](image)

- Flexion
- Neutral
- Extension

- Passive
- Active

- p = 0.034

(B) Ring finger

![Graph B: Moment Arm (mm) vs. Index Position](image)

- Flexion
- Neutral
- Extension

- Passive
- Active
(C) Little finger

Figure 3.4: Average finger moment arm values for: (A) middle, (B) ring, and (C) little fingers. Error bars are standard deviations. Stars indicate a significant difference between passive and active conditions for a given index finger position using a pair-wise comparison test.

Table 3.1: Repeated measure ANOVA results for: (A) Index Finger, (B) Middle Finger, (C) Ring Finger, and (D) Little Finger. Bolded values are significant. DOFs for the factor and error term associated with the factor are reported in subscripts of the F statistic value.

<table>
<thead>
<tr>
<th>Factor</th>
<th>F Statistic</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>FORCE</td>
<td>0.007[1,9]</td>
<td>0.936</td>
</tr>
<tr>
<td>IFP</td>
<td>68.708[2,18]</td>
<td>0.001</td>
</tr>
<tr>
<td>FORCE×IFP</td>
<td>6.679[2,18]</td>
<td>0.007</td>
</tr>
</tbody>
</table>
### B) Middle Finger

<table>
<thead>
<tr>
<th>Factor</th>
<th>F Statistic</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>FORCE</td>
<td>3.191$[1,9]$</td>
<td>0.108</td>
</tr>
<tr>
<td>IFP</td>
<td>1.023$[2,18]$</td>
<td>0.380</td>
</tr>
<tr>
<td>FORCE×IFP</td>
<td>4.317$[2,18]$</td>
<td><strong>0.029</strong></td>
</tr>
</tbody>
</table>

### C) Ring Finger

<table>
<thead>
<tr>
<th>Factor</th>
<th>F Statistic</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>FORCE</td>
<td>3.233$[1,9]$</td>
<td>0.106</td>
</tr>
<tr>
<td>IFP</td>
<td>1.158$[2,18]$</td>
<td>0.336</td>
</tr>
<tr>
<td>FORCE×IFP</td>
<td>0.559$[2,18]$</td>
<td>0.582</td>
</tr>
</tbody>
</table>

### D) Little Finger

<table>
<thead>
<tr>
<th>Factor</th>
<th>F Statistic</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>FORCE</td>
<td>0.139$[1,9]$</td>
<td>0.718</td>
</tr>
<tr>
<td>IFP</td>
<td>1.654$[2,18]$</td>
<td>0.219</td>
</tr>
<tr>
<td>FORCE×IFP</td>
<td>8.224$[2,18]$</td>
<td><strong>0.003</strong></td>
</tr>
</tbody>
</table>

### 3.3.3 Regression Modeling

The stepwise regression models demonstrated that moment arm values are fairly well correlated with anthropometric measurements. Squared values of the correlation coefficients ranged from 0.89 (index finger) to 0.68 (little finger) for the individual finger models (Table 3.2). The circumference of the proximal and middle phalanges was present in several of the models. The measured index MCP joint posture was present in the middle and little finger models. The parameters that reduced the largest amount of error in the model were the proximal phalangeal circumference, hand breadth (first and second order terms), total finger length, and hand length.
Table 3.2 (A) Stepwise regression models for individual finger moment arm values. First and second order anthropometric measurements were used in models. Measured index MCP angle assumes full extension of the MCP joint is 180°, flexion is a decrease from 180° and extension is an increase from 180°.

(A)

### Index Finger Moment Arm

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Coefficient</th>
<th>p-value</th>
<th>Sequential Sum of Squares</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>90.130</td>
<td>0.116</td>
<td>-</td>
</tr>
<tr>
<td>Measured Index MCP Angle (deg)</td>
<td>-0.039</td>
<td>0.000</td>
<td>15.58</td>
</tr>
<tr>
<td>Proximal Phalange Circumference (cm)</td>
<td>-29.980</td>
<td>0.092</td>
<td>6.46</td>
</tr>
<tr>
<td>Middle Phalange Circumference (cm)</td>
<td>2.771</td>
<td>0.001</td>
<td>1.70</td>
</tr>
<tr>
<td>Distal Phalange Length (cm)</td>
<td>-3.158</td>
<td>0.002</td>
<td>1.34</td>
</tr>
<tr>
<td>Subject Height (cm)</td>
<td>0.113</td>
<td>0.000</td>
<td>0.78</td>
</tr>
<tr>
<td>Proximal Phalange Length^2 (cm^2)</td>
<td>0.055</td>
<td>0.077</td>
<td>0.62</td>
</tr>
<tr>
<td>Proximal Phalange Circumference^2 (cm^2)</td>
<td>2.371</td>
<td>0.079</td>
<td>0.56</td>
</tr>
<tr>
<td>Subject Weight (kg)</td>
<td>-0.097</td>
<td>0.000</td>
<td>0.07</td>
</tr>
</tbody>
</table>

R^2 = 0.888

### Middle Finger Moment Arm

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Coefficient</th>
<th>p-value</th>
<th>Sequential Sum of Squares</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>370.500</td>
<td>0.011</td>
<td>-</td>
</tr>
<tr>
<td>Middle Phalange Circumference^2 (cm^2)</td>
<td>-131.220</td>
<td>0.010</td>
<td>7.56</td>
</tr>
<tr>
<td>Middle Phalange Circumference (cm)</td>
<td>11.500</td>
<td>0.009</td>
<td>4.97</td>
</tr>
<tr>
<td>Distal Phalange Circumference^2 (cm^2)</td>
<td>0.284</td>
<td>0.003</td>
<td>3.38</td>
</tr>
<tr>
<td>Hand Length^2 (cm^2)</td>
<td>0.014</td>
<td>0.001</td>
<td>2.05</td>
</tr>
<tr>
<td>Measured Index MCP Angle (deg)</td>
<td>0.009</td>
<td>0.110</td>
<td>0.88</td>
</tr>
</tbody>
</table>

R^2 = 0.711
### Ring Finger Moment Arm

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Coefficient</th>
<th>p-value</th>
<th>Sequential Sum of Squares</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>–42.870</td>
<td>0.054</td>
<td>-</td>
</tr>
<tr>
<td>Proximal Phalange Circumference (cm)</td>
<td>2.910</td>
<td>0.000</td>
<td>6.15</td>
</tr>
<tr>
<td>Distal Phalange Length² (cm²)</td>
<td>–6.875</td>
<td>0.043</td>
<td>0.76</td>
</tr>
<tr>
<td>Hand Breadth² (cm²)</td>
<td>–0.003</td>
<td>0.769</td>
<td>0.57</td>
</tr>
<tr>
<td>Subject Weight (kg)</td>
<td>–0.056</td>
<td>0.012</td>
<td>0.56</td>
</tr>
<tr>
<td>Distal Phalange Length (cm)</td>
<td>33.110</td>
<td>0.053</td>
<td>0.49</td>
</tr>
</tbody>
</table>

\[ R^2 = 0.749 \]

### Little Finger Moment Arm

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Coefficient</th>
<th>p-value</th>
<th>Sequential Sum of Squares</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>–97.660</td>
<td>0.000</td>
<td>-</td>
</tr>
<tr>
<td>Hand Breadth² (cm²)</td>
<td>–1.439</td>
<td>0.000</td>
<td>1.69</td>
</tr>
<tr>
<td>Measured Index MCP Angle (deg)</td>
<td>0.015</td>
<td>0.001</td>
<td>1.39</td>
</tr>
<tr>
<td>Middle Phalange Length² (cm²)</td>
<td>–0.400</td>
<td>0.006</td>
<td>1.39</td>
</tr>
<tr>
<td>Middle Phalange Circumference² (cm²)</td>
<td>–0.026</td>
<td>0.657</td>
<td>1.25</td>
</tr>
<tr>
<td>Hand Breadth (cm)</td>
<td>24.704</td>
<td>0.000</td>
<td>0.97</td>
</tr>
<tr>
<td>Total Finger Length² (cm²)</td>
<td>–0.029</td>
<td>0.103</td>
<td>0.41</td>
</tr>
</tbody>
</table>

\[ R^2 = 0.684 \]

### 3.4 Discussion

All subjects showed an increase in moment arm of the FDS about the MCP joint of the index finger as the finger was moved from neutral position to flexion, which was true for both passive force and active flexion force conditions. These findings, as well as the recorded magnitudes of moment arms, are in agreement with previous research (Brand et al. 1975; Armstrong & Chaffin 1978; Youm et al. 1978; An et al. 1983; Wilson et al. 1999; Fowler et al. 2001). Figure 3.5 summarizes the moment arm results.
Figure 3.5: Schematic of index finger moment arms in the flexed, neutral, and extended positions. Mean and standard deviations of moment arms, under passive force and active flexion force conditions, are given for each position. The p-value for pair-wise comparisons between passive force and active flexion force conditions for each position are given.

The complex relations between the moment arms and the index finger MCP posture and force factors are most likely due to the complex muscle architecture. At the level of the MCP joint both the FDS and FDP tendons pass through the flexor sheath. The FDS has a larger moment arm about the MCP joint than the FDP; thus the FDS is typically recruited more for high force production tasks than the FDP (Brand & Hollister 1999). There are also pulleys along the finger that hold the tendon’s close to the bone to prevent bowstringing, which consequently limit the amount by which the moment arm of these tendons can increase. The advantage of smaller moment arms of the flexor tendons is that small muscle-tendon excursions result in large joint motion. The lack of observed change of moment arm from the neutral to extended index finger MCP posture may have been due to wrapping of the tendons about the head of the metacarpal bone, which limited further reduction of the moment arm from neutral to extension. The points of insertion of the FDS and FDP should also be considered. The FDP tendon inserts on the distal phalange while the FDS tendon inserts on the middle phalange of each finger. The contribution
of the FDS to the force that was produced could have been enhanced if the loop was placed around the middle phalange instead of the distal.

The fact that some changes in moment arms of the non-index, the middle and little, fingers were observed supports the notion that connections among the fingers limit their independence. The changes that occurred in moment arms are not necessarily due only to mechanical connections between the fingers. A study by Kilbreath and Gandevia (1994) showed, using intramuscular EMG, that when a single finger was instructed to flex to lift a weight as low as 2.5% MVC for that finger the EMG activity in other (non-instructed) fingers showed an increase. In turn, the increase of force by the enslaved fingers can induce their moment arm changes, e.g., due to bowstringing effects. It is worth to note that the ring finger MA was the only one not affected by the interaction of force and index finger MCP posture (Table 1B). In the literature on the finger enslaving, the effects of mechanical connections between the fingers were discussed solely in terms of the inter-tendinous transfer of pulling forces (Fahrer 1981; Kilbreath and Gandevia 1994; Leijnse 1997). This study adds a new dimension to this discussion: not only the forces but also the tendon moment arms can be changed as a result of force production by one of the fingers.

The stepwise regression models showed that anthropometric measurements can be used to quickly approximate MAs without the need to use MRI or other imaging methods to scan subjects. The circumferences of the phalanges of the finger’s MA that is being measured appear to be the most important measurement to predict the MA, based on the stepwise regression models. Generally, these terms reduced the most error (sequential sum of squares) and had the most significant p-values. Models such as these can be valuable in the area of modeling muscle mechanics to predict how altering certain parameters would affect function. In particular, such models could be used by surgeons to design implants or determine the best possible manner in order to repair a tendon on a subject-by-subject basis (Wu et al. 2010).

There were several limitations or assumptions used that could be changed in future studies to improve the accuracy and overall quality of the data. Although the tendon excursion and 3D geometric methods have been shown to yield slightly more precise moment arm values (in terms of smaller standard deviations when the same moment arm is repeatedly measured using one of the above mentioned methods (Wilson et al. 1999) we chose to use the 2D geometric method. The 3D scans require longer scan times, which were difficult to achieve.
during active force production. Some subjects felt discomfort from the position they were required to lay in during the measurements and thus had difficulty maintaining the required level of force during the entire scan time. The reason why 3D scans could not be obtained by reconstructing the 2D scans is that the slice thickness was too large to reconstruct images with good enough resolution to accurately measure the moment arms in 3D. The slice thickness (37.0 mm) was as large as it was because the scans had to be performed through the entire hand, in the media-lateral direction, in order to be able to measure the moment arms for each finger. To compensate for our choice of using the 2D geometric method every moment arm was measured five times and an average value was computed. Applying the load at different points of the finger, namely at the middle phalange, could also have improved the study. However, since the level of force production was constrained to remain low this may have been ineffective in further recruiting the FDS. Applying the load to the fingertip allowed for the greatest external moment about the MCP joint to be produced.

5. Conclusions
The main findings were: (1) Moment arms of fingers change due to both changes in joint angle and muscle activation; (2) Changes in one finger’s force production and posture can cause changes in other finger’s moment arms; (3) Moment arms of the FDS scale with various anthropometric measures.
4.1 Introduction

One of the central problems in motor control is the problem of motor redundancy (Bernstein 1967; Turvey 1990). This problem emerges when the number of variables at a selected level of analysis is higher than the number of constraints defined by the task such that an infinite number of solutions are possible. Recently, this problem has been addressed using the concept of a synergy as a neural organization of elemental variables that stabilizes a required value (or time profile) of a potentially important performance variable by co-varying adjustments of the elemental variables (Gelfand and Latash 1998; reviewed in Latash et al. 2002, 2007). A method of quantitative analysis of synergies has been developed within the framework of the uncontrolled manifold hypothesis (UCM hypothesis, Schöner 1995; Scholz and Schöner 1999). The UCM hypothesis assumes that the controller acts in a space of elemental variables, creates in that space a sub-space (UCM) corresponding to a desired value of a selected performance variable, and then tries to limit variability of the elemental variables within the UCM.

This general framework has been used to study multi-digit synergies in prehensile and pressing tasks (reviewed in Zatsiorsky and Latash 2008; Latash and Zatsiorsky 2009). Most of these studies (for a notable exception see Scholz et al. 2003) used analysis of co-variation of elemental variables (typically, forces and moments of force produced by individual digits) across trials to quantify synergies stabilizing such variables as the total force and total moment of force applied to an external object. In these analyses, elemental variables were measured at similar phases of actions.
across repetitive trials (or cycles, in cyclic tasks, Friedman et al. 2009) and two components of their variance were quantified: “good” variance (variance within the UCM) that did not affect the performance variable and “bad” variance (variance orthogonal to the UCM) that did.

Note that in this context the word “stability” has a meaning of “low variability in sequential trials”, which is different from stability in a more direct sense as resistance to external perturbations. A recent study of multi-joint coordination has shown that high synergy indices with respect to a performance variable may be associated with poor stability when an external perturbation is applied (Gorniak et al. 2009).

In this study, we used a simple multi-finger constant force production task, smooth perturbations applied to one of the fingers, and an instruction “do not intervene voluntarily” (cf. Feldman 1966, 1986). Multi-finger synergies stabilizing total force have been documented in several studies with pressing tasks (Latash et al. 2001; Scholz et al. 2002; Shim et al. 2005c), as well as with prehension tasks (Budgeon et al., 2008). Our first question was: Do synergies attenuate the effects of a perturbation applied to one of the fingers on the total force? We used an “inverse piano” apparatus to lift one of the fingers during the steady-state force production. Lifting a finger stretched the flexor muscles and was expected to lead to an increase in the pressing force due to the peripheral spring-like properties of the muscles and the action of the stretch reflex (Liddell and Sherrington 1924; Matthews 1959; Rack and Westbury 1969). We hypothesized that the three other fingers of the hand would show a force decrease such that the total force change will be smaller as compared to the force change of the lifted finger. Note that this prediction links multi-finger synergies to stability of the performance variable (total force) in a direct meaning of the word “stability”.

In an earlier study, we asked the subjects to produce a constant force level and then to tap with one of the fingers (Latash et al. 1998). When the tapping finger lost contact with the surface, its force dropped to zero. Other fingers of the hand showed an out-of-phase increase in their force such that the total force was nearly unaffected. In this experiment, we asked a question whether such error compensation could be observed in the absence of a voluntary action by the subject (under the “do-not-intervene” instruction). We hypothesized —this is our second hypothesis—that synergic mechanisms would act even if a change in force produced by one of the fingers is not produced by the subject voluntarily.

There is a well-known mechanism of finger interaction that leads to positive co-variation of finger forces. It has been addressed as enslaving or lack of individuation (Schieber 1991; Kilbreath
and Gandevia 1994; Zatsiorsky et al. 1998, 2000). When one finger increases its force, this mechanism is expected to lead to an increase in the forces produced by all other fingers. The increase depends on the proximity of the enslaved finger from the master finger: the closer the fingers the larger the enslaving (Zatsiorsky et al. 2000). Previous studies involving multi-finger force stabilizing synergies have not addressed whether or not a proximity effect existed. This study does investigate it. In our experiment, enslaving could be expected to lead to an increase in the forces of all four fingers, when one finger was lifted. We hypothesized, however, that synergic mechanisms that favor negative force co-variation would dominate such that total force is indeed stabilized (the 3rd hypothesis).

To test the three main hypotheses, we used finger displacements of two magnitudes, performed at two rates, applied to each of the four fingers, and varied the initial pressing force between two levels. These manipulations were used to explore the generality of the findings and the dependence of the hypothesized synergic force adjustments on the magnitude of perturbation, possible transient force changes related to the speed of muscle stretch, and target finger.

4.2 Methods and Materials

4.2.1 Subjects
Ten male subjects participated in the experiment. The average age, weight, and height of the subjects were 26.6 ± 3.5 years, 74.7 ± 7.0 kg, and 177.9 ± 7.8 cm, respectively. All subjects were right-handed, in good health, and had no previous history of neuropathies or traumas to the upper limbs. None of the subjects had a history of long-term involvement in hand or finger activities such as professional typing or playing musical instruments. The subjects gave informed consent according to the procedures approved by the Institutional Review Board of the Pennsylvania State University.

4.2.2 Apparatus (the ‘inverse piano’ technique)
Four uni-directional piezoelectric sensors (208C02, PCB Piezotronics) were used for force measurement. The sensors were calibrated prior to data collection to ensure accuracy of data. The sensors were mounted on a steel frame, which was securely attached to the testing station. Sandpaper pads were attached to the face of the sensors to increase friction and to reduce the temperature effect from the skin. Sensors were spaced 30 mm apart in the direction of finger adduction-abduction. The position of the sensors could be adjusted in the finger longitudinal
direction in a range of 75 mm to fit individual subject’s anatomy. A wooden support was made to support the wrist and forearm, as well as to ensure stable contact between the fingers and force sensors. A wooden block was placed under subject’s hand to promote stable hand configuration and avoid pronation/supination during pressing. Analog output signals from the sensors were connected to separate AC/DC conditioners (484B, PCB Piezotronics, Depew, NY, USA), then digitized using a 16-bit analog-digital converter (CA-1000, National Instruments, Austin, TX, USA), mounted on a microcomputer (Dimension 2400, Dell, Round Rock, TX, USA) that was utilized for control, acquisition, and processing of the data.

Force sensors were connected to linear motors (PS01-23x80, Linmot, Spreitenbach, Switzerland) that raised and lowered the sensors (Figure 4.1A). The motors were programmed using LabVIEW (LabVIEW Version 8.0, National Instruments) that sent commands to a controller (E400-AT, Linmot, Spreitenbach, Switzerland). Motors produced smooth vertical movements of the posts with the sensors (the ‘inverse piano’ technique).
Figure 4.1: (A) Schematic of force sensors mounted on linear motors. Linear motors produced motion of the force sensor in the vertical direction. The letters I, M, R, and L refer to the keys corresponding to the index, middle, ring and little fingers, respectively. In the schematic the key under the ring finger is raised. (B) Illustration of feedback given to subjects. A target range (±
5.0 % MVC) was given. The target was shown for the first 5 seconds, disappeared for the next 5 seconds during the key raising/lowering, and then returned for the last 3 seconds of the trial. (C) Example force data from a single trial. Change in force was computed as the forces after the key was raised minus the background force before the key was raised. The background forces were the average finger forces 250 ms before the key was raised.

4.2.3 Experimental Procedure
During testing, subjects were seated facing the testing table with the right upper arm at approximately 45° shoulder abduction in the frontal plane, 45° shoulder flexion in the sagittal plane, and approximately 45° flexion of the elbow. The subjects participated in two measurement sessions. The goal of the first session was to measure maximal voluntary force of the individual fingers (MVC). Subjects were given a 5-s window to press with an instructed finger to achieve maximal force and maintain it for approximately 1 s. The peak force was taken as the MVC value. MVC trials were performed two times for each finger and the higher of the two was used for scaling forces in the experimental trials.

The task given to the subjects was to naturally press with all four fingers on the force sensors and match a target force given on the computer screen. The target force was scaled to the MVC of the finger to be raised and presented as a double line on the screen representing ± 5.0 % of the target force. The subjects were told that the target force represented the sum of the force of all four fingers. This deception was used so that subjects always press with the same natural sharing pattern (Martin et al., 2009). Subjects were told at the end of the experiment of this trick with the feedback and none were aware that the feedback was on one finger’s force, not all combined force of the four fingers. Trials were also visually inspected to ensure that the sharing pattern was consistent across trials, within subjects. After the first 5 seconds the force feedback was removed and one of the force sensors was raised. The beginning of key upward movement occurred 1 second after feedback was removed. Subjects were aware that a key would be raised but did not know which key it would be. The motor maintained its raised position for 2 seconds and then returned to its original height (Figure 4.1B). Force feedback then returned for the remaining 3 seconds of the trial. Subjects were instructed to return to the force target when it re-appeared. Generally, small deviations of the total force of four fingers occurred during the interval of no feedback. These deviations decreased in magnitude with practice.
The instruction given to subjects was once the sensor began to rise “don’t pay attention to changes in finger forces rather maintain same commands sent to fingers prior to the perturbation” and more simply “do not intervene voluntarily”. This instruction may be verbally confusing to some subjects, however, after performance of several trials in which this command is given it tends to become very clear to the subjects. Many subjects, actually said phrases such as “now I understand” after they performed several practice trials. The “do not intervene voluntarily” command has been successfully used with previous experiments in which subjects were not supposed to voluntarily respond to a perturbation. Once the motor stopped its movement the subjects were told to maintain the current finger forces for the remainder of the trial. Subjects were given a short practice session to familiarize themselves with this instruction.

The final vertical displacement of key raised, speed of key raising, initial pressing force, and finger raised were the experimental variables. Two levels of final vertical displacement (1 cm and 2 cm), speed (1 cm/s and 3 cm/s), and initial target pressing force (5 % MVC and 20 % MVC) were used. There were four levels of finger raised (I, M, R, L). Each subject performed a total of 64 trials: 2 height levels × 2 speed levels × 2 target force levels × 4 fingers (I, M, R, L) × 2 trials of each condition = 64 trials. The trials were randomly ordered. If it appeared that the subject did not follow the instructions the trial was repeated. The forces of all the fingers during the trials were visible to the experimenter and thus any unusual pressing pattern, removal of fingers from force transducers, or lack of force increase by the raised finger were immediately detected. Subjects were given a one-minute rest after each of the MVC trials, a five minute rest following the MVC measuring session, and another five minute rest after completion of the first 32 key raising trials. These were given to ensure that fatigue did not affect performance.

4.2.4 Data Processing
A custom LabVIEW program (LabVIEW Version 8.0, National Instruments) was used to collect the force signals and display feedback to subjects. The same program was used to control the motors producing key movements to ensure that the force data was synchronized with the position of the keys. Force data were collected at a frequency of 300 Hz. The force data were digitally filtered using a 4th order low-pass two-way Butterworth filter at 10 Hz using Matlab (Version R2006a, The Mathworks, Inc). All trials were visually inspected to verify that subjects followed the instructions. A criterion for an acceptable trial was the following: (1) the
raised finger increased its force in a smooth manner and (2) it maintained the new force level, with no sudden drop in force and minimal downward drift, until the motor was lowered.

4.2.5 Data Analysis
The data of interest were the change in finger forces during the key raising. The change in finger force was defined as the difference between finger forces at the end of motor movement (to the raised position) minus the background force at the beginning. The forces after the finger was raised were taken as the average finger forces immediately when the key stopped the raising movement to 250 ms afterwards. The background force was computed as the average force 250 ms prior to the initiation of motor movement. For each trial the force changes were calculated for all four fingers. The finger force changes were computed in terms of magnitude of force change and percent MVC of a given finger. The force changes were then analyzed in several ways. First, for each combination of displacement, MVC, and speed the data were averaged across subjects. Averaging was not performed across fingers. Standard errors of the averages were computed.

Generally, all of the non-raised fingers showed a decrease in force. Therefore, another measure, which will be denoted ‘% compensation’, was computed. This quantity represents how much of the total force increase due to the force change of the raised finger was “compensated” for by the other fingers. The % compensation was calculated as: \(100*(\Delta f_{\text{raised}} - \sum \Delta f_{\text{non-raised}}) / \Delta f_{\text{raised}}\). The average force change of fingers as a function of proximity to the raised finger was computed. The finger(s) adjacent to the raised finger were assigned a proximity of 1. Note: when M- and R-fingers were raised, there were two adjacent fingers. Fingers two and three digits away from the raised finger were assigned proximity values of 2 and 3, respectively.

4.2.6 Statistical Analysis
A four-way mixed effects MANOVA was performed to test for the effects of INITIAL FORCE (2 levels: 5% and 20%), DISPLACEMENT (2 levels: 1 cm and 2 cm), SPEED (2 levels: 1 cm/s and 3 cm/s), and FINGER (4 levels: I, M, R, and L). The responses tested were change in raised finger force, in terms of both N and % MVC, change in total non-raised finger force, change in total force (sum of individual finger force changes), and the % compensated values for each trial. To check whether proximity effects were significant, the proximity levels were quantified as
corresponding to whether the finger was 1, 2, or 3 fingers away from the raised finger. A one-way ANOVA, with three levels of proximity was applied, to test for the effect of proximity. A post-hoc pair wise comparison was performed to determine if the proximity levels were significantly different. The response was the change in force of the non-raised finger. Statistical analysis was performed using the statistical software Minitab 13.0 (Minitab, Inc., State College, PA, USA) and SPSS (SPSS Inc., Chicago, IL, USA). The data was tested for sphericity. No statistically significant deviation from sphericity was found. All statistical analysis was performed at a significance level of $\alpha = 0.05$.

4.2.7 Passive Mechanical Effects of Lifting a Finger
To examine the effects of passively raising a finger one subject was asked to complete an additional set of experimental trials. The subject was instructed to rest their hand on the force sensors, close the eyes and keep their hand/forearm muscles as relaxed as possible. Each finger was then raised, using the IP, for all combinations of displacements and speeds used in the experiment. One trial of each condition was recorded. The force data were processed exactly the same as the data from the experimental trials.

4.3 Results
The results will be divided into two sections. The first section will focus on the force change in raised finger. The second section will address the finger interaction.

4.3.1 Force Changes in Raised Fingers
In all trials the force exerted by the raised finger increased. The changes were from $1.39 \pm 0.13$ N (R-finger, INITIAL FORCE 5% of MVC, DISPLACEMENT 1.0 cm, SPEED 1.0 cm/s) to $8.00 \pm 1.00$ N (L-finger, INITIAL FORCE 20% of MVC, DISPLACEMENT 2.0 cm, SPEED 3.0 cm/s). In percent of the MVC, the changes ranged from $4.66 \pm 0.38$ % (I-finger, INITIAL FORCE 5% of MVC, DISPLACEMENT 1.0 cm, SPEED 1.0 cm/s) to $31.88 \pm 2.19$ % (L-finger, INITIAL FORCE 20% of MVC, DISPLACEMENT 2.0 cm, SPEED 3.0 cm/s). All the main effects, with the exception of the SPEED effect on the FORCE and % of the MVC changes were statistically significant. The differences in the increases between the slow and fast speeds were the smallest of the three factors investigated. Of all the factors the INITIAL FORCE factor
produced the largest difference between the two levels. Individual fingers were affected differently by the perturbations. I- finger showed the smallest % MVC change (on average around 7.5 % of its MVC) followed by R-, M-, and L-fingers (21%). ANOVA results are presented in Table 4.1. The interaction effects of the factors were non-significant in all cases.

Table 4.1: Mixed effects MANOVA results. P-values are given. Statistically significant values are boldfaced. Note all interactions were not statistically significant.

<table>
<thead>
<tr>
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<th>Responses</th>
</tr>
</thead>
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<td></td>
<td>Force</td>
</tr>
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</tr>
<tr>
<td>DISPLACEMENT</td>
<td>0.004</td>
</tr>
<tr>
<td>SPEED</td>
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</tr>
<tr>
<td>FINGER</td>
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</tr>
<tr>
<td>INITIAL FORCE × DISPLACEMENT</td>
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</tr>
<tr>
<td>INITIAL FORCE × SPEED</td>
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</tr>
<tr>
<td>INITIAL FORCE × FINGER</td>
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</tr>
<tr>
<td>DISPLACEMENT × SPEED</td>
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<tr>
<td>DISPLACEMENT × FINGER</td>
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<tr>
<td>SPEED × FINGER</td>
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<tr>
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</tr>
<tr>
<td>INITIAL FORCE × DISPLACEMENT × FINGER</td>
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</tr>
<tr>
<td>INITIAL FORCE × SPEED × FINGER</td>
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</tr>
<tr>
<td>DISPLACEMENT × SPEED × FINGER</td>
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</tbody>
</table>

4.3.2 Finger Interaction and Compensation

The results presented below address three questions: (a) the type of interaction – enslaving or compensation, (b) effect of a single-finger perturbation on the total force of all fingers, and (c) were the proximity effects observed?

**Enslaving or compensation?** In all trials the forces of the non-raised fingers decreased. Hence, synergic mechanisms favoring negative force co-variation dominated over possible finger enslaving. The force changes ranged from $-9.12 \pm 1.49$ N (L-finger, INITIAL FORCE 20% of
MVC, DISPLACEMENT 2.0 cm, SPEED 1.0 cm/s) to $-0.29 \pm 0.10$ N (I-finger, INITIAL FORCE 5% of MVC, DISPLACEMENT 1.0 cm, SPEED 1.0 cm/s). On a finger by finger comparison, the higher INITIAL FORCE level always produced a larger decrease in the total force of the non-raised fingers. For all other factors (FINGER, INITIAL FORCE, SPEED) being equal, the larger DISPLACEMENT level also always resulted in a larger decrease in the force of non-raised fingers. SPEED did not have a significant effect on the non-raised finger forces ($p > 0.52$). The raised finger, non-raised finger and total force changes are given in Table 4.2A.

*Effects on the total force.* The total force change, in terms of force (N), during key raising was positive in all but four cases. This means that the compensation was not complete: while all of the non-raised fingers showed a negative change in force this force drop was not sufficient to fully compensate for the force increase in the perturbed finger. Three of the four cases in which the total force change was negative occurred when the L-finger was raised and the INITIAL MVC was 20%. The other case occurred when the R-finger was raised and the initial MVC was 20%. The total force change was the greatest when the M-finger was raised (the worst compensation). There was no clear difference between the levels of displacement (Table 4.2B).

**Table 4.2:** (A) The force changes in raised and non-raised fingers. Mean values were computed across subjects ($\pm$ standard error). Units of force are newtons (N). (B) Mixed effects MANOVA results on the effect of finger perturbation on the force changes of all fingers. P-values are given. Statistically significant values are boldfaced.

<table>
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<tr>
<th>FINGER RAISED</th>
<th>INITIAL MVC (% MVC)</th>
<th>DISPLACEMENT (cm)</th>
<th>SPEED (cm/s)</th>
<th>RAISED ΔF (N)</th>
<th>NON-RAISED ΔF (N)</th>
<th>TOTAL ΔF (N)</th>
</tr>
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<td>1</td>
<td>1.83 ± 0.18</td>
<td>-0.29 ± 0.10</td>
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<td>3</td>
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<td>-0.58 ± 0.08</td>
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<td>2.25 ± 0.31</td>
<td>-0.70 ± 0.19</td>
<td>1.55 ± 0.31</td>
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<td>2.87 ± 0.20</td>
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<td>3.27 ± 0.31</td>
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<td>3</td>
<td>4.09 ± 0.35</td>
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<tr>
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<td>Factor</td>
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<td>% Compensation</td>
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<td>--------------------</td>
<td>--------------------</td>
<td>----------------</td>
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<td>0.594</td>
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</tr>
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</table>

Proximity effects. The proximity effect was found to be significant (p<0.005, F = 5.40), see Figure 4.2. The general trend was that, as distance from the raised finger increased, the absolute magnitude of negative force change (in newtons) decreased.

![Proximity effects](image)

**Figure 4.2:** The effect of a non-perturbed finger location with respect to a perturbed finger ('proximity') on the force change ('compensation'). The proximity values of 1, 2, and 3 refer to the distance of non-raised finger in relation to the raised finger. Values were averaged across all trials. Error bars are standard error. The symbol * indicates that proximity 3 was significantly different than 1 and 2. Proximity 1 and 2 were not significantly different than each other.
4.3.3 Passive Mechanical Effects of Lifting a Finger

The passive mechanical effects (i.e. force changes) of lifting a finger on the non-raised fingers were found to be minimal (Table 4.3). The largest negative force change was -0.21 N and many non-raised fingers showed a positive force change. This provides evidence that force changes during experimental trials were not due to passive mechanical mechanisms.

Table 4.3: Force changes in fingers during passive lifting.

<table>
<thead>
<tr>
<th>Finger</th>
<th>Displacement (cm)</th>
<th>Speed (cm/s)</th>
<th>Change in Finger Forces (N)</th>
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</thead>
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<td></td>
<td></td>
<td></td>
<td>I</td>
</tr>
<tr>
<td>1</td>
<td>1.0</td>
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<tr>
<td>4</td>
<td>2.0</td>
<td>3.0</td>
<td>-0.02</td>
</tr>
</tbody>
</table>

4.4 Discussion

The experiment produced two main results, reproducible across subjects, which supported the three main hypotheses formulated in the introduction. In summary, these results showed that finger force adjustments during lifting of one of the fingers were dominated by synergic effects,
not enslaving effects. These adjustments reduced the effects of the force change of the raised finger on total force, which may be interpreted as stabilization of the total force. We observed no signs of voluntary intervention by the subjects and hence interpret the data as resulting from involuntary synergic adjustments of finger forces.

The first result was that the raised finger always showed an increase in force, as expected. The effect depended on the initial force level, magnitude of finger displacement, and varied across the four fingers. The effect of speed was non-significant for the force changes (in N and % MVC).

The second result was that the non-raised fingers showed a decrease in force. The force decrease partially compensated for the increase in force of the raised finger such that the total force change was diminished. A strong proximity effect was observed: Fingers closer to the raised finger showed larger force adjustments as compared to relatively distant fingers. The following discussion will address implications of the findings for phenomena of finger interaction and features of synergic control.

4.4.1 Force Changes in Raised Fingers
The increase of force of the raised finger appears to be primarily due to peripheral (muscle and tendon) properties. Because the perturbations were applied to active muscles the reactions can barely be called ‘passive’ but it seems that the force increase was not induced by increased efferent activation of the muscles. The ‘passive’ nature of the force rise (in the sense that the level of activation was not substantially changed) does not contradict experimental facts that the amount of force increase depended on the initial force level, magnitude of finger displacement and to a smaller degree on the speed of finger displacement. Both the initial force and displacement magnitude affect the resistance of the muscle-tendon complexes to stretching: with the larger initial force and increased magnitude of displacement the resistance to stretching should increase.

4.4.2 Finger Interaction, Compensation, and Proximity Effect
The hypothesis that a force stabilizing synergy would emerge was supported. The non-raised fingers compensation was typically between 50 and 70 % of the increase in force of the raised finger. The provisional explanation that we offer is that during multi-finger pressing tasks a
synergy is established and—in spite of the instruction ‘do not intervene’— the central controller is acting to stabilize the total output by compensating the immediate effect of perturbation to one finger by adjusting forces of other fingers. Such error compensation is the most prominent feature of the synergies (Latash, 2008).

The error compensation has been documented in several studies in which a finger was perturbed during multi-finger pressing. Types of perturbations that were previously used were finger-tapping (Latash et al., 1998), finger addition/removal (Li S. et al., 2003) and finger fatigue (Kruger et al., 2007). All of these studies found that the non-perturbed fingers compensated for the induced change in the total force to a higher degree than the non-raised fingers in this study, in some cases the compensation was 100%. This may be due to the fact that in these studies the perturbations were induced by the subjects while in this study the perturbation came from an extrinsic source. Perhaps, this signifies an anticipatory component of error compensation, in which the CNS is able to “pre-plan” how it will adjust for an expected perturbation and as a result the % compensation is greater. The inter-finger error compensation was also observed in the prehension studies where the local and synergic effects to the perturbation have been reported (Zatsiorsky et al., 2006; Budgeon et al., 2008).

The effect of proximity of non-perturbed fingers to perturbed finger in previous enslaving studies (Zatsiorsky et al., 1998, 2000) has been found to be highly significant. The findings from this study agree with the aforementioned in the sense that fingers closer to the perturbed finger showed a greater force change; however, in this study the fingers in closer proximity showed a larger negative change. This result was unexpected and may be explained by one of two possibilities. The first is that non-raised finger’s force changes were purely compensatory and there was minimal enslaving between fingers. Had enslaving been involved in the finger interaction then it would have been expected that neighboring non-raised fingers to the raised finger would have displayed smaller negative force changes, or even positive force changes.

The second cause may be that raising a finger induced a mechanical effect on the entire hand, which was more pronounced in the neighboring fingers due to stronger peripheral connections to the raised finger. One could argue that pure mechanical effects explain all the force changes that were observed. Raising of the finger causes: 1) an increase of force in that finger due to the force vs. length properties of muscle and the finger being required to support more of the weight of the hand as it is lifted and 2) a decrease in force of the non-raised fingers.
from the lifting effect that is induced across the entire hand. However, the data collected from
the single subject contradicts this notion. The largest negative force change (-0.21 N) was
substantially smaller than the average negative force changes observed during the experimental
trials. Also, many of the non-raised fingers showed a positive increase in force, which may
suggest that the total force stabilizing synergy was even stronger than originally thought. Further
evidence that the observed force changes were more than pure mechanics is supported by the
Zatsiorsky et al. (2000) study. The authors measured enslaving effects at different points of
force application along the fingers, which essentially changes the contribution of FDP, FDS, and
intrinsic muscle force contribution. The enslaving effects were similar in all conditions of finger
loading, indicating a strong neural component source of enslaving as opposed to only muscular
architecture and mechanics. However, in the present experiment it is quite possible that
mechanics played a greater role in the observed force changes than in previous experiments, due
to the dynamic nature of the lifting perturbation.

4.4.3 Synergies and Stability of Performance

What do synergies do? In the original experiments within the UCM hypothesis framework (Scholz
and Schöner 1999; Scholz et al. 2000; Latash et al. 2001), it was assumed that the main purpose of
synergies was to reduce variability of an important performance variable by co-varying the
inherently noisy outputs of the elements. However, later studies have shown that, during multi-finger
tasks, each finger shows a large increase in the variance of its force (as compared to single-finger
tasks), and the co-variation among the finger forces brings the total force variance down to values
comparable to those observed in one-finger experiments (Shapkova et al. 2008; Gorniak et al. 2008).
An alternative hypothesis has been suggested that synergies allow performing several tasks (ensuring
low variability of several performance variables) simultaneously with the same set of elements
without a negative interference among the tasks (Zhang et al. 2009; Gera et al. 2010; cf. the principle
of superposition, Arimoto et al. 2001; Zatsiorsky et al. 2004). In other words, synergies allow us to
hold a glass of water and simultaneously point with the index finger of the same hand at a target
without spilling the contents of the glass.

Our study addresses a basic feature of the notion of synergies: their relationship to stability of
motor performance. The data suggest that multi-finger interaction may be directly related to
stabilizing a performance variable, that is, to attenuating effects of perturbations applied to one of
the elements (and, as a result, to the performance variable). Furthermore, the result that error compensation was observed rather than enslaving also agrees with this concept.

In a study by Gorniak et al. (2009), the subjects were asked to transport a brick-shaped, very light object held between the two palms and to transport an imaginary object to the same target location. Multi-joint synergies stabilizing the distance between the two midpoints of the palms were computed. They were higher during imaginary object transport. However, when, in some trials, an unexpected transient perturbation was applied to one of the hands, the other hand showed a very quick adjustment in the trials with the real object; these adjustments stabilized the distance between the hands and prevented the object from falling. No such adjustments were seen in the trials with an imaginary object. These results show that low variability in a performance variable ensured by a synergy does not necessarily provide stability of that performance variable if a perturbation takes place. Our results carry a different message: Lifting a finger perturbed the force it produced, but the force adjustments in other fingers attenuated the effects of this change on the total force.

There may be several reasons for the different results of this study and the study by Gorniak and her colleagues. Unlike the study of Gorniak, in our experiments, the perturbations were smooth and the system had ample time to produce corrective force adjustments. Our study did not involve manipulation of imaginary objects. The object of study (the fingers of the hand), the task (force production), and the instruction (do not intervene) differed from those in the two-hand object transport study. At this time, we cannot answer the question, which of the mentioned factors brought about the difference in the results.

4.4.4 Synergic Reactions in Voluntary and Involuntary Actions

Earlier studies of motor synergies explored co-variation of elemental variables across trials to quantify the relative amount of “good” variance in the total amount of variance (reviewed in Latash et al., 2007; Latash 2008). In those studies, the subjects were instructed to perform certain actions, and analyses of variance were run at comparable phases across trials. The current study shows that synergic adjustments of elemental variables are typical not only of voluntary actions but also of reactions to perturbations under the instruction to the subject not to intervene.

The instruction “do-not-intervene” used in our study had also been used in several studies within the equilibrium-point hypothesis of motor control (Feldman, 1966; Latash, 1994). Based on those studies, we have assumed that the reactions to finger lifting were compatible with an
unchanged motor command that may be associated with setting a referent value for a salient variable that translated into a required constant total force in the initial state (Feldman and Levin, 1995; Pilon et al., 2007). As suggested in a recent study, multi-digit synergies may be produced by this pattern of control (Latash et al., 2010). When one finger was lifted, its actual coordinate was taken further away from the presumably unchanged referent coordinate resulting in an increase in that finger’s force. The observed changes in other (motionless) finger forces suggest that their referent coordinates changed as well, despite the instruction “not to intervene”, moving closer to the actual coordinates of the fingertips.

The results suggest that, despite the instruction, there were adjustments in the referent coordinates for the fingers, possibly mediated by sensory receptors (cf. Johansson and Westling, 1984). This suggests that referent coordinates are not set by the controller but emerge given values of (unidentified) neural control variables and sensory information about the actual body configuration (Feldman and Levin, 1995). Lastly, we tend to think that our observed results were mostly due to a force-stabilizing multi-finger synergy. However, we do not dismiss the fact that passive mechanisms were undoubtedly acting in parallel to the presumed synergic mechanisms. Now the challenge is to better design experimental protocols, which will shed light onto the relative contribution of each.
CHAPTER 5

Study #3: Multi-finger Interaction during Involuntary and Voluntary Single Finger Force Changes

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5.1 Introduction

It is well known that finger actions are interdependent. Two patterns of finger interaction have been reported, positive co-variation (known as enslaving) and negative co-variation. During voluntary force production with a subset of fingers, the other fingers of the hand also produce force in the same direction (enslaving, Zatsiorsky et al. 1998, 2000). Enslaving effect gets contribution from mechanical connections between the fingers (Fahrer 1981; Kilbreath and Gandevia 1994; Leijnse 1997), multi-digit motor units in the multi-tendon extrinsic muscles (Kilbreath and Gandevia 1994; Schieber 1995), and overlapping cortical representations of the intrinsic hand muscles (Schieber and Hibbard 1993; Sanes et al. 1995; Rathelot and Strick 2006).

A model was developed, the “mode hypothesis” (Danion et al. 2003, Zatsiorsky et al. 1998, 2002), which accounts for enslaving effects. This model was developed to study the neural mechanisms of finger coordination in multi-finger tasks. The hypothesis states that the neural controller manipulates hypothetical variables (modes) to individual fingers that reflect their intended involvement in the task. The mode magnitude represents an intensity of the central command intended for one finger but sent simultaneously to several fingers. Mode magnitude can vary from 0 to 1, with mode = 0 indicating zero intentional force production and mode = 1 representing maximal force production by a finger. For a more detailed discussion see Zatsiorsky et al. (2002). Analysis in terms of modes (rather than forces) allows, in particular,
addressing issues of task-specific co-variation of commands to fingers (reviewed in Latash et al. 2007).

The second type of finger interaction is characterized by negative co-variation (called in earlier studies error compensation, Latash et al. 1998) of finger forces, or force changes in opposite directions within a subset of fingers. Negative co-variation was found in multi-finger tasks in which subjects were asked to produce constant force with a set of fingers and then tapped with one of the fingers (Latash et al. 1998), added or removed a finger (Li S et al. 2003), increased the force of one finger voluntarily (Martin et al. 2009), or one finger was unexpectedly raised (Martin et al., in press). The negative co-variation of finger forces can be interpreted as resulting from a force-stabilizing synergy. This explanation follows from the definition of a motor synergy as a neural organization of elemental variables (in the present example, the finger forces) that stabilizes a performance variable (total force) by co-varied adjustments of the elemental variables (Gelfand and Latash 1998; reviewed by Latash et al. 2002, 2007).

The goal of this study has been to compare force changes in fingers of the hand when a finger force increases either (a) unintentionally, due to passive lifting; or (b) intentionally due to voluntarily pressing with a single finger.

Assuming that the subject is not voluntarily changing the modes to fingers when one finger is passively lifted, no effects of enslaving on other finger forces are expected. The force of the passively raised finger is expected to increase due to such factors as elastic properties of muscles (Magnusson 1998) and tendons (Benjamin et al. 2008), as well as the stretch reflex (Liddell and Sherrington 1924). In contrast, during intentional single-finger pressing, its mode is expected to increase, and enslaving is expected to lead to increased forces in all the fingers.

Negative co-variation is expected to reflect a pre-existent synergy associated with total force stabilization. A change in the force of the passively raised finger sensed by somatosensory receptors is an error signal, which is expected to lead to an unintentional decrease in all the other finger modes resulting in a drop in their forces. Hence, a task involving accurate, constant force production by a set of fingers is expected to be dominated by synergic mechanisms leading to negative co-variation (cf. Gorniak et al. 2007; Shapkova et al. 2008). So, we hypothesize that an involuntary increase in finger force will be associated with a drop in modes to other fingers and a drop in their forces. In contrast, a voluntary increase in finger force is expected to lead to no
changes in modes to other fingers; however an increase in forces will be observed due to enslaving.

We also explored two additional issues related to finger force adjustments. Previously, it was proposed that during multi-finger pressing the CNS attempts to minimize the ‘secondary moment’ produced about the longitudinal axis of the hand (Li ZM et al. 1998; Vigouroux et al. 2008). We hypothesized that a force changes of a finger, whether voluntary or not, will lead to force changes in other fingers that will be organized to minimize the moment about the longitudinal axis of the hand. The other issue is related to the effects of proximity on finger force adjustments, that is, whether fingers that are located closer to the task finger show larger mode/force adjustment as could be expected based on earlier studies (Zatsiorsky et al. 1998, 2000).

5.2 Methods and Materials

5.2.1 Subjects

Twelve subjects (six male, six female) participated in the experiment. The average age, weight, and height (± SD) of the male subjects were 24.8 ± 3.2 years, 78.9 ± 4.8 kg, and 186.0 ± 4.8 cm, respectively. The average age, weight, and height of the female subjects were 23.0 ± 2.8 years, 62.6 ± 17.7 kg, and 162.1 ± 12.2 cm, respectively. All subjects were right-handed, in good health, and had no previous history of neuropathies or traumas to the upper limbs. None of the subjects were professional typists or musicians, which could affect finger coordination. The subjects gave informed consent according to the procedures approved by the Institutional Review Board of the Pennsylvania State University.

5.2.2 Apparatus (the ‘inverse piano’ technique)

The main piece of equipment was a device called the ‘inverse piano’ (I-Piano). The I-Piano consists of four uni-directional piezoelectric force transducers (208C02, PCB Piezotronics) mounted on top of four linear actuators (PS01-23x80, Linmot, Spreitenbach, Switzerland) (Figure 5.1). Actuators produced smooth vertical movements of the transducers. The I-Piano was mounted to a steel frame that was rigidly attached to the testing station. Each individual transducer/actuator combination was adjustable in the finger longitudinal direction, but not in the medial/lateral direction. Actuators were adjusted prior to each subject’s testing session in a
configuration they reported as being most comfortable, which was typically exemplified by approximately 0 degrees of flexion at MCP joint, 30-45 degrees flexion at PIP joint, and 30-45 degrees of flexion at DIP joint. A wooden block was placed in the palm of the hand to support the hand and limit wrist flexion as well as supination/pronation of the forearm. The block provided support to the hand across the 2-5 metacarpal bones. The thumb was abducted and flexed so that it was against the side of the wooden block and supported in the vertical direction by a wooden platform. The wooden platform extended towards the subject and provided support to the entire forearm, from wrist to elbow.

**Figure 5.1:** Top and side view of force transducer set up. Transducers were equally spaced laterally and adjustable in the forward/backward direction. Each transducer was rigidly attached to a linear actuator.

The transducers were calibrated prior to data collection in the first subject. Sandpaper pads were attached to the contact surface of the force transducers to increase friction and to reduce the temperature effect from the skin. Analog output signals from the transducers were connected to separate AC/DC conditioners (484B, PCB Piezotronics, Depew, NY, USA), then digitized using a 16-bit analog-digital converter (CA-1000, National Instruments, Austin, TX, USA), mounted on a microcomputer (Dimension 2400, Dell, Round Rock, TX, USA) that was
utilized for control, acquisition, and processing of the data. The actuators were programmed using LabVIEW (LabVIEW Version 8.0, National Instruments) that sent commands to a controller (E400-AT, Linmot, Spreitenbach, Switzerland).

5.2.3 Experimental Procedure
The experiment consisted of three separate measurement sessions. During all sessions, subjects were seated facing the testing table with the right upper arm at approximately 45° shoulder abduction in the frontal plane, 45° shoulder flexion in the sagittal plane, and approximately 45° flexion of the elbow. The first session was used to measure individual finger maximum voluntary contractions (MVC). MVC measurements were recorded for each finger individually and all four fingers together in five different hand configurations. The hand configurations were all fingers level (C₀), I-lifted (C₁), M-lifted (C₂), R-lifted (C₃), and L-lifted (C₄). Measurements were made for the different hand configurations because the changes in muscle architecture would affect the force producing capabilities of the fingers. The height of the key for the passive finger lift was 5.0 mm. MVC trials were 5 s long during which subjects were instructed to press with a given finger to achieve maximal force and maintain it for approximately 1 s (Figure 5.2a). The peak force was taken as the MVC value. There were 25 MVC trials (5 MVC measurements × 5 hand configurations = 25).

During the second session subjects had to follow a ramp target force with each finger for all of the hand configurations (Figure 5.2b). The ramp started at 0% MVC and went up to 70% MVC at a slope of 10% MVC/s, thus trials were 7 s in duration. The MVC force levels were based on the MVC values recorded for each hand configuration in the first session. The force data of all four fingers were recorded during each trial. There were 20 ramp trials performed (4 fingers × 5 hand configurations = 20 trials).

The third session was the main experimental session. Subjects were given a force target range to which they were instructed to press with all four fingers and keep the force inside the target range. The feedback was the total force produced by all four fingers. The target range was of 10% MVC ± 5.0% of four-finger pressing in hand configuration C₀. Once the force output initially reached the target range it had to remain within the target range prior to the initial perturbation, otherwise the trial was aborted and restarted. After 5 s one of the transducers was lifted to 5.0 mm at 3.0 cm/s. Subjects were told one of the keys would be lifted and, when this
occurred, “do not intervene voluntarily”. One second prior to the key being lifted, the actual force feedback was removed and replaced with pseudo-feedback for the remainder of the trial. The pseudo-feedback was a sinusoidal signal with noise added that always remained within the force target range. This pseudo-feedback was used so that subjects were not surprised by the sudden change in force from key being lifted and attempt to actively change their finger force to match the target force. After the key was lifted, the next instruction was to wait for about 3 s, and then quickly press down with the lifted finger only to produce a pulse of force. The subjects were told to press with as close to maximal effort as they could without a change in arm posture or fingers losing contact with force sensors. Many of the male subjects were able to press the sensor with a force greater than that being produced by the linear actuator, which caused it to lower back to its initial position. If subjects demonstrated this ability then they were told to attempt to press the motor down to the initial position every time. In terms of pulse speed and duration they were told to produce the force pulse as quick as possible then immediately return back to the target force. The experimenter showed subjects examples of what a desired force pulse profile appeared like.

A short practice session was performed until subjects demonstrated that they were able to follow these instructions. The actual force feedback of the trial was visible to the experimenter and it was quite apparent if the subject followed the instructions. There were 20 total trials (4 fingers × 5 trials per finger = 20 trials). The passive finger lifting phase of the experiment will be referred to as the involuntary phase (Invol) and the finger pressing phase will be referred to as the voluntary phase (Vol). The finger that was passively lifted and then pressed voluntarily will be referred to as the target finger and the other fingers referred to as non-target fingers.
Figure 5.2: Examples of trials. (A) MVC trial (I-Finger). (B) Ramp-target trial (I-Finger). (C) Experimental trial as the feedback appeared to the subject (I-Finger). (D) Finger force data during experimental trial (I-Finger).
5.2.4 Data Processing

A custom LabVIEW program (LabVIEW Version 8.0, National Instruments) was used to collect the force signals and display feedback to subjects. The actuator moves were controlled within the program. This allowed for the exact time of actuator move initiation to be known. Force data were collected at a frequency of 300 Hz. The force data were filtered using a 4th order low-pass two-way Butterworth filter at 10 Hz using Matlab (Version R2006a, The Mathworks, Inc.). All trials were inspected to verify that subjects followed the instructions. The criteria for an acceptable trial was: (1) once the total force was within the target range it remained in the range until the actuator move was initiated, (2) the sharing pattern was steady during the first 5 s, (3) the target finger displayed an increase in force during the upward move of the actuator, and (4) a quick force pulse was produced with a force profile that was qualitatively similar to what the instruction was.

5.2.5 Data Analysis

The data of interest were the changes in both actual forces (F) and mode (MD) values expressed in newtons during passive finger lifting and pressing. The method of computing MD values is described below. The force and mode changes (ΔF and ΔMD) during key lifting were computed as the difference between the values at the time of peak force of the lifted finger minus the average value over 250 ms prior to initiation of key upward movement. To find the onset of the Vol phase, the rate of force change (dF/dt) was calculated for the target finger over the Vol phase of the trial. The maximum dF/dt was identified and the initiation of Vol pressing was assumed to occur when dF/dt reached 5% of this value. Trials were inspected visually to ensure that the identified time of initiation of finger pressing and peak force was correct.

The F data were transformed to MD values. The first step was to construct the enslaving matrix, which was calculated from the ramp-target trials. For each ramp-target trial, linear regression coefficients were computed on the force of each finger against the total force of all four fingers from 0% to 50% MVC range of the instructed finger. The coefficient of the regression line for each finger was entered into the enslaving matrix:
where $b_{j,k}$ is the regression coefficient of individual finger $F_j$ [$j = \{\text{index (i)}, \text{middle (m)}, \text{ring (r)}, \text{little (l)}\}$] when finger $k$ is instructed to press [$k = \{\text{index (i)}, \text{middle (m)}, \text{ring (r)}, \text{little (l)}\}$]. Separate enslaving matrices were computed for each of the five finger configurations ($C_0$, $C_i$, $C_M$, $C_R$, and $C_L$). The mode value in newtons, $MD$, was computed by multiplying the inverse of the appropriate enslaving matrix (for a given finger configuration) by the recorded $F$ values:

$$MD = E^{-1} \begin{bmatrix} F_i \\ F_m \\ F_r \\ F_l \\ \end{bmatrix}$$

The $C_0$ finger configuration enslaving matrix was used to calculate the $MD$ values during key lifting. $MD$ values during the $Vol$ pressing phase were computed using the appropriate raised finger enslaving matrix (finger configuration $C_i$, $C_M$, $C_R$, and $C_L$). The $\Delta MD$ of each finger during passive finger lifting and voluntary pressing was calculated in the same manner as described for $\Delta F$.

Due to gender strength differences, there was a large variation in the magnitude of $\Delta F$ across subjects. In order to compare $\Delta F$ and $\Delta MD$ values across subjects they were normalized to the MVC values of the respected finger. During each phase of the experiment, the $\Delta F$ and $\Delta MD$ of both the target finger and non-target fingers were compared.

An index, called the compensation percentage ($COMP\%$), was calculated to quantify the synergic relationship between the fingers during the $Invol$ phase. It was assumed that a force-stabilizing synergy among the fingers was established during the steady-state phase of each trial. The $COMP\%$ quantifies the strength of the synergy in terms of how much of the $\Delta F$ of the lifted finger is compensated for by $\Delta F$ of the non-lifted fingers, with 100% indicating that the overall effect of total force was nil. The $COMP\%$ is computed as:

$$100\% \frac{1 - (\sum_j \Delta F_j)}{\Delta F_{\text{raised}}}$$

where $F_j$ is the set of individual finger $\Delta F$ [$j = \{\text{index (i), middle (m), ring (r), little (l)}\}$].

$E$ is the enslaving matrix value.
The change in moment about the longitudinal axis of the hand during Invol and Vol was another parameter of interest. The moments produced by the target finger force and all finger forces together about the neutral line (NL) were compared. The NL was the point of application of the resultant normal force by all fingers. The location of the neutral point of normal F application of the fingers was found using the following formula (Zatsiorsky et al. 1998):

\[
NL = \frac{\sum_j F_j L_j}{F_{\text{tot}}}
\]

where NL is the medial-lateral coordinate of the neutral point of normal force application, \(F_j\) [\(j = \{\text{index (i), middle (m), ring (r), little (l)}\}\)] is the finger normal force, \(L_j\) is the moment arm of each finger, and \(F_{\text{tot}}\) is the sum of the normal forces of all fingers. The moment arms (\(L_j\)) of the individual finger forces were measured from the index finger with \(L_i = 0\) mm, \(L_m = 30\) mm, \(L_r = 60\) mm, and \(L_l = 90\) mm. After the perturbation (Invol or Vol) the change in the moment about the NL was computed in regards to: (1) \(\Delta F\) and \(\Delta MD\) of the target finger only (MD\(_j\) = (L\(_j\) – NL)*\(f_j\)), and (2) \(\Delta F\) and \(\Delta MD\) of all fingers (MTOT = \(\sum\)[(L\(_j\) – NL)*\(f_j\)].

The effect of proximity of non-target fingers to target finger was investigated. Fingers were assigned a proximity value of 1, 2, or 3 in terms of the distance from the target finger, where the finger(s) adjacent to the target finger was assigned a value of 1. When either the M- or R-fingers were the target finger there were two adjacent fingers.

5.2.6 Statistical Analysis
Mean and standard errors (SE) of the \(\Delta F\), \(\Delta MD\), proximity index changes, change in moments about NL, were computed across all subject trials of the same condition. Paired t-tests were used to test for a significant difference between various measures between: (1) \(\Delta F\) and \(\Delta MD\) values in the same phase of a trial (Invol or Vol) and (2) between Invol and Vol phases of a trial. One-way repeated measures ANOVAs were used to test for the effect of Finger perturbed (4 levels: I, M, R, and L) on the Invol and Vol responses of: Target Finger \(\Delta F\) and \(\Delta MD\), Non- Target Finger \(\Delta F\) and \(\Delta MD\), Total \(\Delta F\) and \(\Delta MD\). One-way repeated measures ANOVAs were used to test for the effect of Proximity (3 levels: 1, 2, and 3) on the \(\Delta F\) and \(\Delta MD\) in un-perturbed fingers. Tukey pairwise comparisons were performed to test the difference among levels of each ANOVA test.

Statistical analysis was performed using the statistical software Minitab 13.0 (Minitab, Inc., State College, PA, USA) and SPSS (SPSS Inc., Chicago, IL, USA). The data were tested for
sphericity and deviations were corrected using the Greenhouse-Geisser correction. All statistical analysis was performed at a significance level of $\alpha = 0.05$.

5.3 Results

5.3.1 Changes in Forces and Modes during the Involuntary Phase

The force changes ($\Delta F$) and mode changes ($\Delta MD$) values averaged across subjects during the involuntary phase ($Invol$) are illustrated in Figure 5.3.

A)
Figure 5.3: Change in force (ΔF) and mode force (ΔMD) during the involuntary phase (passive finger lifting) for target fingers: (A) I-Finger, (B) M-finger, (C) R-finger, and (D) L-finger. Target fingers all showed an increase in both ΔF and ΔMD. Generally, non-target fingers showed a small decrease in ΔF and ΔMD. Asterisk (*) indicates a significant difference between ΔF and ΔMD of a finger.

5.3.2 Changes in Forces

In all cases, the average ΔF of target fingers was positive and in all but one case the average ΔF of non-target fingers was negative, i.e. negative co-variation, not enslaving was observed. The target finger displayed a ΔF between 10.71 ± 1.89% MVC (I-finger) and 16.60 ± 2.26% MVC (L-finger). For all subjects the total force (i.e. force produced by all fingers) increased. The percentage of ΔF of the target finger compensated for by the negative ΔF of the non-target fingers was computed (COMP%). The COMP% by the non-raised fingers ranged from 17.0 ± 9.0% MVC (L-finger raised) to 24.9 ± 6.4% MVC (R-finger raised), i.e. the compensation was present but not complete (ΔF\text{total} > 0). The one-way repeated measure ANOVAs (Table 5.1A) showed that the effect of Finger perturbed was significant on the ΔF of the target finger, non-
target fingers, and total force. The effect of Proximity of non-target fingers to the target finger was examined. The Proximity effect on the ΔF of non-target fingers was significant (p < 0.001). Fingers with a closer proximity to the target finger had a larger decrease in force during the passive lifting of the target finger. The averaged ΔF data, as a function of proximity to target finger, is presented in Figure 5.4. Pairwise comparisons showed that the ΔF for a proximity of 1 was significantly different than the ΔF for a proximity of 3 (p < 0.01) and a proximity of 2 was significantly different than a proximity of 3 (p < 0.01).

**Table 5.1:** One-way repeated measures ANOVA results. Bold values are statistically significant.

A)

<table>
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<tr>
<th>Response Type</th>
<th>Factor</th>
<th>Target Finger</th>
<th>Non-Target Fingers</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>ΔF</td>
<td>Finger</td>
<td>2.152 3.037</td>
<td>2.573 9.312</td>
<td>2.031 6.738</td>
</tr>
<tr>
<td>ΔMD</td>
<td>Finger</td>
<td>2.275 9.973</td>
<td>1.905 8.781</td>
<td>3.000 12.837</td>
</tr>
</tbody>
</table>

B)

<table>
<thead>
<tr>
<th>Response Type</th>
<th>Factor</th>
<th>Target Finger</th>
<th>Non-Target Fingers</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>ΔF</td>
<td>Finger</td>
<td>3.000 4.779</td>
<td>2.311 10.435</td>
<td>1.943 13.691</td>
</tr>
<tr>
<td>ΔMD</td>
<td>Finger</td>
<td>3.000 8.579</td>
<td>2.433 2.463</td>
<td>3.000 5.278</td>
</tr>
</tbody>
</table>

Note: The effect of *Finger* on ΔF and ΔMD is given for the involuntary phase (passive finger lifting) and voluntary phase (finger pressing). DOF stands for degrees-of-freedom corrected for violations of sphericity.

### 5.3.3 Changes in Mode Magnitudes
Mode changes (ΔMD) of target fingers ranged from 12.05 ± 1.90% MVC (I-finger) to 29.06 ± 3.19% MVC (L-finger). In all cases the ΔMD of non-target fingers was negative. The largest ΔMD of a non-target finger was -6.24 ± 1.24% MVC (L-finger when R-finger raised). The total ΔMD (sum of ΔMD of individual fingers) was positive for all trials. The COMP% by the non-target fingers ranged from 26.6 ± 9.0% MVC (I-finger raised) to 50.6 ± 7.1% MVC (R-finger raised). ΔMD values of Target Finger, Non-Target Finger, and Total ΔMD were all significantly affected by Finger raised (Table 5.1B). A significant Proximity effect was found (p < 0.001), with fingers closer to the target finger displaying a larger negative ΔMD. Pairwise comparisons found that the ΔMD with proximity of 1 was significantly different than the ΔMD for proximity of 2 or 3 (p < 0.001).
Figure 5.4: Change in force (ΔF) and mode force (ΔMD) as a function of proximity from target finger for: (A) Invol and (B) Vol tasks. ΔF during Invol showed smaller changes versus the proximity than ΔMD. The opposite was found for Vol. Asterisks (*) indicate a significant difference between ΔF and ΔM values. Error bars are SE.

5.3.4 Comparison of Force and Mode Changes
The ΔF and ΔMD were compared for both target and non-target fingers. The ΔF and ΔMD of the target fingers were significantly different for all fingers (Figure 5.4), with the ΔMD of the target finger being larger than the ΔF. The ΔF and ΔMD of the non-target fingers were significantly different in 6 of 9 instances. In general, the ΔMD was larger in magnitude than ΔF for the non-target fingers.

5.3.5 Changes in Forces and Modes during the Voluntary Phase
The force changes (ΔF) and mode changes (ΔMD) values averaged across subjects during the voluntary phase (Vol) are shown in Figure 5.5.
Figure 5.5: Change in force ($\Delta F$) and mode force ($\Delta MD$) during the voluntary phase (finger pressing) for target fingers: (A) I-Finger, (B) M-finger, (C) R-finger, and (D) L-finger. Target
fingers all showed an increase in both ΔF and ΔMD. Non-target fingers showed increases in terms of ΔF and near zero changes in terms of ΔMD. Asterisk (*) indicates a significant difference between ΔF and ΔMD of a finger.

5.3.6 Changes in Forces
The target finger showed a large positive ΔF, between 90.61 ± 13.65% MVC (R-finger) and 64.61 ± 6.60% MVC (I-finger). All non-target fingers displayed a positive ΔF, which was larger for fingers adjacent (proximity = 1) to the target finger (proximity effect). The average positive ΔF of non-target fingers ranged from 21.83 ± 4.47% MVC for R-finger (M-finger instructed to press) to 0.71 ± 1.10% MVC for L-finger (I-finger instructed to press). One-way ANOVA showed a significant effect of Finger on the ΔF of the Target Finger, Non-Target Fingers, and Total ΔF (Table 5.1B). A significant Proximity effect was found for ΔF of non-target fingers. Fingers with a closer proximity to the target finger showed larger increase in force during the pressing of the target finger. Pairwise comparisons found that the ΔF of non-target fingers with proximity of 1 was significantly different than the ΔF for proximities of 2 and 3 (p < 0.001).

5.3.7 Changes in Modes
The average ΔMD of the target fingers were between 140.57 ± 25.75% MVC (R-finger) and 68.55 ± 6.69% MVC (I-finger). In 7 of 12 cases a negative ΔMD was observed for the non-target fingers. The range of ΔMD for non-target fingers was between -7.34 ± 19.27% MVC for R-finger (L-finger instructed to press) and 7.10 ± 1.38% MVC for M-finger (I-finger instructed to press). In terms of ΔMD values, the Finger effect was significant on the change in Target Finger and Total ΔMD. There was no significant effect of Proximity on non-target finger ΔMD (p > 0.35).

5.3.8 Comparison of Force and Mode Changes
The ΔF and ΔMD of the target fingers were found to be statistically significantly different for R- and L-fingers (Figure 5.5). On average the ΔMD was larger than the ΔF for all the target fingers. The ΔF and ΔMD of the non-target fingers were significantly different in 5 of 9 instances. In general the ΔMD was smaller in magnitude than the ΔF for the non-target fingers. In many of the cases the ΔMD was very close to zero.
5.3.9 Secondary Moment Stabilization

The moment produced about the NL by target finger ΔF and ΔF of all fingers together (target finger and non-target fingers combined) were significantly different for both phases (Invol and Vol) (p-value < 0.001). The same was found in regards to ΔMD values. In regards to the Invol phase, the total moment change was larger when M-, R- and L- fingers were raised than the moment change produced by the target finger alone. This indicated that the force changes, both ΔF and ΔMD in the non-target fingers did not act to compensate for the moment change due to the target finger perturbation. The opposite was found for Vol. For all Vol target finger trials the total moment was smaller than the moment produced by the target finger alone (Table 5.2). This was true when the moment change was computed in regards to both F and MD values. This indicated that the force changes in the non-target fingers functioned to compensate for the moment change produced by the target finger force increase.

Table 5.2: Mean moment produced about NL by perturbed finger and all fingers (± SE). (A) Involuntary phase. (B) Voluntary phase.

A)

<table>
<thead>
<tr>
<th>Target Finger</th>
<th>Δ Target Finger Moment</th>
<th>Δ Total Moment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Δ F</td>
<td>Δ MD</td>
</tr>
<tr>
<td>I</td>
<td>170.35 ± 15.89</td>
<td>154.35 ± 15.47</td>
</tr>
<tr>
<td>M</td>
<td>-23.64 ± 10.75</td>
<td>-30.96 ± 13.92</td>
</tr>
<tr>
<td>L</td>
<td>-17.16 ± 8.17</td>
<td>-26.57 ± 12.20</td>
</tr>
</tbody>
</table>

B)

<table>
<thead>
<tr>
<th>Target Finger</th>
<th>Δ Target Finger Moment</th>
<th>Δ Total Moment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Δ F</td>
<td>Δ MD</td>
</tr>
<tr>
<td>I</td>
<td>527.38 ± 77.37</td>
<td>561.40 ± 96.15</td>
</tr>
<tr>
<td>M</td>
<td>-807.03 ± 93.47</td>
<td>-1037.31 ± 192.22</td>
</tr>
<tr>
<td>R</td>
<td>-812.61 ± 75.15</td>
<td>-1287.41 ± 230.55</td>
</tr>
<tr>
<td>L</td>
<td>-752.51 ± 89.90</td>
<td>-1281.54 ± 195.35</td>
</tr>
</tbody>
</table>
Note: Moments were computed based on F and MD values. Units of moment are Nmm.

5.4 Discussion
The results agree well with the main hypotheses. In particular, the first hypothesis was that during the involuntary finger force increase (Invol phase) finger force adjustments will primarily reflect a force stabilizing synergy. The data support this hypothesis: For all conditions the target finger displayed an increase in force and the non-target fingers showed a decrease in force. This finding was upheld when the analysis was performed in terms of both force (F) and mode (MD) values. The compensation of the force increase in the target finger by the force drop in the non-target fingers was far from complete, between 20 and 25%.

A previous study (Martin et al. 2011a) showed qualitatively similar results during involuntary force changes. It was found that initial pressing force had a highly significant effect on the force changes observed during passively lifting one of the fingers. It is possible that the low initial pressing force used in this experiment did not allow stronger effects of the force-stabilizing synergy to emerge. Higher compensation values were reported by Latash et al. (1998). In that study subjects were asked to tap with one finger after initially pressing with I-, M-, and R-fingers to 30% MVC. Compensation by non-tapping fingers for the tapping finger force drop to zero was, on average, between 94% and 102%.

The second hypothesis was that, during the voluntary force production by the target finger, the force of the non-target fingers would increase without a change in modes to those fingers that is exclusively due to enslaving. During the Vol phase all of the non-target fingers showed substantial increases in force but only very small changes in mode values. This signifies that, when instructed to press with a target finger, subjects were able to direct the command (the mode) almost entirely to the target finger with force changes in the other fingers produced by the enslaving. The changes in the non-target finger forces displayed a strong proximity effect similar to that documented in previous enslaving studies (Zatsiorsky et al. 1998; 2000). However, the changes in the mode values showed no proximity effect, which supports the conclusion that subjects were able to send the pressing command solely to the target finger.

The third hypothesis was that during both phases the force changes of non-target fingers would act to reduce the moment about the longitudinal axis of the hand. The data do not allow support the claim that the synergic reactions during the Invol phase acted to minimize the
secondary moment. However, during the Vol phase this hypothesis was upheld. When analyzed in terms of both forces and modes, the total moment change was smaller than the moment change induced by the target finger alone. This was true for all target fingers. A similar finding was reported by Vigouroux et al. (2008); however, they used a four-finger pressing task instead of single-finger pressing used in our experiment.

5.4.1 Factors Contributing to Force Changes
Several mechanisms could lead to force changes. The first, most basic, mechanism is purely mechanical. There are mechanical effects of passively lifting a finger that can cause changes in the forces of other fingers. A study (Martin et al. 2011a) that was performed prior to this study investigated force changes during the Invol phase. Several levels of initial pressing force, vertical displacement and vertical speed were used. To ensure that the force changes were not purely passive force changes were recorded while subjects passively rested their non-raised fingers on the sensors. The negative force changes observed in such conditions were smaller than during active finger pressing, they even turned positive in some cases. The conclusion was that the force changes during the experimental trials could not be explained solely by the passive mechanics of finger lifting. This does not mean that the forces cannot be transmitted due to pure mechanical reasons at all. Forces can be transmitted among the fingers ‘passively’ since the fingers are mechanically connected by various tissues. This would be expected to be more prominent in the Vol than Invol phase due to the higher forces, and thus higher internal strains. It is almost certain that mechanics do contribute to the force changes; however, they are evidently not the sole cause. Another method to assess whether or not force-changes are due to mechanical effects is to measure the latency between the lifted finger and non-lifted finger force changes. This works well for some experimental tasks; however, for this particular study we did not deem it appropriate. The force changes of the non-lifted fingers were quite small, and it was difficult to define when they started to deviate from the background force. Based entirely on visual inspection, the force changes of non-lifted fingers did appear to have a greater than zero-latency, which supports the contention that force changes were due to more than pure mechanical effects.

Another potential cause of the force changes are reflex responses. Changes in muscle length induce the stretch reflex (Liddell and Sherrington 1924; Matthews 1959). However, given
the small amplitude of finger raise and the low speed of this motion, the reflex effects were likely modest (Matthews 1959; Rack and Westbury 1969). Also, the stretch reflex evoked during the Invol phase in the extrinsic flexors would produce a force increase in all non-task fingers, not a force decrease as observed in the experiments.

A third mechanism of the observed force changes is enslaving. As already mentioned enslaving can be due to mechanical connections between the fingers (Fahrer 1981; Kilbreath and Gandevia 1994; Leijnse 1997), multi-digit motor units of the extrinsic muscles (Kilbreath and Gandevia 1994; Schieber 1995), and overlapping cortical connections (Schieber and Hibbard 1993; Sanes et al. 1995; Rathelot and Strick 2006). The enslaving effects were assumed to be present in both the Invol and Vol phases. They were expected to dominate in the Vol phase and might have been masked in the Invol phase by the more dominant total force-stabilizing synergic relationship that was established prior to the finger lifting.

A total force-stabilizing synergy is the last mechanism of force changes in the fingers that we will be considering. We use a definition of a synergy as a neural organization of elemental variables in a way that reduces the variability of an important performance variable (reviewed in Latash et al. 2007; Latash 2008). For a multi-finger pressing task, in which the instruction was to produce a certain level of force, the elemental variables would be each finger’s force or mode while the performance variable is the total force. Negative force changes displayed by the non-target fingers in response to the positive force change of the target finger during the Invol phase may be seen as signs of such a synergy. Several recent studies provide support to the possibility that a total force stabilizing synergy commonly exists among the fingers during multi-finger pressing (Gorniak et al. 2007; Shapkova et al. 2008).

Aside from the above mentioned factors that could cause force changes there are other factors that affect the magnitude of the force changes by altering motor unit recruitment thresholds. McNulty and Cresswell (2004) studied the effect of varying muscle length and load on the recruitment behavior of low-threshold motor units in the flexor digitorum superficialis. They found that at shorter muscle lengths the recruitment threshold was decreased with increased loads. At longer muscle lengths the recruitment threshold was less affected by external load, equivalent to initial pressing force in our study. These factors should be taken into consideration when interpreting the results of this study.
Perhaps the main limitation of this study was that our protocol did not allow the individual mechanisms (i.e. mechanical, neural, etc.) of force changes to be estimated. As previously stated, finger interaction is a complex combination of mechanical and neural factors. Recently, several studies have used EMG in an attempt to estimate the force distribution of extrinsic forearm muscle motor units across the fingers (Keen et al. 2004; Butler et al. 2005). Butler et al. (2005) recorded EMG from individual motor units of the flexor digitorum superficialis during flexion at various contraction levels. The results showed that below 50% MVC the recruitment of motor units serving individual digits was quite independent. Keen et al. (2004) performed a similar experiment involving the extensor digitorum. The main finding was that the force output of single digits from microstimulation of single motor units of the extensor digitorum was also quite concentrated to individual digits. These studies point toward the conclusion that, at least in terms of the neural enslaving factors, fingers are more independent during low level force production. This suggests that at low force production levels the forces produced by fingers are very close to the intended force production of the central nervous system, minus the enslaving that occurs due to mechanical factors. This would allow for fine object manipulation, which commonly utilizes relatively low force production.

Another potential limitation was that the force changes by the target finger were quite different between the Invol and Vol phases. However, we would like to state the following facts to justify our comparison between the two phases. First, the composition of modes has been shown to be consistent over a wide range of force magnitudes (Zatsiorsky et al. 1998; Danion et al. 2003). Second, force/mode co-variation patterns stabilizing total force in multi-finger tasks have been documented over a range of force magnitudes comparable with the range of forces in this study (e.g., Latash et al. 2002; Shim et al. 2005). Third, the force sharing pattern during multi-finger tasks has also been shown to be consistent over a wide range of forces (Li et al. 1998). Overall, these observations suggest that the difference in the force ranges in the Vol and Invol phases might not have corrupted the results.

5.4.2 Negative vs. Positive Force Co-variation

The two basic patterns of finger interaction were clearly exemplified during the Invol and Vol phases of the experiment. The Invol phase was characterized by a negative co-variation of finger forces (error compensation, Latash et al. 1998). Error compensation is a fundamental feature of
motor synergies and, as previously demonstrated, transcends tasks in which the performance variable (such as total force) is the same but perturbations differ (tapping, finger addition/removal, passive finger lifting, Latash et al. 1998; Li S. et al 2003; Martin et al. 2009, 2010).

The Vol perturbation was a clear example of finger enslaving (Zatsiorsky et al. 1998; 2000). Similar to previous studies, the task was to produce force with a single finger; however, other fingers also showed substantial increases in their force production. The force production of the non-target, or enslaved fingers, displayed the same fundamental characteristics as previously documented: 1) relatively large force changes that ranged from 21.83 ± 4.47% MVC (R-finger, M-pressing) to 0.71 ± 1.10% MVC (L-finger, I-pressing); 2) proximity effect in which the adjacent (proximity = 1) fingers to the target finger produced the largest forces; and 3) a higher independence, or less enslaving, of the I-finger compared to other fingers. The changes in the mode values of non-target fingers during the Vol phase were, on average, very close to zero. This indicates that the amount of enslaving during rapid finger pressing differed very little from the enslaving trials that were performed to compute the enslaving matrices.

The common connection, in terms of control, between error compensation and enslaving is that both have a strong neural origin. The fact that the subjects essentially switched from one pattern to another within a single short trial suggests that the CNS is capable of regulating which pattern emerges with relative ease and that the mechanical connections between the fingers play less of a role in the finger force interaction than the neural component. Further evidence supporting the notion that finger interaction depends more on neural mechanisms than the architecture of the periphery is that obviously the connections between the fingers didn’t change between Invol and Vol phases yet different interaction patterns emerged. Perhaps, the next step in this line of research is to design experimental protocols that can identify the relative contribution of each mechanism to the observed force changes.

5.4.3 Interpretation within the Equilibrium-Point Hypothesis

The equilibrium-point hypothesis (Feldman 1966, 1986) was originally developed for single-muscle control; it assumes that the voluntary command to a muscle can be adequately described as changes in the threshold of the tonic stretch reflex. Later, the hypothesis was developed for multi-muscle systems and whole-body movements in the form of the referent configuration.
hypothesis (Feldman, Levin 1995). Recently, the main ideas of the referent configuration hypothesis have been merged with the ideas of synergic control of multi-element systems (Latash 2010a,b; Latash et al. 2010). This approach considers a multi-level hierarchical control system where, at each level, control variables represent levels of sub threshold depolarization of neuronal pools that, in their interaction with the external force field, specify referent coordinates of important performance variables. The difference between the referent and actual coordinates of a variable drives muscle activation directed at moving the actual coordinate towards the referent one. If an external obstacle prevents movement, active force generation is observed at equilibrium.

When the subject was asked to produce a certain value of the total force, a referent coordinate of a “virtual finger” (an imaginary digit with the mechanical effect equal to that of all the actual fingers combined, Arbib et al. 1985) was established at the highest, task level of the hierarchy. This coordinate served as an input into a synergic organization that produced referent coordinates for individual fingers that differed in different trials as long as the effects of this variability on the referent coordinate of the virtual finger were small. This is reflected in negative across trials co-variation of finger forces (and modes) stabilizing the total force value (see Latash et al. 2001; Gorniak et al. 2007; Shapkova et al. 2008). When a finger was passively lifted, the instruction “not to interfere” implied no changes in the referent coordinate of the virtual finger. The mentioned synergic mechanism, however, used somatosensory information on the target finger force increase to drive adjustments of referent coordinates to non-target fingers. These adjustments resulted in reproducible changes in the non-target finger modes. Since the point of virtual finger force application shifted away from the referent coordinate, there was an increase in the total finger force (that is, negative co-variation produced only partial compensation of the target finger force change).

During the Vol phase, when one finger was instructed to produce force, the task was effectively split into two: The target finger was controlled at the highest hierarchical level. Besides, the total force of the three non-target fingers was expected to remain unchanged. As a result, there was no synergic interference between the target and non-target fingers resulting in no adjustments in non-target finger referent coordinates (and no mode changes).

Another finding that allows interpretation within this theoretical scheme is the minimization of secondary moments supported by the findings on the neutral line (NL)
coordinate changes. Referent configuration does not have to be limited to a single variable such as, for example, total force which was used to set tasks in our study. In particular, a set of referent values for several performance variables may be set at the highest, task-related, hierarchical level. One of such variables may be coordinate of the NL in the medio-lateral direction (supported by Latash et al. 2001; Scholz et al. 2002). Note that several recent studies have shown that multi-digit synergies are able to stabilize several variables at the same time, even if explicit feedback and task formulation focused on only one of those variables (Zhang et al. 2008; Klous et al. 2010) indirectly supporting our interpretation.

Overall, the results of this study fit well the framework of the equilibrium-point hypothesis coupled with the idea of multi-finger synergies.

Although we used a rather artificial task and experimental design to study finger interaction, the findings have direct implications for finger interaction during many common situations encountered when manipulating objects. The involuntary phase may be compared to a situation when a person is holding an object and it suddenly deforms, for example as during holding a plastic cup filled with water. The voluntary phase may be compared to holding an object and then changing finger location, lifting a finger or re-positioning it on the object.

Acknowledgments
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CHAPTER 6

Study #4: Comparison of Inter-Finger Connection Matrix Computation Techniques

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6.1 Introduction
Coordinated finger interaction is critical to properly perform numerous everyday tasks. Several characteristic behaviors of finger interaction apparently complicate finger force production. Enslaving is the term that has been used for the documented behavior of fingers producing force unintentionally when other fingers intentionally produce force (Zatsiorsky et al. 1998; Zatsiorsky et al. 2000). Another phenomenon of finger interaction is referred to as force deficit (Ohstuki 1981; Li et al. 1998). Force deficit refers to lower forces produced by individual fingers in a multi-finger maximal voluntary contraction (MVC) task than in a single-finger MVC task. The force deficit increases with the number of fingers asked to produce maximal force (Li et al. 1998).

The mode control hypothesis was proposed to account for neural commands (NCs) from the central nervous system (CNS) being delivered to muscles and resulting in a pattern of movement or force production by the fingers (Zatsiorsky et al. 1998; Li et al. 2002; Danion et al. 2003). The hypothesis accounts for both enslaving and force deficit. The basic assumption of the hypothesis is that the CNS manipulates finger modes (NCs to individual fingers) and that sending a NC to a single finger results in force production by other fingers as well. The NCs are scaled from 0 to 1; 0 corresponding to no intentional force production and 1 being maximal force production. The mathematical relation proposed by Danion et al. (2003) was:

\[ [F] = G[IFC][NC] \]  \hspace{1cm} (6.1)
where \([F]\) is a (4×1) vector of finger forces, \(G\) is gain factor that is inversely proportional to a power function of the number of fingers explicitly involved in the task, \([IFC]\) is a (4×4) inter-finger connection matrix that accounts for enslaving and does not depend on the number of explicitly involved fingers, and \([NC]\) is a (4×1) vector of NCs. This simple model was found to account for finger forces well in the MVC tasks involving different numbers of intentionally active fingers.

Neural network (NN) models have also been used to relate NCs to forces produced by fingers (Zatsiorsky et al. 1998; Li et al. 2002; Zatsiorsky et al. 2004). Previous NN models have been comprised of three layers: (1) the input layer that models a central neural drive; (2) the hidden layer; and (3) the output layer that models the force output of fingers and receives inputs both from the input and middle layers. The input from the middle layer is scaled by the inverse of the number of the fingers explicitly involved in the task. As shown by Zatsiorsky et al. (1998) the action of the NN can be described by an equation:

\[
[F] = \left(\frac{1}{N}\right)[w][NC] + [v][NC]
\]

where \([w]\) is a (4×4) matrix of connection weights between the fingers, \([v]\) is a (4×4) diagonal matrix and \(N\) is the number of explicitly involved fingers. The previous studies based the NN model on all fifteen combinations of single- and multi-finger MVC pressing tasks. It was found that the NN modeling approach fitted finger forces during these tasks relatively well.

A number of previous studies (Latash et al. 2001; Scholz et al. 2002; Shim et al. 2005; Singh et al. 2010) have transformed finger forces to NCs and performed analysis on these values. In these papers the NCs were referred to as finger modes. Finger modes are NCs that have been transformed to force units so that they have a physical meaning when interpreting the data. Several key differences existed in these studies. First the NCs were defined using neither MVC nor NN methods, but one-finger accurate sub-maximal force ramp production that covered the range of typical finger forces that were expected during the main experiment. Secondly, NCs (i.e. finger modes) were expressed in units of N to make comparison with actual performance variables such as total force and total moment of force transparent. A mode of 1 N to a finger corresponded to a command to that finger leading to a force distribution across all fingers such that the total force was 1 N. Note that NCs between 0 and 1 make the same command magnitudes to different fingers corresponding to different force magnitudes.
The purpose of this paper is to compare the techniques proposed by Danion et al. (2003) and the NN modeling approach for estimating finger forces from NCs. The performance of the two techniques has been previously compared only in the MVC tasks (Danion et al. 2003). Yet in many applications the NCs are computed for sub-maximal finger forces (Latash et al. 2002; Zatsiorsky et al. 2002). Comparison of the two techniques for sub-maximal finger forces is challenging because in this case the true NCs are unknown (in MVC tasks they are assumed to be either 0 or 1). One way to do this is to compute the percentage of “outliers”, i.e. the cases when the NCs fall out of the 0 to 1 range. Such “outliers” were documented previously in a sub-maximal prehension task (Zatsiorsky et al. 2002). A NC less than 0 could theoretically occur if due to the co-activation of the extensors the force due to enslaving was decreased (i.e. flexion moment of the flexor muscles is decreased by extension moment generated by the extensor muscles). A NC greater than 1 could occur if the force produced by a finger was greater than what was measured during a single-finger MVC task involving that finger. This may occur due to an inaccurate single-finger MVC measurement. Another indicator of the better method is the degree to which the transformation from forces to NCs preserves the general tendency of the data distribution. In another study (Martin et al., in press) we have found that the force data are confined to a two-dimensional plane in the four-dimensional space of finger forces. The planarity signifies that the finger force sharing pattern may reflect the minimization of a cost-function (Park et al. 2010; Park et al. 2011; Park et al. 2012; Terekhov et al. 2010). If the CNS controls the finger forces through the NCs, then one can expect that the NC values are also confined to a plane.

We chose the following criteria of performance: (1) the precision of finger force prediction in the MVC tasks; (2) the percentage of outliers (i.e. NCs outside of the 0 to 1 range) in sub-maximal tasks; and (3) the preservation of planarity in the NCs.

6.2 Methods
6.2.1 Subjects
Eleven right-handed male participants (age: 26.7 ± 4.1 yrs, weight: 80.5 ± 7.8 kg, height: 18.23 ± 7.9 cm, hand length: 19.0 ± 1.2 cm, and hand width: 8.4 ± 0.3 cm; mean ± SD across subjects) volunteered to participate in the current study. None of the subjects had a previous history of illness or injury that would affect the function of their upper arm, hand, or fingers. Hand length
was measured from the tip of the middle finger to the distal crease at the wrist. Hand width was measured as the distance across metacarpophalangeal (MCP) joints of fingers 2 to 5, with the fingers in approximately neutral ab/adduction. Prior to performing the experiment subjects signed an informed consent form approved by the Pennsylvania State University.

6.2.2 Equipment
Pressing forces were measured using four uni-directional piezoelectric force transducers (208C02, PCB Piezotronics, Depew, NY). The force transducers were fixed to an aluminum plate that was securely fastened to a table. The aluminum plate had slots cut so that the each of the individual force transducers could be adjusted in the forward-backward direction in order to accommodate for different finger lengths of subjects. Sandpaper covers were placed on the surface of the force transducers to increase friction.

Analog output signals from the force transducers were sent to an AC/DC conditioner (5134B, Kistler, Amherst, NY, USA) then digitized with a 16-bit analog to digital converter (CA-1000, National Instruments, Austin, TX, USA). A LabVIEW program (LabVIEW version 8.0, National Instruments, Austin, TX, USA) was written to provide feedback and control data acquisition during the experiment. The force signals were collected at 100 Hz. Post-processing of the data was performed using custom software written in Matlab (Matlab 7.4.0, Mathworks, Inc, Natick, MA).

6.2.3 Experimental Procedures
During the study subjects were seated in a chair facing a computer screen. The right forearm rested on a padded support and the tip of each finger was positioned in the center of a force transducer. The distal interphalangeal (DIP), proximal interphalangeal (PIP), and MCP joints were all flexed in a posture that subjects felt was comfortable. The upper arm was positioned in approximately 45° shoulder abduction in the frontal plane, 45° shoulder flexion in the sagittal plane, and approximately 45° flexion of the elbow.

The experimental data were collected in two sessions. During the first session subjects were instructed to press with all one-, two-, three- and four-finger combinations (I, M, R, L, IM, IR, IL, MR, ML, RL, IMR, IML, IRL, MRL, and IMRL) to achieve their MVC. Note the following abbreviations were used: I = index; M = middle; R = ring; and L = little. Subjects
were asked to increase force in a ramp like manner and to avoid a quick pulse of force production. They were required to maintain the force for at least 1 s before relaxing. Sufficient (at least, 30-s) rest was given between trials to avoid fatigue.

The main purpose of the second experimental session was to collect the data necessary for the inverse optimization (ANIO) analysis performed in another study (Martin et al. *in press*). The data obtained in this session were also used for the present study. Subjects were asked to produce a specified total force and total moment \( (F_{TOT}; M_{TOT}) \) combination while pressing with all four fingers. \( F_{TOT} \) produced by the fingers was the sum of normal forces of the four fingers. \( M_{TOT} \) produced by the fingers was computed as the moment produced about an axis passing mid-way between the M- and R-fingers. Subjects were required to produce both pronation (PR) and supination (SU) moments. The task set consisted of twenty-five combinations of five levels of \( F_{TOT} \) (20, 30, 40, 50 and 60% of MVC of all four fingers) and five levels of \( M_{TOT} \) (High PR, Low PR, 0, Low SU, and High SU). The high and low moments were scaled to 28% and 14%, respectively, of the moment the index finger could produce in a single finger MVC trial about the neutral axis.

### 6.2.4 Data Processing

The force signals were filtered using a 4\(^{th}\) order low-pass Butterworth filter at 10 Hz. The force data that was extracted from the MVC trials were the individual finger forces at the point when the peak MVC occurred for the instructed fingers. For the second session the individual finger force data from each trial were averaged over a 2-s time period in the middle of each trial (2- to 4-s windows), where steady-state values of \( F_{TOT} \) and \( M_{TOT} \) were observed. For all trials four data points (average finger forces) were extracted and used in the further analyses.

### 6.2.5 Enslaving Matrix and Neural Command Computation

The finger forces from the MVC trials were used to construct the IFC matrices describing finger interaction. We compared the performance of two methods for IFC matrix computation. The first method (Danion et al. 2003), which will be referred to as the MVC method, only uses the forces from single-finger MVC trials. For each single-finger MVC trial the forces produced by the four fingers are placed in a column of the \([IFC]\) matrix. To account for force deficit \([IFC]\) is multiplied by a gain factor \(G\). The value of \(G\) depends on the number of fingers \(N\) involved in a
pressing task (Danion et al. 2003):

\[ G = 1/N^{0.712} \]  

(6.3)

The \([IFC]\), with force deficit accounted for, is given by:

\[
[IFC_{MVC}] = \left(\frac{1}{N^{0.712}}\right) \begin{bmatrix}
W_{L,I} & W_{I,M} & W_{I,R} & W_{L,L} \\
W_{M,I} & W_{M,M} & W_{M,R} & W_{M,L} \\
W_{R,I} & W_{R,M} & W_{R,R} & W_{R,L} \\
W_{L,I} & W_{L,M} & W_{L,R} & W_{L,L}
\end{bmatrix}
\]  

(6.4)

The finger connection weights \((w_{i,j})\) represent the force produced by finger \(i\) when finger \(j\) is instructed to press.

The NCs for the trials with sub-maximal force production, i.e. for the second experimental session, were computed by rearranging equation 1:

\[
[NC] = [IFC]^{-1}[F]
\]  

(6.5)

### 6.2.6 Neural Network Modeling

The second method of the \([IFC]\) computation uses a three-layer NN model (Zatsiorsky et al. 1998; Li et al. 2002; Zatsiorsky et al. 2004). The mathematical description of the NN is provided in Zatsiorsky et al. (1998) and Li et al. (2002). The input pattern vector was of the form:

\[
[NC] = [NC_I NC_M NC_R NC_L]^T
\]  

(6.6)

where \(NC_i\) is the NC to the \(j\)th finger; \(NC_j\) equals 1 if the finger was instructed to produce the force and 0 otherwise. The desired output pattern vector, which is the force collected in the corresponding MVC trial, was of the form:

\[
[F^d] = [F_I^d, F_M^d, F_R^d, F_L^d]^T
\]  

(6.7)

where \(F_j^d\) is the desired force output of the \(j\)th finger from the MVC experimental trials. The NN was trained using all fifteen MVC combinations. The NN returned the vector of model finger forces

\[
[F] = [F_I, F_M, F_R, F_L]^T.
\]  

(6.8)

The weight coefficients of the NN, \(w_{jk}\) and \(v_k\), were chosen to minimize the discrepancy between the model finger forces and those collected in the MVC trials. The discrepancy was characterized be the error function, \(E\), defined as the sum of squares error over all input MVC conditions:

\[
E = \sqrt{\frac{1}{15} \sum_{i=1}^{15} \| [F]_i - [F^d]_i \|^2}
\]  

(6.9)

The action of the NN on the NCs can be summarized by the linear matrix equation (2):
\[ [F] = (1/N) [w][NC] + [v][NC] \]  \hspace{1cm} (6.10)

where \([w]\) is a \((4 \times 4)\) matrix of inter-finger connection weights, \([v]\) is a \((4 \times 4)\) diagonal matrix, and \(N\) is the number of fingers involved in the task. \(N = 4\), since all fingers produced force during the trials of the second session. The \([IFC]\) that was used to compute the NCs from the session two data was computed as:

\[ [IFC_{NN}] = \left( \frac{1}{N} \right) [w] + [v] \]  \hspace{1cm} (6.11)

The NN was trained using a back-propagation algorithm (Bose & Liang 1996). The number of training epochs was set to 500 epochs. The learning rate was 0.01. The number of epochs was sufficient for the convergence of the algorithm with the selected learning rate. A set of different initial conditions was tested and for all of them the algorithm converged to the same minimum. The average value of the error function (across subjects) was 3.68 ± 1.13 N.

6.2.7 Prediction of Experimental Forces

The \(IFC_{MVC}\) and \(IFC_{NN}\) matrices of each subject were used to predict finger forces in each of the fifteen MVC trials using equation 5. The finger(s) that were instructed to press had the NC value set to 1, the NC value of non-instructed fingers was set to 0. The predicted force was compared to the experimental force for all four fingers. The absolute error was computed for each finger as the absolute value of the difference between the experimental and predicted forces.

6.2.8 Planarity of Data

We evaluated the planarity of the data by performing the principal component analysis (PCA). Since the transformation between forces and NCs is linear it is natural to expect the planarity to be preserved in the NCs. In the presence of unavoidable deviation of the actual force data from a perfect plane, the transformation of forces to NCs could potentially enhance any deviations from planarity of the force data. Thus, we checked which method better produced NCs with a planarity closer to the original force data. This was done by performing PCA on the force data set and the NC data sets computed from each method. The variance explained in the first two PCs was assumed to be indicative of whether or not the data was confined to a 2D plane. Previously, it was assumed that if greater than 90% of the variance was explained in the first two PCs then the data was confined to a 2D plane (Park et al. 2010; Park et al. 2011a; Park et al. 2012; Terekhov et al. 2010).
6.2.9 Percentage of Outliers
The finger forces from the second experimental session were transformed into NCs. The number of NCs that were: (1) less than 0 and (2) greater than 1 was computed. The entire data set contained 1100 total data points (11 subjects × 5 moments × 5 force levels × 4 fingers). The occurrences of NC values less than 0 and greater than 1 were counted in terms of the entire data set, as well as on a finger-by-finger basis.

6.2.10 Statistical Methods
The mean error of the predicted forces was computed across subjects for the total force and individual finger forces. Mean values of the variance explained by the first two principal components were computed on the Fisher z-transformed values; then the inverse z-transformation was performed on the mean values. A repeated-measure (RM) ANOVA was performed to test the effect of multi-finger pressing COMBINATION (11 levels: IM, IR, IL, MR, ML, RL, IMR, IML, IRL, MRL, and IMRL), NC computation METHOD (2 levels: MVC and NN) and FINGER (4 levels: I, M, R, and L) on the force error of individual fingers in the four-finger MVC task. Note: the RM ANOVA was only performed for multi-finger combinations since all the single-finger combinations of the MVC method had zero error. The PCA variance responses were z-transformed prior to performing the RM ANOVA. Statistical analyses were performed using the SPSS software package (SPSS Inc., Chicago, IL, USA). The significance level was set to $\alpha = 0.05$.

6.3 Results
The results are presented in the following order: (1) inter-finger connection matrices [IFC], (2) accuracy of force prediction and (3) accuracy of neural command (NC) reconstruction.

The mean forces for each of the MVC pressing tasks were computed and for all tasks enslaving forces (force production by non-instructed fingers) were present (Table 6.1). Mean enslaving forces ranged from 0.80 ± 0.29 N (L-finger in MVC$_{IM}$ task) to 8.28 ± 1.67 N (M-finger in MVC$_{R}$ task). Qualitatively both IFC$_{MVC}$ and IFC$_{NN}$ are similar (Table 6.2) with the instructed finger force (diagonal elements) several times higher than the non-instructed finger’s forces (off-diagonal elements). For all tasks, the diagonal element values are higher in IFC$_{NN}$ than in
IFC\textsubscript{MVC}. In fourteen of sixteen cases the values of the non-instructed fingers forces are lower in IFC\textsubscript{NN} than IFC\textsubscript{MVC}. The two cases that are the exceptions are the L-finger forces when M-finger was instructed to press and when R-finger was instructed to press.

**Table 6.1** Mean MVC forces for all finger combinations. Standard errors are in parentheses.

<table>
<thead>
<tr>
<th>Finger Combination</th>
<th>Forces</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
</tr>
<tr>
<td>I</td>
<td>34.92 (2.26)</td>
</tr>
<tr>
<td>M</td>
<td>6.71 (1.57)</td>
</tr>
<tr>
<td>R</td>
<td>2.07 (0.63)</td>
</tr>
<tr>
<td>L</td>
<td>1.59 (0.71)</td>
</tr>
<tr>
<td>IM</td>
<td>24.78 (2.11)</td>
</tr>
<tr>
<td>IR</td>
<td>22.27 (1.77)</td>
</tr>
<tr>
<td>IL</td>
<td>21.99 (2.56)</td>
</tr>
<tr>
<td>MR</td>
<td>3.57 (1.68)</td>
</tr>
<tr>
<td>ML</td>
<td>3.23 (1.45)</td>
</tr>
<tr>
<td>RL</td>
<td>2.12 (0.72)</td>
</tr>
<tr>
<td>IMR</td>
<td>19.31 (1.33)</td>
</tr>
<tr>
<td>IML</td>
<td>18.55 (2.14)</td>
</tr>
<tr>
<td>IRL</td>
<td>19.12 (2.10)</td>
</tr>
<tr>
<td>MRL</td>
<td>2.66 (1.16)</td>
</tr>
<tr>
<td>IMRL</td>
<td>20.19 (2.03)</td>
</tr>
</tbody>
</table>
Table 6.2 Mean inter-finger connection matrices computed using MVC and neural network modeling methods. Column headings are of the finger instructed to press. Standard error is in parentheses.

<table>
<thead>
<tr>
<th></th>
<th>MVC Method</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
<td>M</td>
<td>R</td>
<td>L</td>
</tr>
<tr>
<td>I</td>
<td>13.01 (0.84)</td>
<td>2.50 (0.59)</td>
<td>0.77 (0.24)</td>
<td>0.59 (0.26)</td>
</tr>
<tr>
<td>M</td>
<td>1.65 (0.82)</td>
<td>10.96 (0.98)</td>
<td>3.09 (0.62)</td>
<td>1.29 (0.60)</td>
</tr>
<tr>
<td>R</td>
<td>0.74 (0.30)</td>
<td>2.05 (0.42)</td>
<td>10.01 (1.17)</td>
<td>2.75 (0.51)</td>
</tr>
<tr>
<td>L</td>
<td>0.50 (0.15)</td>
<td>0.41 (0.20)</td>
<td>1.22 (0.26)</td>
<td>7.78 (0.71)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>NN Method</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
<td>M</td>
<td>R</td>
<td>L</td>
</tr>
<tr>
<td>I</td>
<td>16.16 (1.72)</td>
<td>1.16 (0.61)</td>
<td>0.28 (0.23)</td>
<td>0.41 (0.14)</td>
</tr>
<tr>
<td>M</td>
<td>1.44 (0.45)</td>
<td>15.34 (1.30)</td>
<td>1.11 (0.31)</td>
<td>0.00 (0.18)</td>
</tr>
<tr>
<td>R</td>
<td>0.47 (0.13)</td>
<td>1.98 (0.42)</td>
<td>11.32 (0.99)</td>
<td>1.09 (0.21)</td>
</tr>
<tr>
<td>L</td>
<td>0.31 (0.25)</td>
<td>0.57 (0.41)</td>
<td>1.67 (0.38)</td>
<td>11.36 (1.07)</td>
</tr>
</tbody>
</table>

The error between the experimental and predicted forces was quantified (Figures 6.1-6.3). Both methods predicted the total forces with a relatively high degree of accuracy. The largest errors were observed in the three- and four-finger tasks. The RMSE error across all combinations is less for the NN method (3.68 ± 0.34 N) than the MVC method (4.43 ± 0.46 N); however, there is no significant difference (p > 0.1) between the METHODS. For the force error of individual fingers the NN method results in smaller absolute errors for the majority of multi-finger tasks (Figures 6.2 & 6.3). The RM ANOVA performed on the individual finger force errors in the multi-finger MVC tasks resulted in finding a significant effect of METHOD ($F_{1,10} = 10.266, p < 0.01$); however the effects of FINGER ($F_{3,30} = 2.324, p > 0.09$) and COMBINATION ($F_{10,100} = 0.994, p > 0.45$) were non-significant.
Figure 6.1: Comparison of total forces during MVC trials to those predicted by the MVC and neural network based methods. Error bars are standard errors.
Figure 6.2: Comparison of the absolute force error between individual experimental finger forces and forces predicted by the MVC and neural network based methods for: A) index finger, B) middle finger, C) ring finger, and D) little finger. Data for all finger combinations are shown. Error bars are standard errors.
Figure 6.3: Mean absolute error for multi-finger tasks between experimental forces and forces predicted by the MVC and neural network based methods. Absolute errors were averaged across all finger pressing combinations. Error bars are standard error.

As in indicator of which method produced more accurate reconstructed values of the NCs the percentage of values outside of the range of 0 to 1 was computed for the data from the second experimental session (Table 6.3). The percentage of values less than 0 was 2.7% and 0.1% for the MVC and NN methods of computing NCs, respectively. The percentage of values greater than 1 was 8.7% and 3.4% for the MVC and NN based NC’s, respectively. For the MVC method the most occurrences of NCs less than 0 was for the index finger. The NN method had almost no occurrences of NC values less than 1. For both methods the ring and little fingers displayed the most instances of values greater than 1. None of the subjects produced a NC greater than 1 for the index finger for either method.

Table 6.3: Percentage of neural command values less than 0 and greater than 1 observed in the second experimental session. Percentage of values for MVC and NN methods are given. The data set consisted of 275 values per finger.

<table>
<thead>
<tr>
<th>Finger</th>
<th>% of Values Less Than 0 MVC</th>
<th>% of Values Less Than 0 NN</th>
<th>% of Values Greater Than 1 MVC</th>
<th>% of Values Greater Than 1 NN</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>8.0%</td>
<td>0.0%</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td>M</td>
<td>2.8%</td>
<td>0.0%</td>
<td>8.4%</td>
<td>3.2%</td>
</tr>
<tr>
<td>R</td>
<td>0.0%</td>
<td>0.4%</td>
<td>12.4%</td>
<td>6.8%</td>
</tr>
<tr>
<td>L</td>
<td>0.0%</td>
<td>0.0%</td>
<td>14.0%</td>
<td>3.6%</td>
</tr>
</tbody>
</table>

The NN method better preserved the planarity of the original force data (Figure 6.4). In other words, the variance explained by PC1+PC2 on the NCs computed with the NN method (94.6 ± 7.1%) was closer to the variance explained by the first two PCs on the force data (96.6 ± 7.4%) than that on the NCs computed using the MVC method (90.8 ± 7.2%). The effect of METHOD (F₁,₁₀ = 30.855, p < 0.001) on the variance explained in the first two PCs was significant.
Figure 6.4: Variance explained by the principal component (PC) one and two of the principal component analysis. The variance of forces and NC computed using both the single-finger MVC and neural network method is presented. Error bars are standard error.

6.4 Discussion

The results indicate that the neural network (NN) method outperforms the MVC method with respect to all three chosen criteria: it provides more accurate predictions of finger forces; the NN method produces a greater percentage of NCs between 0 and 1; and it preserves the planarity of the original force data better than the MVC method.

There are a number of constraints, both in the periphery and centrally, that limit the independence of finger interaction (for review see Schieber and Santello, 2004). The mechanical connections, multi-digit motor unit architecture in the extrinsic muscles, and cortical representation may all differ among people. Architectural properties of a single muscle (first dorsal interosseous) have been shown to display significant variability across healthy persons (Infantolino and Challis, 2010). These differences could be due to practice, training, strength, or age. Although our subjects were all fairly similar in terms of sex, age, strength, and daily use of the fingers the [IFC] were quite unique to individual subjects. Taking this into consideration it is
not surprising that the NN method, which provides a broader representation of enslaving and force deficit across finger pressing combinations, outperformed the MVC method in our study.

A previous study investigated differences between [IFC] of twenty subjects (Gao et al. 2003) computed using the NN method. The subjects were similar to those in our study in that they were all young, healthy males with no reported activities that would abnormally alter their finger independence. The [IFC] were normalized to the MVC values and it was reported that after the normalization the main differences between subjects were in the force sharing patterns and the amount of enslaving.

It appears that the main difference between the MVC and NN methods is their ability to predict force sharing patterns, as well as, model enslaving. Figure 1 shows that both methods predicted the total force of the fingers in the multi-finger MVC trials with similar accuracy. In many cases the absolute error of the MVC method was even less than that of the NN method. The NN method set itself apart from the MVC method in its ability to predict the individual finger forces in the multi-finger MVC trials, which translates to the force sharing pattern. The [IFC] contain sixteen elements, diagonal and off-diagonal. The diagonal elements are several times larger than the off-diagonal elements. The relative magnitude of the off-diagonal elements is an important factor in determining the transformation scaling (singular values) of the [IFC].

In conclusion, finger interaction is a complex behavior due to mechanical connections and central factors. The force sharing patterns of fingers in a given task are affected by both enslaving and force deficit. Subtle, yet significant, physiological differences between subjects lead to differences between finger forces and thus different individual finger inter-connection matrices. It appears better to use the neural network method to model finger interaction as it more accurately predicts individual finger forces. It should be stated that the MVC method, which only requires four trials, did demonstrate an adequate ability to predict the total force of multi-finger MVC trials but was not able to match the NN method in its ability to predict single-finger forces in multi-finger MVC trials.

Acknowledgements
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CHAPTER 7

Study #5: Does the Brain Optimize and Stabilize the Motor Behavior in the Same Space of Elemental Variables? Evidence from a Finger Pressing Study.

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Submitted to: Journal of Neurophysiology, June 2012

7.1 Introduction
It is broadly accepted that the brain does not necessarily use the same variables to control movements as the researchers use to describe them (Bernstein, 1967). For instance, the joint torques, which could be the perfect elementary variables (EV) from the engineer's point of view, are unlikely to be used by the brain. Evidence suggests that the brain does not control each muscle individually, but it does so through more general commands. Each command defines a pattern of activity in several muscles and the overall behavior is shaped by the superposition of those patterns (Krishnamoorthy et al. 2003, d'Avella et al. 2003, Ivanenko et al 2004). These patterns are often subject-specific and can vary from task to task within the same subject (Danna-Dos-Santos et al. 2008). However, even for the same task different sets of the EVs can be involved in a hierarchical manner. For example, in grasping at the highest level of the control hierarchy the brain operates with the thumb and the virtual finger (the virtual finger is the combined effect of the four fingers) while at the lower level the commands to the virtual finger are translated into the individual finger commands (Latash et al. 2010).

Nearly every motor task is redundant with respect to the number of effectors - the sharing between the thumb and the virtual finger can correspond to different grip forces, the same efforts of the virtual finger can be implemented with different finger forces, etc. (Bernstein 1967; Latash, 2012). At every level of the control hierarchy the brain has freedom to choose among many possible solutions. The fact that its choice is rather reproducible suggests that the brain
optimizes a certain criterion - a cost function. At the same time, the movements are executed in a noisy environment and hence they inevitably deviate from the optimal performance. In order to compensate for this deviations the brain has to implement stabilization mechanisms, which would shape the variability of the effectors to minimize the imprecision in important performance variables (PVs). Consequently, for the same task and the same level of control hierarchy the brain has to solve at least two problems: (1) optimize the distribution of the task among the effectors and (2) stabilize the task-relevant PVs against motor variability.

Though there are no doubts that different EVs can be employed by the brain for different motor tasks and at different levels of the control hierarchy, it is not clear whether the two problems – optimization and stabilization – are solved using the same EVs. In order to address this question we will consider the problem of force sharing among individual fingers. For this problem two sets of EVs have been proposed: the forces of individual fingers and the so-called neural commands (NCs). The NCs reflect a well-known fact that the fingers are hard to control independently, e.g. flexing a finger also makes other fingers move. This phenomenon is called enslaving (Zatsiorsky et al. 1998; Zatsiorsky et al. 2000). A hypothesis has been suggested (Zatsiorsky et al. 1998; Li ZM et al. 2002) that to control the finger forces the central controller sends out hypothetical NCs to the fingers that are transformed by a matrix modifier, which accounts for the effect of enslaving.

In this study we aim at finding out which of the two types of EVs – the forces or the NCs – is used for optimization and which is used for stabilization in the a task when total force and total moment of force are prescribed. To determine which EVs are involved in each aspect of behavior we will use two recently developed research tools – the analytical inverse optimization (ANIO, Terekhov et al. 2010; Terekhov & Zatsiorsky 2011; Niu et al. 2012 a, b; Park et al. 2011 a, b; 2012) and the uncontrolled manifold analysis (UCM, Scholz and Schöner 1999; reviewed in Latash 2002). The ANIO allows for reconstructing the unknown cost function from experimental recordings and the UCM approach provides the tools for decomposing the variance of the EVs involved in the task into the variance that either does not affect an important PV (‘good variance’) or affects it (‘bad variance’). These two methods complement each other: the ANIO describes the general tendency in the motor performance, which is common over a range of performance values and preserved in spite of the inter-trial variability, while UCM addresses the structure of the inter-trial differences.
7.1.1 On the coordinate sensitivity of ANIO

The ANIO method allows for reconstructing an unknown cost function from the experimental data under assumption that this cost function is additive with respect to certain known EVs. For the finger pressing tasks it can be assumed that the brain minimizes a cost function additive with respect to either the finger forces:

\[ J_F(F_1,F_2,F_3,F_4) = g_1^F(F_1) + g_2^F(F_2) + g_3^F(F_3) + g_4^F(F_4) \]  
(7.1)

or with respect to the NCs:

\[ J_{NC}(NC_1,NC_2,NC_3,NC_4) = g_1^{NC}(NC_1) + g_2^{NC}(NC_2) + g_3^{NC}(NC_3) + g_4^{NC}(NC_4). \]  
(7.2)

Here \( F_i \) and \( NC_i \) are the forces and the NCs of the individual fingers, respectively, for the index- (\( i=1 \)), middle- (\( i=2 \)), ring- (\( i=3 \)) and little-fingers (\( i=4 \)); \( g_i^F \) and \( g_i^{NC} \) are unknown scalar functions representing the costs of each finger force or NC.

The ANIO method can be used to reconstruct the cost functions \( J_F \) and \( J_{NC} \). More importantly for the current study, the method will fail if the given data distribution cannot be accounted for by a cost function that is additive with respect to the chosen EVs (see example of in Xu et al., submitted 2012.).

In most cases the same cost function can be either additive with respect to one set of EVs or with respect to another, but not with respect to both at the same time. To illustrate this statement consider a cost function for two fingers:

\[ J(F_1,F_2) = k_1 (F_1)^2 + k_2 (F_2)^2, \]  
(7.3)

where \( k_1 \) and \( k_2 \) are arbitrary positive coefficients. Let's build an artificial set of EVs, \( EV_1 \) and \( EV_2 \), defined as:

\[ EV_1 = 0.55 F_1 + 0.45 F_2, \]  
(7.4)
\[ EV_2 = 0.45 F_1 + 0.55 F_2. \]  
(7.5)

The cost function \( J \) can be rewritten with respect to new variables:

\[ J(EV_1, EV_2) = (30.25 k_1 + 20.25 k_2) (EV_1)^2 + (30.25 k_1 + 20.25 k_2) (EV_2)^2 + 24.75 (k_1 + k_2) EV_1 EV_2. \]  
(7.6)

The function \( J \) evidently cannot be additive with respect to \( EV_1 \) and \( EV_2 \), because it would require that \( k_1 = -k_2 \), which is impossible to satisfy for positive coefficients \( k_1 \) and \( k_2 \). There do exist sets of EVs for which certain cost functions can be additive in all of the sets, yet such sets and the cost functions are rare (see the Discussion section).
Since in most cases the same cost function can be either additive with respect to the forces or with respect to the NCs, but not with respect to both of them, we hypothesize (Hypothesis 1) that ANIO will fail for one of the set of EVs. In the previous studies (Park et al. 2010; 2011a, b; 2012) it was shown that ANIO works well for the finger forces, which allows us to expect that it will fail for the NCs.

### 7.1.2 On the coordinate sensitivity of UCM

The UCM method can be used to evaluate the degree of coordination, or synergy, between the multiple elements. It compares the variability of the task-relevant PV – like total finger force or total moment of finger forces – with the variability of the EVs, which would be observed if they were not coordinated. This method is sensitive to the change of the coordinates, or, in other words, to the choice of the EVs (Sternard et al. 2010). Theoretically, one can expect that the same data distribution can be interpreted as stabilizing or destabilizing a certain PV, depending on which EVs were selected to perform the analysis. To illustrate this fact consider the problem of stabilization of total pressing force produced by two fingers:

\[ F_1 + F_2 = F_{\text{total}} \]  \hspace{1cm} (7.7)

Let's assume that experimentally measured forces are distributed in the ellipse shown in Figure 7.1A. It is clear from the figure that the forces are coordinated to minimize the variance of the PV, \( F_{\text{total}} \). Now, let's see how the same distribution will look like for the elementary variables, \( EV_1 \) and \( EV_2 \), provided in (equations 7.4 and 7.5). The force stabilization constraint on the EVs is the same as on forces:

\[ EV_1 + EV_2 = F_{\text{total}}. \]  \hspace{1cm} (7.8)

For the new variables the same data set will be distributed in an ellipse shown in Figure 7.1B. This ellipse is oriented against the stabilized direction, meaning that the variance of \( EV_1 \) and \( EV_2 \) are coordinated to destabilize \( F_{\text{total}} \). Of course, these variables make no physiological sense; they are here only to illustrate how the choice of the EVs can influence the properties of the data distribution. Now, if the judgment is to be made on which set of variables, \( F_1 \) and \( F_2 \) or \( EV_1 \) and \( EV_2 \), is more probably used by the brain to produce \( F_{\text{total}} \), it will be in favor of the forces, because their distribution stabilizes the PV.
This example shows that the UCM method can be used as an indirect evidence for the EVs used in the performance stabilization. Given the clear evidences of the finger force coupling provided by enslaving we hypothesize (Hypothesis 2) that the UCM analysis will elicit significantly higher degree of coordination for the NCs than for the forces.

![Diagram](image)

**Figure 7.1:** The coordinate sensitivity of the UCM analysis. A: the inter-trial variance of two finger forces, $F_1$ and $F_2$, in the total force stabilization task. The resulting ellipse is elongated along the UCM (dashed line), which corresponds to all finger forces whose sum equals the target value. B: the variance of the same data set as in A, but plotted in the artificially constructed coordinates, EVs (see the text); the variance ellipse is oriented orthogonal to the UCM (dashed line). This example shows how the same data can be interpreted as stabilizing or destabilizing certain performance variable depending on the choice of the EVs. This property of the UCM analysis provides means for testing the plausibility of certain EVs being used by the CNS in the performance stabilization process.

### 7.2 Methods

#### 7.2.1 Subjects

Eleven right-handed male participants (age: 26.7 ± 4.1 yrs, weight: 80.5 ± 7.8 kg, height: 182.3 ± 7.9 cm, hand length: 19.0 ± 1.2 cm, and hand width: 8.4 ± 0.3 cm; mean ± SD across subjects) volunteered to perform the current study. None of the subjects had a previous history of illness.
or injury that would affect the function of their upper arm, hand, or fingers. Hand length was measured from the tip of the middle finger to the distal crease at the wrist. Hand width was measured as the distance across metacarpophalangeal (MCP) joints of fingers 2 to 5, with the fingers in approximately neutral abd/adduction. Prior to performing the experiment subjects signed an informed consent form that was approved by the Office for Research Protections of the Pennsylvania State University.

7.2.2 Equipment
Pressing forces were measured using four uni-directional piezoelectric force transducers (208C02, PCB Piezotronics, Depew, NY). The transducers were rigidly fixed to metal rods mounted to an aluminum plate that was securely fastened to a table. The aluminum plate had slots so that the each of the individual rod-transducer couplings could be adjusted in the forward/backward direction in order to accommodate for different finger lengths of subjects.

Analog output signals from the transducers were sent to an AC/DC conditioner (5134B, Kistler, Amherst, NY, USA) then digitized with a 16-bit analog-to-digital converter (CA-1000, National Instruments, Austin, TX, USA). A LabVIEW program (LabVIEW Version 8.0, National Instruments, Austin, TX, USA) was written to control feedback and data acquisition during the experiment. The force signals were collected at 100 Hz. Post-data processing was performed using custom software written in Matlab (Matlab 7.4.0, Mathworks, Inc, Natick, MA).

7.2.3 Procedures
During the study subjects were seated in a chair facing a computer screen. The right forearm rested on a padded support and the tip of each finger was positioned in the center of a force transducer. The distal interphalangeal (DIP), proximal interphalangeal (PIP), and MCP joints were all flexed in a posture that subjects felt was comfortable. A wooden block supported the palm of the hand. The block limited wrist flexion and supination/pronation of the forearm. The upper arm was positioned in approximately 45° shoulder abduction in the frontal plane, 45° shoulder flexion in the sagittal plane, and approximately 45° flexion of the elbow. The experiment consisted of three sessions, all of which were performed on the same day.

The goal of the first session was to determine the maximum voluntary contractions (MVCs) of the fingers. The session required subjects to press with all one-, two-, three- and four-
finger combinations (I, M, R, L, IM, IR, IL, MR, ML, RL, IMR, IML, IRL, MRL, and IMRL; where I stands for the index, M for the middle, R for the ring, and L for the little finger) to achieve their MVC. Subjects were asked to increase force in a ramp-like manner and to avoid a quick pulse of force production. They were required to maintain the force for a minimum of 1 s before relaxing. Sufficient rest was given between trials to avoid fatigue. The results obtained in this session were used for (a) normalizing the target finger forces in the subsequent experimental sessions and (b) computation of the individual IFC matrices (explained later in the text).

The purpose of the second experimental session was to collect the data necessary for the inverse optimization (ANIO) analysis. The session entailed producing a set of specified total force ($F_{\text{Target}}$) and total moment ($M_{\text{Target}}$) combinations while pressing naturally with all four fingers. The total force produced by the fingers was computed as the sum of normal forces of the four fingers. The total moment produced by the fingers was computed as the moment produced about an axis passing mid-way between the M- and R-fingers. Subjects were required to produce both pronation (PR) and supination (SU) moments. The task set consisted of twenty-five combinations of five levels of $F_{\text{Target}}$ (20, 30, 40, 50 and 60% of individual MVC$_{\text{IMRL}}$) and five levels of $M_{\text{Target}}$ (2PR, 1PR, 0, 1SU, and 2SU). The moment levels were computed based on the 14% of the MVC$_{\text{I}}$ using the following equation:

$$M_{\text{Target}} = 0.14 S_f d_f MVC_{\text{I}}$$

(7.9)

where $d_f$ and $S_f$ represent the moment arm of the $j$th finger and the moment scaling factor. $S_f$ values used were: $-2, -1, 0, 1,$ and $2$, corresponding to 2PR, 1PR, 0, 1SU and 2SU respectively. The total moment produced by the fingers was given by the equation:

$$M_{\text{Produced}} = d_I F_I + d_M F_M + d_R F_R + d_L F_L$$

(7.10)

The values of $d$’s were measured from the midline between the M- and R-fingers to the centers of the sensors. They did not change during the experiment and were: $d_I = -4.5$ cm, $d_M = -1.5$ cm, $d_R = 1.5$ cm, and $d_L = 4.5$ cm for the I-, M-, R-, and L-fingers, respectively. The $M_{\text{Target}}$ levels were set using $S_f$. Subjects performed five repetitions of each $F_{\text{Target}}$ and $M_{\text{Target}}$ combination. A total of 125 trials were performed (5 $F_{\text{Target}}$ levels $\times$ 5 $M_{\text{Target}}$ levels $\times$ 5 trials) in a randomized order. Each trial lasted for 5 s. Approximately 10 s of rest were given between the trials. In addition, several five-minute breaks were given during session two.

The purpose of the third session was to collect the data for performing the uncontrolled manifold (UCM) analysis. The session consisted of an additional 75 trials. For five of the
conditions in session two the subjects performed fifteen more trials. The conditions were: 1) 20\% F_{Target} & 2PR M_{Target}, 2) 40\% F_{Target} & 2PR M_{Target}, 3) 20\% F_{Target} & 2SU M_{Target}, 4) 40\% F_{Target} & 2SU M_{Target} and 5) 40\% F_{Target} & 0 M_{Target}. These conditions were selected in order to cover the largest range of experimental conditions while also minimizing fatigue of the subjects, which is why the 60\% F_{Target} condition was not included. These trials were 5 s long with 10 s of rest given between trials. Trials were performed in random blocks of the five conditions (i.e. all 15 trials of each condition were performed in a block of trials).

The three experimental sessions took between 1.5 to 2 hours. None of the subjects complained of pain or fatigue during or after the experimental sessions.

7.2.4 Data Analysis

For all trials the force signals were filtered using a 4th order low-pass Butterworth filter at 10 Hz. In the first session, the peak force data were extracted for future analysis. For the second and third sessions, the individual finger force data from each trial were averaged over a 2 s time period in the middle of each trial (2- to 4-s windows), where steady-state values of total force and total moment were observed. For each trial the average finger force of each finger was extracted and used in the further analyses.

The data analysis then included the following steps:

7.2.4.1: Computation of the inter-finger connection [IFC] matrices via neural network (NN) models; the data from the first experimental session were used.

7.2.4.2: Reconstruction of the NCs from the recorded finger forces using the IFC matrices determined in the previous step. This procedure was performed separately for the data recorded in the second and third experimental sessions, respectively.

7.2.4.3: The ANIO analysis on the forces and NCs obtained in the second experimental session.

7.2.4.4: The UCM analysis of the forces and NCs obtained in the third experimental session.

7.2.4.1 Computation of the IFC matrices via neural network (NN) models
A three-layer NN model with both direct and indirect input-output connections was used. The mathematical description of the network is explained in Zatsiorsky et al. 1998, Li et al. 2002 and Gao et al. 2003. The NN model produced an $[IFC]$ matrix for each subject.

### 7.2.4.2 Reconstruction of the neural commands

The force data from the second and third experimental sessions were transformed to NCs using the following computational steps.

Due to the fact that the transfer functions of the individual neurons of the network are linear and in both sessions the number of active fingers was the same, the output vector of finger forces $[F]$ for the entire network due to an input vector of neural commands $[NC]$ can be described with a matrix equation (Zatsiorsky et al. 2002): $[F] = [IFC] [NC]$, where $[IFC]$ is the inter-finger connection matrix, $[F]$ and $[NC]$ are the four-dimensional vectors of finger forces and NCs, respectively. Knowing the $[IFC]$ for each subject we can compute the NCs corresponding to the forces recorded in sessions 2 and 3 using formula:

$$[NC] = [IFC]^{-1} [F]$$  \hspace{1cm} (7.11)

This procedure was applied to all average force data from each trial in the sessions two and three.

### 7.2.4.3 Inverse optimization (ANIO)

The inverse optimization analysis was performed on the data obtained in the second experimental session. A detailed description of the ANIO approach is available in Terekhov et al. 2010, Terekhov, Zatsiorsky 2011, and Niu et al. 2012b (a brief description of the method is also provided in Park et al. 2010; Park et al. 2011a, b; Park et al. 2012; Niu et al. 2012a). Appendix E contains a description of the details most relevant to this study.

The ANIO method allows for the determination of an unknown objective function based on an experimental data set, which were finger forces and NCs in this study. The ANIO assumes that the cost function, which generated the data, is additive with respect to certain known EVs (equations 7.1 and 7.2). The equation 7.2 assumes that the cost function is additive with respect to the forces, while the equation 7.3 assumes it to be additive with respect to the NCs. Since the force of each finger depends on all NCs, we expect that only one of these assumptions to be true, i.e. we expect that ANIO will fail for one of the sets of EVs. However, because we estimate the cost functions from non-perfect experimental data, which is limited and subject to noise, it may
happen that additive cost functions with respect to forces and to the NCs are able to explain the experimental data with almost equal precision. The probability of this outcome will be estimated in Appendix G.

The ANIO procedure includes two steps: (i) preselecting a parameterized class of the cost functions (e.g. additive polynomials), and (ii) estimating the parameters (coefficients) from the experimental data.

(i) Preselecting the class: planarity of the data distribution. Principal component analysis (PCA) was performed on the force data and on the NC data. The amount of variance explained by the first two principal components (PCs) was used to test whether or not the data were confined to a two-dimensional hyperplane. Following the convention used in the previous ANIO studies (Park et al. 2010; 2011a, b; Park et al. 2012; Niu et al. 2012 a, b) it was accepted that the experimental data were confined to a two-dimensional hyper-plane if the first two PCs accounted for over 90% of the variance.

If the data points are indeed distributed along a two-dimensional plane in the four-dimensional space, then the cost function should be searched on the class of additive quadratic cost functions of either finger forces or NCs (see Appendix E for an explanation).

For finger forces:

\[ J_F = \frac{1}{2} \sum_{j=1}^{4} k_j^F (F_j)^2 + \sum_{j=1}^{4} w_j^F (F_j) \]  
(7.12)

For NCs:

\[ J_{NC} = \frac{1}{2} \sum_{j=1}^{4} k_j^{NC} (NC_j)^2 + \sum_{j=1}^{4} w_j^{NC} (NC_j) \]  
(7.13)

where \( k_j^X \) and \( w_j^X \) are unknown second and first order coefficients for data type \( X_j \). Note that they might differ for forces and for NCs.

Unlike the previous studies (Terekhov et al. 2010; Park et al. 2010; Park et al. 2011a,b) here we used slightly different normalization procedure: instead of assuming the \( k_i \) equals one, we demanded that the sum of the squares of the second order coefficients was equal to one: \( k_I^2 + k_M^2 + k_R^2 + k_L^2 = 1 \). The new method of normalization preserves the standard deviation of the coefficients after normalization.
(ii) Estimation of the cost function coefficients. The experimental constraints can be modeled with linear equations on finger forces or NCs. For the finger forces the constraints are:

\[
[C][F] = [B]
\]

\[
[C] = \begin{bmatrix}
1 & 1 & 1 & 1
\end{bmatrix}
\]

(7.14) (7.15)

where \([C]\) is the matrix of constraints on the total force (first row) and total moment of force (second row), and \([B] = [F_{\text{Target}}, M_{\text{Target}}]^T\) is the vector of target values of the total force and total moment of force. Written with respect to the NCs the constraints are:

\[
[C][IFC][NC] = [B]
\]

(7.16)

On the whole, ANIO was performed on: (1) finger forces and (2) NCs computed from the NN finger interaction matrix.

The accuracy of the ANIO with respect to the forces and NCs was checked. The dihedral angle (D-angle; Terekhov et al. 2010; Park et al. 2010; Park et al. 2011a, b; Park et al. 2012) between the planes of experimental observations and optimal solutions was used as a measure of the ability of the cost function to capture the experimental data. The ANIO method returns the cost function for which the D-angle is minimal (or close to minimal), thus a large D-angle would signal that the data are inconsistent with the assumption that the cost function was additive with respect to the selected elementary variables. We assumed that the cost function acceptably fit the data if the D-angle was less than 5° (Park et al. 2010; Park et al. 2011a, b; Park et al. 2012).

7.2.4.4 Analysis of performance variability

Analysis within the UCM hypothesis quantifies trial-to-trial variance for a given experimental condition. The trials from the third experimental session as well as the five trials from the second session that matched the experimental conditions used in session three were combined for this analysis, giving a total of twenty trials per condition. The variance of the EVs (finger forces or NCs) was decomposed into two components, variance within the UCM (\(V_{\text{UCM}}\)) and variance orthogonal to the UCM (\(V_{\text{ORT}}\)). \(V_{\text{UCM}}\) does not affect the PVs (\(F_{\text{Target}}\) and \(M_{\text{Target}}\)), while \(V_{\text{ORT}}\) does affect those values. The analysis was performed relative to \(F_{\text{Target}}, M_{\text{Target}}\) and both \(F_{\text{Target}} \& M_{\text{Target}}\) (\(FM_{\text{Target}}\)). The computational steps to compute \(V_{\text{UCM}}\) and \(V_{\text{ORT}}\) are described in previous papers (Park et al. 2010; Park et al. 2011a; Park et al. 2012). The \(V_{\text{UCM}}\) and \(V_{\text{ORT}}\) presented in the
results were normalized by the total variance \(V_{TOT}\) in order to compare values between forces and NCs. An index to describe the relative variance in the UCM was computed as:

\[
\Delta V = \frac{V_{UCM} - V_{ORT}}{V_{TOT}}
\]  

(7.17)

where \(V_{TOT}\) is the total variance. Each variance index was computed per degree-of-freedom in the corresponding spaces (Robert et al. 2008). The variance index \(\Delta V\) was transformed using a Fisher z-transformation \(\Delta V_z\) prior to statistical analysis. The variance index was computed for two different sets of the EVs: (1) finger forces and (2) NCs. For each type of EV the variance index was computed for three PVs: (1) \(F_{\text{Target}}\), (2) \(M_{\text{Target}}\) and (3) \(FM_{\text{Target}}\).

\subsection{7.2.5 Statistics}

Repeated measure ANOVAs (RM ANOVAs) were employed to address the study goals. In particular we were interested in answering the following three questions:

(1) Are the 4-dimensional NC vectors distributed —similarly to the finger forces— along a 2-dimensional plane? To answer this question we performed the analysis on the variance accounted for in the first two PCs (PC1 + PC2), transformed using Fisher z-transformation prior to the RM ANOVA, with the factor of ELEMENTARY VARIABLES (2 levels: forces and NCs).

(2) Does the ANIO method performed on the NC data perform better than ANIO of the actual finger forces? To answer that we analyzed the dihedral angles between the planes of the actual values of the elementary variables (forces and NCs) and their values predicted with the ANIO approach.

(3) Are there differences in the structure of the variance between the NC and force data? Three RM ANOVAs were performed on (3a) z-transformed \(\Delta V\) index, (3b) normalized \(V_{UCM}\) and (3c) normalized \(V_{ORT}\) to examine the effect of ELEMENTARY VARIABLE (2 levels: forces and NCs) and PERFORMANCE VARIABLE (3 levels: \(F_{\text{Target}}\), \(M_{\text{Target}}\) and \(FM_{\text{Target}}\)).

The difference in the variance explained was tested for significance using the Wilcoxon signed rank test. Statistical analyses were performed using the Minitab 13.0 (Minitab, Inc., State College, PA, USA) and SPSS (SPSS Inc., Chicago, IL, USA). All the data was tested for sphericity and deviations were corrected using the Greenhouse-Geisser correction. A significance level was set at \(\alpha = 0.05\).
7.3 Results
The experimental results will be presented in the following order: (1) Principal Component Analysis (PCA), (2) Analytical Inverse Optimization (ANIO) and (3) Uncontrolled Manifold (UCM) analysis. Results on (1) inter-finger connection [IFC] matrices from the neural network modeling and (2) reconstruction of hypothetical neural commands are presented in Appendix D. The statistical modeling results regarding: (1) the planarity of the NC distribution and (2) the additivity of the cost functions are presented in Appendix G.

3.1 Principal Component Analysis
The planarity of the data sets was checked using principal component analysis (Table 7.1). The variance accounted for by the first two PCs was slightly higher for the force data (96.2±0.6 %) than for the NC data (94.1±0.7 %). The fact that the variance explained for both types of data was greater than or equal to 90% in the first two PCs indicates a planar data distribution. This finding allowed us to estimate the cost functions based on the ANIO approach.

Table 7.1: Percent of variance explained by PC1 and PC 2. Median and range of variance in PC1, PC2 and PC1 + PC2 are given.

<table>
<thead>
<tr>
<th></th>
<th>PC1 Median</th>
<th>Range (min, max)</th>
<th>PC2 Median</th>
<th>Range (min, max)</th>
<th>PC1 + PC2 Median</th>
<th>Range (min, max)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forces</td>
<td>72.63</td>
<td>(56.83, 80.76)</td>
<td>24.67</td>
<td>(13.57, 38.15)</td>
<td>96.67</td>
<td>(92.42, 98.26)</td>
</tr>
<tr>
<td>Neural Commands</td>
<td>66.60</td>
<td>(53.53, 78.27)</td>
<td>29.13</td>
<td>(14.93, 39.82)</td>
<td>94.40</td>
<td>(90.47, 97.60)</td>
</tr>
</tbody>
</table>

7.3.2 Analytical Inverse Optimization
The ANIO method was successfully applied to the NC data. This allowed for the comparison of the optimization results between force and NC data. The mean dihedral angle (D-angle) was slightly smaller for the NC data (4.39±0.89°) than for the force data (4.46±1.21°). The effect of ELEMENTARY VARIABLE \(F_{1,10} = 0.158, p > 0.700\) on the z-transformed D-angle was not significant. The mean second and first order ANIO coefficients were only compared
qualitatively since the units are arbitrary. For both types of data the second order coefficients were positive, the M- and R-finger first order coefficients were positive, and the I- and L-finger first order coefficients were negative. The overall conclusion is that the inverse optimization of the NCs worked approximately as well as the inverse optimization of the finger forces did.

7.3.3 Uncontrolled Manifold Analysis

The UCM analysis was performed to compare the structure of the variance of the NC data to that of the force data relative to the selected PVs: (1) total force (FTarget), (2) total moment (MTarget) and (3) both total force & total moment (FMTarget). The ∆Vz index, which represents the relative magnitudes of the variability along the UCM and orthogonal to it, was higher for the NC data than for the force data, in regards to all PVs (Figure 7.2). The main effects of ELEMENTARY VARIABLE (F1,10 = 36.744, p < 0.001) and PERFORMANCE VARIABLE (F2,20 = 48.708, p < 0.001) on the ∆Vz index were both significant. The coordination index ∆Vz tended to be the largest for MTarget and the smallest for FMTarget: ∆Vz(MTarget) > ∆Vz(FTarget) < ∆Vz(FMTarget). This tendency was observed both for forces and NCs and for all experimental conditions. For all three PVs the mean normalized VUCM was higher for NC data than for the force data. The main effects of ELEMENTARY VARIABLE (F1,10 = 7.287, p < 0.05) and PERFORMANCE VARIABLE (F2,20 = 248.137, p < 0.001) were both found to be significant on VUCM. In terms of VORT, the mean normalized VORT was lower for NC data than for the force data. The main effects of ELEMENTARY VARIABLE (F1,10 = 7.663, p < 0.05) and PERFORMANCE VARIABLE (F2,20 = 5.034, p < 0.05) were significant on VORT. Larger differences were observed between force and NC data in regards to VORT than VUCM. For the PVs FTarget, MTarget and FMTarget the percent difference in the VORT for forces and NC was 116.9%, 77.1%, and 75.9%, respectively (NC VORT < force VORT). The percent differences observed in the VUCM were much smaller, 2.5%, 0.8%, and 2.7% for FTarget, MTarget, and FMTarget, respectively (NC VUCM > force VUCM). The results for VUCM and VORT indicate that the main difference between the structure of the variance for the forces and NCs is that the NC data distributions have less “bad” variance.
Figure 7.2: Normalized difference between variance in UCM and variance orthogonal to UCM with respect to: (A) total force and moment, (B) total force, and (C) total moment. Error bars are standard errors.

7.4 Discussion

The current study aimed at answering the question of whether the brain uses the same single set of elementary variables (EVs) to optimize and to stabilize the motor behavior, or instead it uses two different sets, one for optimization and another one for the stabilization. We formulated two hypotheses: 1) the ANIO method will fail when applied to the finger force data using the NCs as elementary variables and 2) the UCM will show higher degree of coordination for the NCs than for the forces. The experimental data confirmed the second hypothesis only. To our surprise, ANIO worked almost equally well for the forces and the NCs.

First of all, we would like to note that the results obtained in the paper are consistent with the previous studies. The IFC matrices (Appendix D) agreed well with the previously published data (Zatsiorsky et al. 1998; Zatsiorsky et al. 2000; Li et al. 2002; Danion et al. 2003). The same can be said about the ANIO results (Park et al. 2010, 2011a,b; Park et al. 2012) and the results of the UCM analysis performed for the finger forces used as elementary variables (Latash et al.
2001; Park et al. 2010). Such a consistency of the findings strengthens our belief that the data obtained here for finger forces can be considered representative and used as a benchmark for comparison with the outcome of similar NC analyses.

7.4.1 UCM analysis

We start with discussing the results of the UCM analysis as they are more straightforward. For both forces and NCs as EVs, the UCM analysis indicated that the majority of the variance was along the UCM ($\Delta V > 0$). This finding supports the notion that there was a multi-element synergy stabilizing the PVs. The quantitative UCM results favor NCs over forces. The “bad” variance was dramatically lower in the NC space than in the force space in regards to all PVs, i.e. $F_{\text{Target}}$, $M_{\text{Target}}$, $FM_{\text{Target}}$. This translated into the differences in the synergy index ($\Delta V$). The synergy index ($\Delta V_z$) was highest when computed in regards to $M_{\text{TOT}}$ performance set ($\Delta V_M > \Delta V_F > \Delta V_{FM}$); although $\Delta V_M$ and $\Delta V_F$ were very close in magnitude. This finding agrees with prior studies that found $\Delta V_M > \Delta V_F > \Delta V_{FM}$ (Park et al. 2010, 2011a; Park et al. 2012).

The following explanation is offered as to why the NC data outperformed the force data. Due to enslaving, finger forces display a certain degree of positive co-variation in regards to $F_{\text{TOT}}$; thus $\Delta V$ could be expected to be lower in the force space than in the NC space. Transforming the forces to the NCs is assumed to remove enslaving effects, effectively making individual finger NCs independent of one another. The higher $\Delta V$ values during the analysis of $M_{\text{TOT}}$ stabilization using NCs are less trivial. Indeed, the effects of positive force co-variation due to the enslaving on the total moment of force depend on particular patterns of enslaving. In earlier studies (Zatsiorsky et al. 2000), it has been shown that the enslaving patterns reduce the magnitude of the total moment produced by the fingers in pronation-supination. Given the importance of rotational hand actions in everyday life, it is possible that the specific patterns of enslaving observed in healthy adults are optimal to ensure higher stability of the total moment of force.

Similar to previous studies, the fact that the variance within the UCM was higher than the variance in the orthogonal sub-space suggests that the across-trial variability was attenuated by the negative co-variation among EVs and hence the observed variability cannot be explained by some kind of a “neuromotor noise” (Schmidt et al. 1979; Newell and Carlton 1988; Harris and Wolpert 1998).
Overall, the UCM method worked significantly better for the NCs than for forces. In our view, this is not a simple consequence of the mapping between the two sets of variables and, hence, these results provide support to the hypothesis that the stabilization of the total force and moment of force is more probably controlled in the NC than in force coordinates.

7.4.2 ANIO analysis

The results of the ANIO analysis are much less clear: the ANIO worked nearly as well for the forces and for the NCs. For both coordinate systems the cost functions were quadratic. As it is explained in Appendix E, the quadratic structure of the cost function follows from the planarity of the data distribution. More precisely, if the data distribution is planar, then there can be only two possibilities: either 1) the data can be explained by an additive cost function and then this cost function is quadratic, or 2) the data cannot be explained by an additive cost function at all (for the chosen elementary variables; an example of this case can be found in Xu et al. 2012). The planarity of the data was evaluated by the percentage of variance explained by the first two PCs; it was well above 90% for all subjects in terms of both the forces and the NCs.

Not every planar data distribution can be explained by an additive cost function. As it is shown in Appendix E, there is a rather small class of planes in a four-dimensional space, such that every plane from this class can be explained by an additive cost function, for given EVs. The theoretically probability that an arbitrary plane belongs to this class is close to zero. Because of the noise in the data we cannot expect that the experimental plane estimated with PCA belongs to this class. Instead, we require that the dihedral angle (D-angle) between the experimental plane and the closest plane from the class is sufficiently small. In other words, D-angle can be used as a measure of how likely it is that the experimental plane can be explained by an additive cost function for given elementary variables.

Our result show that the D-angles are small (< 5°) and do not differ significantly between the NC- and the force-based analysis, suggesting that both cost functions equally well capture the general tendency of the force sharing. Thus, we can conclude that the two cost functions perform equally well, and hence, either of them might be used by the CNS.

This finding is rather strange because, as explained above, the planes that are explainable by an additive cost functions are rare. Moreover, the mapping between the NCs and the forces makes the individual finger forces the functions of all four NCs, and hence the same cost
function is unlikely to be additive with respect to both the NCs and to the forces. Of course, one cannot exclude that these results were observed by pure coincidence. To estimate the probability of such a coincidence we ran statistical simulations, described in detail in Appendix G. At the first step, we estimated the probability that a random plane in the space of forces can be explained by an additive cost function with respect to the forces. For each subject we generated 10,000 random planes in the space of forces (only non-negative force values were used), such that they could explain all combinations of total force and total moment of force used in the experiments. We call these planes *feasible*. Then we computed the percentage of those planes, for which the D-angle was < 5° and a hypothetical cost function corresponding to the plane that had positive second order coefficients. We found that such planes constitute 10.3±6.2% of all feasible planes (the values denote average and standard deviation across all subjects). Hence, the probability that an arbitrary experimental plane can be explained by an additive cost function with accuracy corresponding to D-angle < 5° is about 0.10. Note that this happened in all subjects, although the experimental planes differed among them. It is hard to estimate the joint probability because, on the one hand, these events are not entirely independent: if it happened in one subject, it is more likely to happen in another, but on the other hand, they are not imperatively connected. It is clear that the joint probability is below 0.10, yet we cannot guarantee that it is below the typical, conventional level of significance (0.05).

At the next step, we checked the probability of encountering an experimental plane that can be at the same time explained by a cost function additive with respect to the forces and by a cost function additive in with respect to the NCs. We repeated the same procedure as before, but now we computed the percentage of planes for which the same conditions were satisfied both for the forces and for the NCs. Such planes constituted just 5.0±1.3% of all feasible planes. It means that an arbitrary experimentally feasible plane has about 0.05 probability to be explainable by additive cost functions both for the forces and the NCs taken as EVs. The experimental planes were different in all subjects, yet in all of them they had this property. Though it is hard to give an estimate of probability of such observation to occur by a pure chance, it is definitely below 0.05 and, thus, we think it may reflect the underlying control mechanisms.

To summarize, we found that the sharing of the finger forces observed for different combinations of total force and moment of force can be explained both by a cost function additive with respect to forces and a cost function additive with respect to the NCs. This property
is unlikely to be observed by a pure chance and, hence, it may reflect internal mechanisms used by the CNS for the motor control. However, we must conclude that we cannot distinguish which EVs – the forces or the NCs – are more likely employed by the CNS for the optimization of the finger force sharing.

7.4.3 Interaction between the optimization and stabilization

The results of the current study are rather difficult to interpret. On the one hand, we found that the NCs outperformed the forces in the UCM analysis and thus are more likely to be employed in the stabilization aspect of the task. This assumption is also confirmed by the effect of enslaving itself which suggests that the CNS has no direct control of the finger forces (see review in Schieber & Santello 2004). On the other hand, ANIO worked equally well for the forces and the NCs meaning that both coordinates are equally probable as the EVs for the optimization. Moreover, the latter property is not common: the probability of encountering it by pure chance in all subjects is below 0.05.

Though the latter observation deserves closer investigation, we can propose a simple interpretation for it. Note that using additive functions is beneficial for the CNS. The additive cost functions have a nice property that an increase of the cost due to a change in one EV does not depend on the values of the other EVs. As a consequence, local search algorithms, like gradient descent, which may be employed by the CNS (Ganesh et al 2010) can be implemented in additive cost functions in much easier way than in non-additive ones. So, the CNS may favor additive cost functions, and it may perform optimization in the coordinates, with respect to which the employed cost function is additive.

The interpretation we offer here is that the CNS might prefer to use the NCs as the EVs both for optimization and stabilization, but at the same time the cost function it wants to optimize is additive with respect to the finger forces. The fact that the finger forces are adjusted to the expected force and moment of force in advance (Johansson & Westling 1988; Olafsdottir et al. 2005; Shim et al. 2006) suggests that the CNS determines the optimal solution in a feed-forward manner. The optimization can become rather tricky if it is performed on forces, because they are not directly accessible by the CNS. However, at the same time, the goal of the optimization can be additive with respect to the forces: for instance the CNS may care about minimization of fatigue of the individual fingers (as suggested for muscles by Crowninshield & Brand 1981) or
total energy expenses associated with the task (Alexander 1999), or reducing the deformation of the individual finger pads (Pataky 2005), – all these measures are additive with respect to the finger forces, not with respect to the NCs. So, to optimize the values additive with respect to the forces the CNS may construct an intermediate cost function additive with respect to the NCs, such that its minimization will at the same time minimize the cost function of forces. Such a two-level scheme will also allow the CNS to adopt the mechanisms, which are responsible for stabilization and which operate in the space of the NCs, in order to satisfy the constraints of the optimization.

A hypothetical scheme that implements the described processes is presented in Figure 7.3. This scheme is a slight modification of the central back-coupling (CBC) scheme introduced by Latash et al. (2005). The tasks – the total force and the total moment of force – are transmitted into the performance variable stabilization neurons (PV), whose responsibility is to stabilize the performance variables by shaping the variability of the feed-forward commands, produced by the NC neurons. The NC neurons project on PV stabilization neurons as a part of the stabilization loop, but at the same time they project onto the optimization neurons \( J' \), which in turn back-project on the NC neurons, implementing the gradient descent optimization of the NCs. Finally the outputs of the NCs are mixed through the \([IFC]\) matrix to yield actual finger forces. There must exist a sensory feedback contributing to the PV stabilization, but currently it is not included into the scheme as the main focus is on the feed-forward processes. Note that the optimization neurons do not care about satisfying the task constraints; they try to bring NCs to a minimum of the cost function. The action of the \( J' \) neurons is partly counterbalanced by the PV stabilization neurons, which stabilize the task, by correcting the NCs in the direction orthogonal to the UCM. Due to the combined functioning of these two mechanisms the conditioned minimum of the cost function is achieved. Moreover, we can expect that the subjects will tend to deviate from the precise satisfaction of the task constraints towards the unconditioned minimum of the cost function. Experimental investigation of this fact falls out of the scope of the current study.

This interpretation allows giving a possible answer to the question addressed in the title of the study. The CNS probably uses the same EVs for the optimization and stabilization of the finger forces. In our study these EVs are the NCs. This finding is not surprising for the stabilization, because the CNS has no direct access to the finger forces, only to the NCs. In optimization, in turn, it seems that the CNS minimizes a cost function which is additive with
respect to the forces, yet it substitutes the optimization with an intermediate cost function additive with respect to the NCs. The benefits of such substitution are that the CNS can execute local search optimization in the variables it has direct access to – the NCs – and the same mechanisms, which are used in stabilization, can also be employed in optimization to ensure the optimal values satisfy the task constraints.

**Figure 7.3**: The hypothetical scheme of feed-forward control of the finger forces. The central controller assigns the values of the performance variables, which are shared among the NC neurons. The stabilization of the PVs is assured by the loop connecting the NCs and the PVs. At the same time another loop combines the NC and $J_i$ neurons implementing an algorithm similar to gradient decent. Without the stabilization loop the optimization would converge to unconditioned minimum of the cost function, i.e. to zero finger forces. The presence of the stabilization loop constraints the optimization so that the PVs remain close to their desired values. Finally the outputs of the NC neurons are combined together using $[IFC]$ matrix to yield the finger forces.

### 7.4.4 Study limitations
We would like to mention a few limitations of the study. The first is that only one trial at each MVC condition was collected in order to avoid fatigue. Typically, several trials of an MVC force are collected and either averaged (Zatsiorsky et al. 2002) or the highest value taken as the true MVC (Li S. et al. 2000). Inaccurate MVC forces would have the greatest effect on the \([IFC]\) matrix computed from the NN model. This would, in turn, cause the computed the NCs to be slightly inaccurate.

Another limitation of the study is that it was assumed that the NCs were between 0 and 1. Several of the subject’s NCs were computed to be outside of this range for a few of the trials (both negative NCs and NCs greater than 1). This result is most likely in part linked to the limitation mentioned above. It is also plausible that during some of the conditions the subjects were able to either decrease enslaving by activating extensor muscles or produced forces larger than they did in the MVC trials. The supination effort tasks may have caused subjects to produce quite large forces with their little fingers since the moment was scaled to the MVC of the index finger. Subjects with higher index to little finger MVC ratios may have been producing forces above the recorded little finger MVC. We speculate that this is due to psychological effects of the tasks.

The last limitation is that the range of \([F_{\text{Target}}; M_{\text{Target}}]\) used, especially moments, only captured a small subset of what subjects were capable of producing. Using a greater range of target forces and moments could have resulted in a more accurate cost function approximation. However, we felt that the potential benefit of collecting a larger range of \([F_{\text{Target}}; M_{\text{Target}}]\) was outweighed by the extra fatigue these additional trials would have induced on subjects. We felt it was better to limit the total number of trials collected to obtain the most accurate set of forces over the space of \([F_{\text{Target}}; M_{\text{Target}}]\) task constraints used.
CHAPTER 8

Discussion and Conclusions

8.1 General Overview

The dissertation includes five studies. The studies focused on the effect of perturbations on finger interaction (Chapters 3-5), modeling finger interaction (Chapter 4) and control of finger interaction (Chapters 5). The results were analyzed in terms of finger forces and hypothetical commands to fingers. The following summarizes the individual studies and revisits the initial hypotheses.

Study #1 (Chapter 3): looked at changes in the moment arms (MAs) of the FDS tendon about the MCP joint of all fingers under different MCP joint and force production conditions of the index finger. The major findings were: 1) the index finger MCP joint position and force production had no significant effect on the FDS MAs of the other fingers about the MCP joint, 2) the MA about the MCP of the FDS of the index finger increased in the flexed position when the subject actively produced force, and 3) regression models using basic anthropometric measurements were able to accurately predict the MAs of all fingers.

Hypothesis: The index finger FDS moment arm would show systematic changes with MCP joint position and force production level.

Result: The hypothesis was found to be true in regards to the MCP joint position. In regards to the force production level the FDS moment arm of the index finger increased in the flexed position in the active condition but decreased in the neutral and extended positions in the active condition.

Study #2 (Chapter 4): examined the changes in forces of fingers during a four-finger pressing task due to a vertical lifting perturbation that was applied to a single finger. It was found that raising a finger resulted in an increase in the force of that finger and a decrease in the force of the non-raised fingers. Thus, it was concluded that a total force stabilizing synergy was the mechanism of the force changes. The initial pressing force, amplitude of the finger lift, and finger lifted were all significant factors affecting the force changes.
Hypothesis: Synergistic reactions would be observed in response to the involuntary perturbation, or in other words, the non-raised fingers would show a force decrease to stabilize the total force.

Result: The hypothesis was found to be true.

Study #3 (Chapter 5): investigated the changes in forces and finger modes in response to involuntary perturbations and voluntary pressing of a single finger that resulted in a force increase of that finger. The involuntary perturbation was qualitatively the same vertical lifting perturbation as used in study #2. The involuntary perturbation resulted in: 1) an increase in force and finger mode of the perturbed finger and 2) a decrease in force and finger mode of the non-perturbed fingers. The voluntary pressing, which always followed the involuntary perturbation, required subjects to produce a quick pulse of force with the lifted finger. It was found that: 1) the pressing finger showed an increase in force and finger mode, while the non-pressing fingers displayed 2) an increase in force, and 3) no change in finger mode. The results were formulated within the referent configuration hypothesis.

Hypothesis: The first hypothesis was due to the involuntary perturbation the force and finger modes of other fingers will decrease. The second hypothesis was due to the voluntary pressing of a single finger the force and finger mode of the pressing finger will increase, the forces of the non-pressing fingers will increase and the finger modes of the non-pressing fingers will not change.

Result: Both hypotheses were found to be true.

Study #4 (Chapter 6): compared two methods of computing finger inter-connection matrices and the accuracy of NC reconstruction from the matrices computed by each method. The methods compared were one in which only single finger MVC trials were used (Danion et al. 2003) and a neural network (NN) model of finger interaction. Both methods result in a finger inter-connection matrix that accounts for both enslaving and force deficit behaviors. It was found that both methods displayed a similar ability to predict the total force across different combinations of fingers producing MVCs; however, the NN method better predicted individual finger forces in the multi-finger MVC trials. Additionally, the NN method outperformed the single finger MVC trial method in regards to the accuracy of NCs computed from sub-maximal forces and preserving the planarity of the sub-maximal force data set.
Hypothesis: The neural network model will outperform the single-finger MVC method due to its ability to better predict enslaving and force deficit in multi-finger trials.

Result: The hypothesis was found to be true.

Study #5 (Chapter 7): explored which of the two types of elemental variables, forces and NC, is more likely used in the optimization of the finger force sharing and which type is used for the stabilization of performance. The optimization of finger force sharing was investigated using the ANIO method. The stability of performance was compared using uncontrolled manifold (UCM) analysis. It was found that ANIO could be successfully performed on NC data and the optimization results performed approximately just as well for NC data as it did for force data. The UCM analysis results favored NCs, which could have been expected based on the fact that the enslaving behavior is effectively removed during the transformation from forces to NCs. Statistical analysis was used to test the probability of the results. The results were found to be non-trivial, not a mere consequence of the transformation from forces to NCs.

Hypothesis: The first hypothesis was that ANIO will work in the space of finger forces but not in the space of NCs. The second hypothesis was that the UCM results will favor the NCs due to the enslaving behavior.

Result: The first hypothesis was found to be incorrect as ANIO worked equally as well in the space of forces as in the space of NCs. The second hypothesis was found to be true.

8.2 Discussion of Main Results

The results of this dissertation support the idea of synergistic control of movements characterized by a hierarchical organization of elements. The results suggest that the CNS may not directly control mechanical variables, such as finger forces, but sends descending commands that control hypothetical variables, which in turn result in certain patterns of movement or force production. The ideas of synergistic control and hypothetical variables are united in the referent configuration (RC) hypothesis.

Synergistic control: The co-variation of individual fingers in order to match a specified performance goal exemplifies a true synergy in the context of motor control. The experimental paradigms of studies #2, 3 and 5 required finger forces to co-vary in order to meet a performance goal that was either total force or a combination of total force and total moment. In all cases,
subjects demonstrated the ability to establish a synergistic relationship among the fingers in order to stabilize specified performance goals. Studies #2 and 3 (Chapters 4 and 5) showed that the synergistic relationship acted to stabilize the performance goal due to an unexpected (involuntary) perturbation. Study #3 then showed that the controller is able to quickly abolish the synergistic relationship when faced with performing a new task that is different from the previous (voluntary pressing). The final study (Chapter 7) demonstrated that the concepts of optimality and structured variability can co-exist and help to explain a synergic relationship. Furthermore, it was shown that NCs could be the elemental variables manipulated, not finger forces. The controller may select the sharing pattern of elemental variables using an optimization approach while the performance variable is stabilized through co-variation of the elemental variables. Studies #1 (Chapter 3) and #4 (Chapter 6) illustrated why complex anatomy of the hand, as well as, certain behaviors (i.e. enslaving and force deficit) make performing multi-finger interaction difficult. Additionally, synergistic control of the fingers is assumed to be organized into a hierarchical structure with the virtual finger at the highest level and the individual fingers at the lower level. The results from study #5, along with previous work (Latash et al. 2001; Latash et al. 2002; Scholz et al. 2002; Danion et al. 2003) suggests there may be an additional level below the individual finger forces level – a level of hypothetical neural commands.
**Figure 8.1:** Illustration of hierarchical structure of synergistic multi-finger interaction. The diagram consists of three layers: 1) neural commands, 2) finger forces, and 3) virtual finger. At each level a synergy exists among the elements whose purpose is to stabilize the output of the above layer in regards to certain performance variables.

**Hypothetical variables:** the plausibility of hypothetical control variables was explored in the final study. This was the first time in which: 1) ANIO was applied to NCs and 2) the UCM performance between forces and NCs was compared. Based on the results it seems reasonable that the controller may manipulate hypothetical variables in order to produce desired finger forces. It was discussed (Chapter 7) that the UCM results may have favored the hypothetical variables due to the simple fact that enslaving and force deficit is essentially removed from the hypothetical variables. This fact may be viewed as support for the notion that the controller uses NCs to produce finger forces - it does not need to worry about the enslaving or force deficit effects of the commands. A scheme that unites control using NCs to regulate finger forces was presented in study #5. The central back coupling scheme was suggested previously (Latash et al. 2005) and essentially utilizes threshold control to stabilize the system output.

**RC Hypothesis:** The RC hypothesis uses physiological variables to explain the control of movements with the underlying idea of threshold control (Feldman and Levin, 1995). Within the context of the RC hypothesis are the ideas of synergistic relations among elements and hypothetical physiological variables that result in a mechanical output. The RC hypothesis states that the CNS controls movements by setting a RC in which all involved muscles would achieve zero activation. Often in the case of isometric pressing the RC is not possible to obtain (i.e. the force sensors don’t allow for fingers to reach the RC). In this case there is a difference between the RC and the actual configuration of fingers. In accordance with the RC hypothesis, the larger this difference is the greater the muscle activation is. A moment could be produced in the framework of the RC by setting a referent orientation of the hand. These ideas were tested and supported experimentally in a previous study of prehension (Latash et al. 2010). Unfortunately, we cannot directly test the RC hypothesis but can perform experiments in which the RC hypothesis predicts a certain outcome. The finger lifting perturbation applied in studies #2 and 3 is such an experiment. The RC hypothesis would predict that due to the lifting of a finger that
finger would increase its force production as its actual configuration became farther from the referent configuration. This was found to be true in the studies. Some people may argue that the decrease in forces of the other fingers may have been a purely mechanical effect. The argument is that lifting a single finger resulted in the whole hand being lifted slightly, thus the observed decreased in forces of other fingers. However, if this were true then lifting either the index or little fingers would cause a rotation of the hand/forearm about a longitudinal axis. This in turn would cause the opposing lateral-most finger to increase its force instead of decrease. This did not occur in the trials and data from a single subject was presented that refutes this claim. For a decrease in the forces of the other fingers the RC hypothesis would require that their RC be moved closer to their actual configuration, since they did not move. This complies with the idea that RCs emerge given values of (unidentified) neural control variables and sensory information about the actual body configuration (Feldman and Levin, 1995). This further suggests that a synergic relationship among the neural control variables exists. To restate what was said previously, the concepts of synergies and hypothetical NCs fit quite well within the RC hypothesis.

8.3 Future Work
The studies included in this dissertation provided a foundation for future studies that may expand on the results. Finger interaction is an attractive area of research because of its importance to performing many daily tasks, as well as, the relative ease in which finger forces can be recorded. The following are possible tracks for future investigations:

1. The subjects used in the studies were all young, healthy adults. It would be beneficial to collect data from populations that have a decreased ability to perform tasks involving the fingers. It may also be interesting to obtain data from populations with increased finger dexterity, such as musicians.
2. Comparing responses to perturbations, cost functions, and variance structure between left and right hands (i.e. non-dominant and dominant) may also provide interesting results that help to further current understanding of control of the hand.
3. The results from the MRI study (chapter 3) showed that relatively small amounts of force production by the fingers (~10-15% MVC) causes significant changes in moment arms of the tendons about the MCP joint. It would be useful to know if these changes are
transmitted more proximally in the hand, specifically at the carpal tunnel level in the wrist, as this is a region that is commonly injured. 

4. The force changes of the fingers due to an involuntary perturbation to a single finger resulted in changes in the other fingers as well. In addition to analyzing the magnitude of the force changes the time course of these force changes should be analyzed as well. Based on the delay between the perturbations and the onset of force changes it could be discerned whether the changes were purely reflexive or if there was a substantial mechanical effect of perturbation contribution to the force changes.

5. One of our reasons for studying finger interaction is to gain a better understanding of how movements in general are controlled and thus another line of research could be applying similar paradigms used in this dissertation to other movements.

8.4 Conclusion
Hundreds of times a day we perform tasks in which proper control of finger forces is required. Often while performing these tasks the contribution of individual fingers may change due to involuntary reasons (i.e. a finger slipping from the object) or voluntary reasons (i.e. grasping and object then removing a finger to point at something). Additionally, the net force and moment requirements of fingers are not necessarily static during a task. For example, when pouring water from a glass as more water is poured out the weight of the glass and moment effort of the fingers change as water leaves the glass. Nonetheless, we are able to properly coordinate our finger forces and perform all of these tasks with ease and little thought to what we are doing. Better comprehending how a healthy CNS controls finger movements should lead to improvements in rehabilitation methods, treatments, diagnoses, and surgeries for those suffering from certain impairments limiting their finger use. This dissertation demonstrated that although the mechanical interaction of fingers is complicated the control does not necessarily have to be as well. Relatively simple relationships and regulation schemes may be used by the CNS to coordinate finger forces in order to produce a desired output. Hopefully, as technology continues to advance, our ability as researchers to measure what exactly is occurring during movements will improve and lead to a better understanding of the human motor system.
REFERENCES


Gao F, Latash ML, Zatsiorsky VM (2005b). In contrast to robots, in humans internal and manipulation forces are coupled. 9th International Conference on Rehabilitation Robotics, June 28 – July 1.


APPENDIX A

Anatomy and Physiology

This appendix complements Chapter 2.

The following figures illustrate various anatomical features of the hand. The tables describe various anatomical and physiological properties.

A.1 Bones

Figure A.1: Bones in Human Hand. Source: http://images.yourdictionary.com/hand.
A.2 Muscles

Table A.1: Insertions, Origins, and Actions of Extrinsic Hand Muscles. Adapted from: Tortora, 2005.

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Origin</th>
<th>Insertion</th>
<th>Action</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flexor Pollicus Longus (FPL)</td>
<td>Anterior surface of radius and interosseous membrane</td>
<td>Base of distal phalanx of thumb</td>
<td>Flexes distal phalanx of thumb at interphalangeal joint.</td>
</tr>
<tr>
<td>Flexor Digitorum Profundus (FDP)</td>
<td>Anterior medial surface of body of ulna</td>
<td>Base of distal phalanx of each finger</td>
<td>Flexes distal and middle phalanges of each finger at interphalangeal joints, proximal phalanx of each finger at metacarpophalangeal joint, and hand at wrist joint.</td>
</tr>
<tr>
<td>Flexor Digitorum Superficialis (FDS)</td>
<td>Medial epicondyle of humerus, coronoid process of ulna, and a ridge along lateral margin of anterior surface of radius</td>
<td>Middle phalanx of each finger</td>
<td>Flexes middle phalanx of each finger at proximal interphalangeal joint, proximal phalanx of each finger at metacarpophalangeal joint, and hand at wrist joint.</td>
</tr>
<tr>
<td>Extensor Pollicus Brevis (EPB)</td>
<td>Posterior surface of middle of radius and interosseous membrane</td>
<td>Base of proximal phalanx of thumb</td>
<td>Extends proximal phalanx of thumb at metacarpophalangeal joint, first metacarpal of thumb at carpometacarpal joint, and hand at wrist joint.</td>
</tr>
<tr>
<td>Extensor Pollicus Longus (EPL)</td>
<td>Posterior surface of middle of ulna and interosseous membrane</td>
<td>Base of distal phalanx of thumb</td>
<td>Extends distal phalanx of thumb at interphalangeal joint, first metacarpal of thumb at carpometacarpal joint, and abducts the wrist.</td>
</tr>
<tr>
<td>Extensor Digitorum Communis (EDC)</td>
<td>Lateral epicondyle of humerus</td>
<td>Distal and middle phalanges of each finger</td>
<td>Extends distal and middle phalanges of each finger at interphalangeal joints, proximal phalanx of each finger at metacarpophalangeal joint, and hand at wrist joint.</td>
</tr>
<tr>
<td>Extensor Digit Minimi (EDM)</td>
<td>Lateral epicondyle of humerus</td>
<td>Tendon of extensor digitorum on fifth phalanx</td>
<td>Extends proximal phalanx of little finger at metacarpophalangeal joint and hand at wrist joint.</td>
</tr>
</tbody>
</table>
Figure A.3: Intrinsic Hand Muscles. Source: http://www.medicalook.com/human_anatomy.
**Table A.2:** Insertions, Origins, and Actions of Intrinsic Hand Muscles. *Adapted from: Tortora, 2005.*

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Origin</th>
<th>Insertion</th>
<th>Action</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Thenar</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Abductor Pollicus</td>
<td>Flexor retinaculum, scaphoid, and trapezium</td>
<td>Lateral side of proximal phalanx of thumb</td>
<td>Abducts thumb at carpometacarpal joint</td>
</tr>
<tr>
<td>Brevis</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Opponens Pollicus</td>
<td>Flexor retinaculum and trapezium</td>
<td>Lateral side of first metacarpal (thumb)</td>
<td>Moves thumb across palm to meet little finger (opposition) at the carpometacarpal joint</td>
</tr>
<tr>
<td>Flexor Pollicus Brevis</td>
<td>Flexor retinaculum, trapezium, capitate, and trapezoid</td>
<td>Lateral side of proximal phalanx of thumb</td>
<td>Flexes thumb at carpometacarpal and metacarpophalangeal joints</td>
</tr>
<tr>
<td>Adductor Pollicus</td>
<td>Oblique head: capitate and second and third metacarpals;</td>
<td>Medial side of proximal phalanx of thumb by a</td>
<td>Adducts thumb at carpometacarpal and metacarpophalangeal joints</td>
</tr>
<tr>
<td></td>
<td>transverse head: third metacarpal</td>
<td>tendon containing a sesamoid bone</td>
<td></td>
</tr>
<tr>
<td><strong>Hypothenar</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Abductor Digiti Minimi</td>
<td>Pisiform and tendon of flexor carpi ulnaris</td>
<td>Medial side of proximal phalanx of little</td>
<td>Abducts and flexes little finger at metacarpophalangeal joint</td>
</tr>
<tr>
<td></td>
<td></td>
<td>finger</td>
<td></td>
</tr>
<tr>
<td>Flexor Digiti Minimi Brevis</td>
<td>Flexor retinaculum and hamate</td>
<td>Medial side of proximal phalanx of little</td>
<td>Flexes little finger at carpometacarpal and metacarpophalangeal joints</td>
</tr>
<tr>
<td></td>
<td></td>
<td>finger</td>
<td></td>
</tr>
<tr>
<td>Opponens Digiti Minimi</td>
<td>Flexor retinaculum and hamate</td>
<td>Medial side of fifth metacarpal (little finger)</td>
<td>Moves little finger across palm to meet thumb (opposition) at the carpometacarpal joint</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td><strong>Intermediate</strong></td>
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</tr>
</tbody>
</table>
### Lumbricals

- **Lateral sides of tendons and flexor digitorum profundus of each finger**
- **Lateral sides of tendons of extensor digitorum on proximal phalanges of each finger**
- **Flex each finger at metacarpophalangeal joints and extend each finger at interphalangeal joints**

### Palmar Interossei

- **Sides of shafts of metacarpals of all digits (except the middle one)**
- **Sides of bases of proximal phalanges of all digits (except the middle one)**
- **Adduct each finger at metacarpophalangeal joints; flex each finger at metacarpophalangeal joints**

### Dorsal Interossei

- **Adjacent sides of metacarpals**
- **Proximal phalanx of each finger**
- **Abduct fingers 2-4 at metacarpophalangeal joints; flex fingers 2-4 at metacarpophalangeal joints; and extend each finger at interphalangeal joints.**

### A.3 Innervation & Sensation

**Table A.3: Innervation of Hand Muscles.**

<table>
<thead>
<tr>
<th>Nerve</th>
<th>Muscles Innervated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Median</td>
<td>flexor digitorum superficialis, flexor pollicus longus, flexor digitorum profundus, thenar muscles</td>
</tr>
<tr>
<td>Radial</td>
<td>extensor digitorum communis, extensor digiti minimi, extensor pollicis longus, extensor pollicis brevis, and abductor pollicis longus</td>
</tr>
<tr>
<td>Ulnar</td>
<td>flexor digitorum profundus, hypothenar muscles</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Receptor</th>
<th>Adapting Speed</th>
<th>Skin Layer</th>
<th>Receptive Field Size</th>
<th>Respond To</th>
</tr>
</thead>
<tbody>
<tr>
<td>Merkel Cells</td>
<td>Slow</td>
<td>Epidermis</td>
<td>Small, 2-3 mm diameter</td>
<td>Normal Forces, Spatial Details</td>
</tr>
<tr>
<td>Meissner’s Corpuscles</td>
<td>Fast</td>
<td>Epidermis</td>
<td>Small, 3-5 mm diameter</td>
<td>Quick pressure changes, tangential forces</td>
</tr>
<tr>
<td>Ruffini Endings</td>
<td>Slow</td>
<td>Dermis</td>
<td>Large, up to 50 mm diameter</td>
<td>Stable skin deformation</td>
</tr>
<tr>
<td>Pacinian Corpuscles</td>
<td>Fast</td>
<td>Subcutis</td>
<td>Large</td>
<td>Rapid mechanical deformation, vibrations</td>
</tr>
</tbody>
</table>
APPENDIX B

MRI Study Supplemental Material
This appendix complements Chapter 3.

B.1 Anthropometric and MVC Measurements

Hand length was measured from the most distal crease at the wrist to the tip of the longest finger. Hand breadth was measured on the palmar surface at the level of the MCP joints of digits 2-5 with the fingers in a relaxed state of ab/adduction. Measurements of the fingers were taken on the dorsal surface. Phalange distances were measured from the approximate joint centers, based on visual inspection. Phalange circumferences were measured around the approximate midpoint of each phalange. Individual and four-finger maximum voluntary contractions (MVCs) were recorded. Subjects placed their four fingers on uni-dimensional force transducers (208C02, PCB Piezotronics, Depew, NY, USA) and were instructed to press as hard as they could for five seconds. Two trials of each MVC were recorded and the average computed. The force deficit (Li et al. 1998) was computed as:

\[
\text{Force Deficit} = 100\% \times \frac{F_{\text{multi-finger MVC}}}{\sum F_i, \text{single-finger MVC}} \quad (B.1)
\]

where \( F_{\text{multi-finger MVC}} \) is the four-finger MVC and \( \sum F_i, \text{single-finger MVC} \) is the sum of MVC’s produced by fingers \( (i = \text{index, middle, ring, and little}) \) during the single-finger MVC tests.

Table B.1 Subject anthropometric and MVC measurements (mean ± STD). Units of length and force are cm and newtons, respectively.

<table>
<thead>
<tr>
<th>Measure</th>
<th>Mean ± STD</th>
<th>Measure</th>
<th>Mean ± STD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (yr)</td>
<td>23.20 ± 3.82</td>
<td>Index MVC</td>
<td>36.36 ± 10.53</td>
</tr>
<tr>
<td>Height (cm)</td>
<td>177.66 ± 7.54</td>
<td>Middle MVC</td>
<td>30.74 ± 8.79</td>
</tr>
<tr>
<td>Weight (kg)</td>
<td>72.22 ± 6.46</td>
<td>Ring MVC</td>
<td>22.63 ± 7.34</td>
</tr>
<tr>
<td>Hand Length</td>
<td>19.18 ± 0.84</td>
<td>Little MVC</td>
<td>20.56 ± 5.71</td>
</tr>
<tr>
<td>Hand Breadth</td>
<td>8.54 ± 0.67</td>
<td>4-finger MVC</td>
<td>73.55 ± 17.22</td>
</tr>
<tr>
<td>Wrist Circumference</td>
<td>16.66 ± 0.67</td>
<td>Force deficit (%)</td>
<td>50.24 ± 22.89</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Measure</th>
<th>Mean ± STD</th>
<th>Measure</th>
<th>Mean ± STD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Index Finger Measurements</td>
<td></td>
<td>Middle Finger Measurements</td>
<td></td>
</tr>
<tr>
<td>Total Length</td>
<td>9.82 ± 0.50</td>
<td>Total Length</td>
<td>10.89 ± 0.44</td>
</tr>
<tr>
<td>Measure</td>
<td>Mean ± STD</td>
<td>Measure</td>
<td>Mean ± STD</td>
</tr>
<tr>
<td>---------------------------------</td>
<td>------------</td>
<td>---------------------------------</td>
<td>------------</td>
</tr>
<tr>
<td>Proximal Phalange Length</td>
<td>4.88 ± 0.32</td>
<td>Proximal Phalange Length</td>
<td>5.22 ± 0.19</td>
</tr>
<tr>
<td>Middle Phalange Length</td>
<td>2.79 ± 0.30</td>
<td>Middle Phalange Length</td>
<td>3.17 ± 0.25</td>
</tr>
<tr>
<td>Distal Phalange Length</td>
<td>2.42 ± 0.15</td>
<td>Distal Phalange Length</td>
<td>2.57 ± 0.21</td>
</tr>
<tr>
<td>Proximal Phalange Circumference</td>
<td>6.58 ± 0.38</td>
<td>Proximal Phalange Circumference</td>
<td>6.41 ± 0.34</td>
</tr>
<tr>
<td>Middle Phalange Circumference</td>
<td>5.77 ± 0.19</td>
<td>Middle Phalange Circumference</td>
<td>5.70 ± 0.21</td>
</tr>
<tr>
<td>Distal Phalange Circumference</td>
<td>5.17 ± 0.22</td>
<td>Distal Phalange Circumference</td>
<td>5.19 ± 0.19</td>
</tr>
</tbody>
</table>

**Ring Finger Measurements**

<table>
<thead>
<tr>
<th>Measure</th>
<th>Mean ± STD</th>
<th>Measure</th>
<th>Mean ± STD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Length</td>
<td>10.33 ± 0.60</td>
<td>Total Length</td>
<td>8.18 ± 0.57</td>
</tr>
<tr>
<td>Proximal Phalange Length</td>
<td>4.89 ± 0.47</td>
<td>Proximal Phalange Length</td>
<td>4.06 ± 0.37</td>
</tr>
<tr>
<td>Middle Phalange Length</td>
<td>3.14 ± 0.33</td>
<td>Middle Phalange Length</td>
<td>2.42 ± 0.32</td>
</tr>
<tr>
<td>Distal Phalange Length</td>
<td>2.58 ± 0.18</td>
<td>Distal Phalange Length</td>
<td>2.23 ± 0.24</td>
</tr>
<tr>
<td>Proximal Phalange Circumference</td>
<td>6.21 ± 0.34</td>
<td>Proximal Phalange Circumference</td>
<td>5.51 ± 0.29</td>
</tr>
<tr>
<td>Middle Phalange Circumference</td>
<td>5.37 ± 0.35</td>
<td>Middle Phalange Circumference</td>
<td>4.91 ± 0.22</td>
</tr>
<tr>
<td>Distal Phalange Circumference</td>
<td>4.90 ± 0.12</td>
<td>Distal Phalange Circumference</td>
<td>4.58 ± 0.23</td>
</tr>
</tbody>
</table>

**Little Finger Measurements**

**Figure B.1:** Illustration of hand and finger measurements. (A) Palmar measurements. (B) Dorsal measurements.
APPENDIX C

Neural Network Modeling

This appendix complements Chapters 6 and 7.

C.1 Background

Neural network models have previously been used to model finger interaction (Zatsiorsky et al. 1998; Li et al. 2002; Zatsiorsky et al. 2004). It is well known that the individual finger forces are not independent (reviewed in Schieber & Santello 2004). In particular: (A) Activation of one finger induces also involuntary activity of other fingers, the phenomenon known as finger enslaving (Zatsiorsky et al. 1998; Zatsiorsky et al. 2000). In four-finger tasks, the inter-finger interactions can be described by \((4 \times 4)\) inter-finger connection [IFC] matrices (Zatsiorsky et al. 1998; Danion et al. 2003; Zatsiorsky et al. 2004). (B) The interaction depends on the number of fingers involved in the task: when the number of fingers increases the force production level decreases, the phenomenon known as force deficit (Ohtsuki 1981; Li et al. 1998).

The neural network model used previously was successful in its ability to predict the behaviors of enslaving and force deficit that limit the independence of fingers. The previously used neural network model consisted of three layers. The first layer (input layer) models the central neural drive (Figure C.1). The second layer (hidden layer) models the multiple connections among the fingers. They represent NCs that get dispersed across multiple fingers and is a combination of values reflecting intentional involvement of individual fingers. The enslaving effects are modeled by the connection weights from the hidden to the output layer and the force deficit by setting the output of the hidden layer being inversely proportional to the number of fingers involved. The third layer (output layer) represents the forces produced by the fingers. The NN includes also direct input-output connections. The direct connections represent possible one-to-one links between the NCs and finger forces.
Figure C.1: Schematic representation of the neural network model. Model includes three layers: 1) input, 2) hidden, and 3) output layer. The input layer receives neural commands from the central nervous system. The hidden layer accounts for the enslaving effects. There are also direct connections from the input to output layers. The output of the model is the forces produced by individual fingers.

C.2 Neural Network Computation

The network was trained using a back-propagation algorithm (Bose & Liang 1996). The input pattern vector was of the form:

\[ [NC] = [NC_I, NC_M, NC_R, NC_L]^T \]  \hspace{1cm} (C.1)

where NC\(_j\) is the neural command to the \(j\)th finger. The desired output pattern vector was of the form:

\[ [F^d] = [F_{I}^d, F_{M}^d, F_{R}^d, F_{L}^d]^T \]  \hspace{1cm} (C.2)

where \(F_j^d\) is the desired force output of the \(j\)th finger from the MVC experimental trials. The network was trained using all fifteen MVC combinations collected in the first session. If the finger was intended to produce maximal force the input value NC\(_i\) of that finger was 1. If the finger was not intended to produce force the input value of that finger was 0. The force output of the network was of the form:
\[ [F] = [F_l, F_M, F_R, F_L]^T \]  
\hspace{1cm} (C.3)

where \( F_j \) is the neural network model force output of the \( j \)th finger. The objective of the training of the network was to minimize the error function, \( E \), by adjusting the network weights and gain coefficients. The error function \( E \) was defined as the RMSE over all fifteen input MVC conditions:

\[ E = \frac{1}{\sqrt{15}} \sum_{i=1}^{15} ||[F_i] - [F^d_i]||^2 \]  
\hspace{1cm} (C.4)

where \( [F_i] \) and \( [F^d_i] \) are actual and desired outputs of the NN for combination \( i \) of instructed fingers. The NN error analyses were performed on the individual MVC data.

The networks were trained using a gradient descent method. The number of training epochs was set to 500 epochs. The learning rate was 0.01. The parameters of the learning algorithm were the same as in [Zatsiorsky et al. 1998; Li et al. 2002; Zatsiorsky et al. 2004]. For such parameters it was shown in [Zatsiorsky et al. 1998; Li et al. 2002] that the learning algorithm converges to the minimum of the error function.
APPENDIX D

Inter-finger Connection Matrices and Neural Command Reconstruction

This appendix complements Chapter 6.

D.1 Inter-finger Connection Matrices
The \([IFC]\) matrices displayed characteristics that were expected and agreed with previous results (Zatsiorsky et al. 1998; Li et al. 2002; Zatsiorsky et al. 2004; Table A4.1). Typical characteristics of enslaving were observed. The mean force deficits (\(\pm\) STD) of the I-, M-, R-, and L-fingers in the IMRL MVC task compared to the single finger MVC tasks were 39.9 \(\pm\) 22.6 \%, 27.8 \(\pm\) 17.9 \%, 37.9 \(\pm\) 17.0 \%, and 33.7 \(\pm\) 20.4 \%, respectively. The diagonal elements of the \([IFC]\) matrices were positive for all subjects and in all cases the smallest diagonal element of a given subject’s interaction matrix was larger than the largest off-diagonal element. Across subjects 23 of the 132 off-diagonal elements were negative (17.4 \%). In most occurrences of negative off-diagonal elements the absolute magnitude was less than 0.25 (16 of 23 occurrences). A companion paper (Martin et al. 2012c) discusses the \([IFC]\) matrices in greater detail.

Table D.1. Mean neural network finger interaction matrix. Column headings are of the finger instructed to press. Standard error is in parentheses.

<table>
<thead>
<tr>
<th>Instructed Finger</th>
<th>I</th>
<th>M</th>
<th>R</th>
<th>L</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>16.16  (1.72)</td>
<td>1.16 (0.61)</td>
<td>0.28 (0.23)</td>
<td>0.41 (0.14)</td>
</tr>
<tr>
<td>M</td>
<td>1.44 (0.45)</td>
<td>15.34 (1.30)</td>
<td>1.11 (0.31)</td>
<td>0.00 (0.18)</td>
</tr>
<tr>
<td>R</td>
<td>0.47 (0.13)</td>
<td>1.98 (0.42)</td>
<td>11.32 (0.99)</td>
<td>1.09 (0.21)</td>
</tr>
<tr>
<td>L</td>
<td>0.31 (0.25)</td>
<td>0.57 (0.41)</td>
<td>1.67 (0.38)</td>
<td>11.36 (1.07)</td>
</tr>
</tbody>
</table>

D.2 Neural Command Reconstruction
Exemplary NCs are shown in Figure D.1. The general pattern of NCs agreed with the expected results: (1) the I-and M-finger NCs were highest for the PR effort tasks, (2) the R- and L-finger NCs were highest for the SU effort tasks, and (3) for all fingers the NCs increased as the force level increased. The group average NCs for several of the moment and force combinations are
presented in Table D.2. There were instances when NCs were outside the 0 to 1 range. The percentage of values less than 0 was 0.1% and the percentage of values greater than 1 was 3.4% for the entire experimental data set of NCs from session 2 (1375 data points; 11 subjects × 125 session 2 trials). The NC values are analyzed and discussed in greater detail in the companion paper (Martin et al. 2012c).
Figure D.1: Exemplary data from the data set of one subject showing experimental forces (column 1) transformed to neural commands (column 2) and the optimal neural commands (column 4) for each finger (index – row 1, middle – row 2, ring – row 3, little – row 4).

Table D.2 Mean neural command values for the boundary force and moment level combinations. Standard errors are given.

<table>
<thead>
<tr>
<th>Moment</th>
<th>Force (% MVC)</th>
<th>I</th>
<th>M</th>
<th>R</th>
<th>L</th>
</tr>
</thead>
<tbody>
<tr>
<td>2PR</td>
<td>20</td>
<td>0.33 ± 0.04</td>
<td>0.31 ± 0.04</td>
<td>0.14 ± 0.02</td>
<td>0.06 ± 0.03</td>
</tr>
<tr>
<td>2PR</td>
<td>60</td>
<td>0.60 ± 0.05</td>
<td>0.81 ± 0.09</td>
<td>0.77 ± 0.06</td>
<td>0.41 ± 0.07</td>
</tr>
<tr>
<td>0</td>
<td>20</td>
<td>0.13 ± 0.02</td>
<td>0.27 ± 0.03</td>
<td>0.32 ± 0.03</td>
<td>0.18 ± 0.03</td>
</tr>
<tr>
<td>0</td>
<td>60</td>
<td>0.45 ± 0.04</td>
<td>0.72 ± 0.06</td>
<td>0.85 ± 0.03</td>
<td>0.60 ± 0.08</td>
</tr>
<tr>
<td>2SU</td>
<td>20</td>
<td>0.07 ± 0.01</td>
<td>0.14 ± 0.03</td>
<td>0.35 ± 0.03</td>
<td>0.50 ± 0.06</td>
</tr>
<tr>
<td>2SU</td>
<td>60</td>
<td>0.30 ± 0.03</td>
<td>0.64 ± 0.07</td>
<td>0.97 ± 0.07</td>
<td>0.79 ± 0.09</td>
</tr>
</tbody>
</table>
APPENDIX E

Analytical Inverse Optimization

This appendix complements Chapter 7.

E.1 Uniqueness Theorem

Uniqueness Theorem states the sufficient conditions for a solution of the inverse optimization problem to be unique. The uniqueness theorem is proved for inverse optimization problems with additive cost functions and linear constraints. The cost function $J$ of $n$ variables $x_1, \ldots, x_n$ is additive if:

$$J([X]) = \sum_{j=1}^{n} g_j(x_j) \rightarrow \min$$  \hspace{1cm} (E.1)

where $g_i$ are scalar functions, $[X] = (x_1, \ldots, x_n)^T$. The cost function $J$ is minimized subject to linear constraints:

$$[C][X] = [B]$$  \hspace{1cm} (E.2)

where $[C]$ is a $k \times n$ matrix of constraints and $[B]$ is a $k$-dimensional vector. Note: $k$ is equal to the number of constraints and $n$ is equal to the number of EVs.

We assume that every experimental point $[X]$ corresponds to the minimum of the cost function $J$ on the constraints (E.2) for a certain vector $[B]$. Hence, at every point $[X]$ the cost function $J$ must satisfy the Lagrange principle, which in this case requires that:

$$[\mathcal{C}] J'([X]) = 0$$  \hspace{1cm} (E.3)

Where $J'([X]) = (J'_{x_1}, \ldots, J'_{x_n})^T$ (prime symbol signifies derivative over the variable):

$$[\mathcal{C}] = [I] - [C]^T([C][C]^T)^{-1}[C]$$  \hspace{1cm} (E.4)

where $[I]$ is the $n \times n$ unit matrix. The derivation of the equation E.3 can be found in Terekhov et al. 2010.

Now let's assume that there are two additive cost functions $J_1([X])$ and $J_2([X])$ producing the same set of experimental data $X^*$. Evidently, both functions must satisfy Lagrange principle at every point of $X^*$. We would like to know, what are the constraints of the experimental data $X^*$, which would guarantee that the functions $J_1$ and $J_2$ coincide.
The answer is given by The Uniqueness Theorem. It states that if two nonlinear functions \( J_1([X]) \) and \( J_2([X]) \) satisfy the Lagrange principle for every point \([X]\) in the set \( X^* \) with the constraints matrix \([C]\) and:

1. \( J_1 \) and \( J_2 \) are additive,
2. \( X^* \) is a smooth \( k \)-dimensional hypersurface
3. the number of constraints \( k \) is greater or equal to 2,
4. the matrix \([\tilde{C}]\) defined in equation E.4 cannot be made block-diagonal by simultaneous reordering of the rows and columns with the same indices (such constraints are called non-splittable; Terekhov et al. 2010).

then:

\[
J_1([X]) = r J_2([X]) + [Q]^T[C][X] + \text{const} \tag{E.5}
\]

for every \( x \) inside the hyper-parallelepiped surrounding the hypersurface \( X^* \). The hyper-parallelepiped is defined as follows: \( X_{\bar{x}}^* = \{[X] \mid \text{for every } j \exists [X-] \bar{x} \text{ in } X^*: x_j = \bar{x}_j\} \), \( r \) is a non-zero scalar value and \( q \) is an arbitrary \( k \)-dimensional vector. Thus, the Uniqueness Theorem states that if any solution to the inverse optimization problem, \( J_1([X]) \), is found then the true additive cost function \( J_2([X]) \) is equal to \( J_1([X]) \) up to multiplication by the unknown scalar \( r \) and adding the unknown linear terms \([Q]^T[C][X]\).

The conditions of the Uniqueness Theorem are impossible to satisfy exactly in real experiments, because it requires that (1) the data forms a \( k \)-dimensional hypersurface, that implies infinite number of data points to be available, and (2) the data is precise, while in reality it is always disturbed by motor variability and measurement noise. Yet, as it was shown in Terekhov & Zatsiorsky (2011) the cost function can be approximately determined even from imprecise and limited data if the other conditions of the Uniqueness Theorem are satisfied.

### E.2 The link between the planarity of the data and quadratic cost functions

In the current study we assumed that the cost functions are additive quadratic polynomial. This assumption follows straightforwardly from the planarity of the data distribution and the Uniqueness Theorem. Indeed, a plane in \( n \)-dimensional space can be represented by a matrix equation:

\[
[A][X] + [D] = 0, \tag{E.6}
\]
where $[A]$ is a $n \times (n-2)$ matrix and $[D]$ is a $(n-2)$-dimensional vector. If every point $[X]$ of the plane (E.6) is a solution of the optimization problem (E.1)-(E.2) and matrix $[C]$ in (E.2) has two rows, then the cost function $J$ must satisfy Lagrange principle (E.3) on the plane. For a quadratic cost function:

$$J_1([X]) = k_1x_1^2 + ... + k_nx_n^2 + w_1x_1 + ... + w_nx_n \quad (E.7)$$

the equation (E.3) takes the form:

$$2[C][K][X] + [C][W] = 0 \quad (E.8)$$

where $[K]$ is a diagonal matrix with the coefficients $k_i$ on the diagonal and $[W] = (w_1, ..., w_n)^T$. Note that since the rank of matrix $[C]$ equals $n-2$, the equation (E.8) also defines a plane. If there exist such coefficients $k_i$ and $w_i$ ($k_i > 0$) that the equations (E.6) and (E.8) define the same plane, then the function (E.7) is a possible solution for the inverse optimization problem (E.1), (E.2), (E.6). Then according to the Uniqueness Theorem the true cost function is:

$$J_2 = rJ_1([X]) + [Q]^T[C][X] + \text{const} = r [X]^T[K][X] + ([P]^T + [Q]^T[C]) [X] + \text{const}$$

and, hence, it is also quadratic.

Now we would like to check if for every plane (E.6) there exist such coefficients $w_i$ and $k_i$ that this plane can be represented as (E.8). If such coefficients do not exist, then the plane (E.6) cannot be explained by any cost function, additive with respect to $x_1, ..., x_n$. The latter does not exclude that this plane can be explained by a non-additive cost function, or by a cost function additive with respect to another set of variables.

There are two reasons why the coefficients may not exist. First, it may happen that they exist, but some of $k_i$ are negative. Second, it may happen that no coefficients at all can fit the plane (E.6) with equation E.8. We will give additional explanations for the second possibility as it plays an important role in the current algorithm of the cost function determination. The algorithm itself will be presented in the next paragraph.

For the planes (E.6) and (E.8) to coincide there must exist such $n \times (n-2)$ matrix $[U]$ that:

$$[C][K] = [U][A]. \quad (E.9)$$

This equation can be seen as an equation on the elements of the matrices $[K]$ and $[U]$. The matrix equation (E.9) is equivalent to $n^2$ scalar equations, but since the matrix $[C]$ has rank $(n-2)$, only $(n-2)\times n$ out of $n^2$ equations make sense. The unknowns are $n$ elements of the diagonal matrix $[K]$ and $n \times (n-2)$ elements of the matrix $[U]$. Again, since only $n(n-2)$ out of $n^2$ equations must be satisfied, the matrix $[U]$ has only $(n-2)^2$ meaningful unknown elements. Summing everything up,
for the planes (E.6) and (E.8) to coincide, \((n-2)^2+n\) unknowns must satisfy \(n(n-2)\) equations. These \(n(n-2)\) equations always admit zero solution when all elements of \([K]\) and \([U]\) vanish. This is not a feasible solution because for a zero \([K]\) the equation (E.8) does not define a plane. In order to have a solution with non-zero coefficients \(k_i\), the number of equations must be at least one less than the number of unknowns. This is the case only for \(n=3\), where the number of equations equals 3 and the number of unknowns equals 4. In four-dimensional space the number of equation is 8, while the number of unknowns is just 7. Such system of equation cannot always be resolved and, hence, not every plane in a four-dimensional space can be explained with a cost function additive with respect to \(x_1,\ldots,x_n\). More precisely, such planes constitute a low-dimensional subset in the set of all planes and hence, the probability of a random plane to have this property tends to zero. It does not exclude, however, that this plane can be explained by a quadratic cost function additive with respect to another set of variables. Note that as the experimental plane is not known precisely it can happen that for the estimated plane (E.6) there exist no coefficients \(k_i\), but they do exist for a plane, which is close to the estimated one. This idea lies behind the ANIO algorithm described below.

E.3 ANIO algorithm

ANIO algorithm used in the current study searches for the parameters of a quadratic additive cost function that would fit the experimental data the best. The details of the algorithm can be found in (Terekhov et al. 2010). The input to the algorithm is the experimental plane in the form (E.6), which we defined by the two largest eigenvectors of the data co-variation matrix and the vector of the data barycenter. The algorithms searches for the coefficients \(k_i\), \(w_i\) of a cost function (E.7), such that the dihedral angle between planes (E.6) and (E.8) is minimized. The dihedral angle was computed using Matlab function \textit{subspace}, the minimization was performed using \textit{fminunc} function of Matlab Optimization Toolbox. The parameters \(w_i\) are determined form the data barycenter. We assume that the algorithm succeeded if the dihedral angle does not exceed 5° and all coefficients \(k_i\) are positive.

Note that according to Uniqueness Theorem the vector \([W]\) cannot be determined uniquely. In the current paper we chose vector \([W]\) which would have the minimal length among all possible vectors. As it is shown in (Terekhov et al. 2010), such vector \([W]\) can be computed as:
\[ [W] = -[\tilde{\mathcal{C}}][K][\bar{X}], \]  

(E.10)

where \([\bar{X}]\) is the vector of average experimental data.
APPENDIX F

Uncontrolled Manifold Analysis

This appendix complements Chapter 7.

F.1 Force Computational Steps

Computational steps of the Uncontrolled Manifold (UCM) Analysis to compute variance within the UCM ($V_{UCM}$) and variance orthogonal to the UCM ($V_{ORT}$) relative to total force ($F_{Target}$), total moment ($M_{Target}$) and total force & total moment ($FM_{Target}$). The EVs were finger forces ($F_i$) or neural commands ($NC_i$). The PVs are: 1) $F_{Target}$, 2) $M_{Target}$ or 3) $F_{Target}$ and $M_{Target}$.

$V_{UCM}$ and $V_{ORT}$ for finger forces:

1. Changes in EVs that sum up to the changes in the PV - $F_{Target}$, $M_{Target}$, or $FM_{Target}$:
   \[
   dF_{Target} = [1 1 1 1] \cdot [dF_i \ dF_M \ dF_R \ dF_L] \quad (F.1a)
   \]
   \[
   dM_{Target} = [d_i \ d_M \ d_R \ d_L] \cdot [dF_i \ dF_M \ dF_R \ dF_L] \quad (F.1b)
   \]
   \[
   dFM_{Target} = [1 1 1 1; d_i \ d_M \ d_R \ d_L] \cdot [dF_i \ dF_M \ dF_R \ dF_L] \quad (F.1c)
   \]

2. UCM is defined as an orthogonal set of vectors ($e_i$) in the space of elemental forces that did not change the net normal force (PV = $F_{Target}$), net moment (PV = $M_{Target}$), or net normal force and moment (PV = $FM_{Target}$):
   \[
   0 = [1 1 1 1] \cdot e_i \quad (F.2a)
   \]
   \[
   0 = [d_i \ d_M \ d_R \ d_L] \cdot e_i \quad (F.2b)
   \]
   \[
   0 = [1 1 1 1; d_i \ d_M \ d_R \ d_L] \cdot e_i \quad (F.2c)
   \]

3. The de-meaned forces are projected onto these directions and summed to produce:
   \[
   f_\parallel = \sum_{i}^{n-p} (e_i^T \cdot df) \cdot e_i \quad (F.3)
   \]
   where $n$ is the number of degrees-of-freedom of EVs ($n = 4$) and $P$ is the number of degrees-of-freedom of the PV ($P = 1$).

4. The de-meaned forces orthogonal to the null-space is computed as:
   \[
   f_\perp = df - f_\parallel \quad (F.4)
   \]
5. The amount of variance per degree-of-freedom parallel to the UCM is:
\[ V_{UCM} = \frac{\Sigma |f_1|^2}{(n-p)N_{trials}} \] (F.5)

6. The amount of variance per degree-of-freedom orthogonal to the UCM is:
\[ V_{ORT} = \frac{\Sigma |f_4|^2}{PN_{trials}} \] (F.6)

7. The normalized difference between these variances is measured by \( \Delta V \):
\[ \Delta V = \frac{V_{UCM} - V_{ORT}}{V_{TOT}} \] (F.7)

where \( V_{TOT} \) is the total variance, per degree-of-freedom, computed as:
\[ V_{TOT} = \frac{\Sigma n \text{var}(f_i)}{n} \] (F.8)

**F.2 Neural Command Computational Steps**

\( V_{UCM} \) and \( V_{ORT} \) for NCs:

8. Changes in EVs that sum up to the changes in the PV - \( F_{\text{Target}} \), \( M_{\text{Target}} \), or \( FM_{\text{Target}} \):
\[ dF_{\text{Target}} = [1 1 1 1] \cdot [IFC] \cdot [dNC_i \ dNC_M \ dNC_R \ dNC_L] \] (F.9a)
\[ dM_{\text{Target}} = [d_i \ d_M \ d_R \ d_L] \cdot [IFC] \cdot [dNC_i \ dNC_M \ dNC_R \ dNC_L] \] (F.9b)
\[ dFM_{\text{Target}} = [1 1 1 1; \ d_i \ d_M \ d_R \ d_L] \cdot [IFC] \cdot [dNC_i \ dNC_M \ dNC_R \ dNC_L] \] (F.9c)

9. UCM is defined as an orthogonal set of vectors \( (e_i) \) in the space of elemental NCs that did not change the net normal force (PV = \( F_{\text{Target}} \)), net moment (PV = \( M_{\text{Target}} \)), or net normal force and moment (PV = \( FM_{\text{Target}} \)):
\[ 0 = [1 1 1 1] \cdot [IFC] \cdot e_i \] (F.10a)
\[ 0 = [d_i \ d_M \ d_R \ d_L] \cdot [IFC] \cdot e_i \] (F.10b)
\[ 0 = [1 1 1 1; \ d_i \ d_M \ d_R \ d_L] \cdot [IFC] \cdot e_i \] (F.10c)

10. The de-meaned NCs are projected onto these directions and summed to produce:
\[ NC_{||} = \sum_i^{n-p} (e_i^T \cdot dNC) \cdot e_i \] (F.11)
where \( n \) is the number of degrees-of-freedom of elemental variables \((n = 4)\) and \( P \) is the number of degrees-of-freedom of the performance variable \((P = 1)\).

11. The de-meaned NCs orthogonal to the null-space is computed as:
\[
NC_{\perp} = dNC - NC_{\parallel}
\] (F.12)

12. The amount of variance per degree-of-freedom parallel to the UCM is:
\[
V_{UCM} = \frac{\sum|NC_{\parallel}|^2}{(n-P)N_{trials}}
\] (F.13)

13. The amount of variance per degree-of-freedom orthogonal to the UCM is:
\[
V_{ORT} = \frac{\sum|NC_{\perp}|^2}{PN_{trials}}
\] (F.14)

14. The normalized difference between these variances is measured by \( \Delta V \):
\[
\Delta V = \frac{V_{UCM} - V_{ORT}}{V_{TOT}}
\] (F.15)

where \( V_{TOT} \) is the total variance, per degree-of-freedom, computed as:
\[
V_{TOT} = \frac{\sum_{i=1}^{n} \text{var}(NC_{\perp})}{n}
\] (F.16)

In order to compare \( V_{UCM} \) and \( V_{ORT} \) between NCs and forces a normalization procedure was performed. \( V_{UCM} \) and \( V_{ORT} \) were normalized by dividing the values by \( V_{TOT} \).
APPENDIX G

Feasibility of Experimental Results

This appendix complements Chapter 7.

The application of ANIO to the forces and the NCs yielded unexpected results: it worked nearly equally well for both sets of elementary variables. To see if this could happen by pure coincidence we ran statistical tests in which we generated random experimentally feasible planes (described below). We tested the planes for satisfaction of each of two conditions: 1) the D-angle is small in the space of forces, 2) the D-angle is small both in the space of forces and in the space of NCs. A detailed description of the procedure is explained below.

G.1 Feasible planes

The planes were originally defined in the space of the finger forces. We call a plane feasible if it contains points, in which the task constraints – total force and moment of force – are satisfied by positive finger forces. This property is important because in statistical modeling we must exclude the planes, which can never, even hypothetically, be obtained in the experiments. For example, the plane of the UCM, which is defined by the matrix $[C]$, cannot be admitted because at every point of this plane the values of the total force and the total moment of force are the same, and hence they can never satisfy the experimental constraints for different task values.

The procedure starts with generating two random orthonormal 4-dimensional vectors $[A_1]$ and $[A_2]$. Each element of the vectors was randomly drawn from the uniform $[-1, 1]$ distribution and then the vectors were made orthonormal using Gram-Schmidt process. These vectors define a plane in the four-dimensional space.

To check if the plane is feasible we searched for a parallel shift $[A_0]$ of the plane, such that the experimental constraints were satisfied by positive finger forces. We used quadratic programming as a tool for that. The corresponding problem was:

$$\begin{align*}
[A_0]^T[A_0] & \rightarrow \text{min}, \\
[F]^i & = [A_0] + [A_1] \beta_1^i + [A_2] \beta_2^i, \ i = 1,...,20, \\
[C][F]^i & = [B]^i, \\
[F]^i_j & \geq 0, \ j = 1,...,4,
\end{align*}$$

(G.1) (G.2) (G.3) (G.4)
where \([F]^i\) is a vector of hypothetical finger forces computed for each pair of total force and total moment of force used in the experiments; their values are given by the vector \([B]^i\). The subsidiary scalar values \(\beta_1^i\) and \(\beta_2^i\) were used to define the vector \([F]^i\) belonging to the tested plane, which in turn was defined by the orthonormal vectors \([A_1], [A_2]\) and the shift \([A_0]\). The last inequality above requires that the constraints are satisfied by positive values of finger forces. For each random plane we checked that the described quadratic programming problem has a solution. We used \texttt{quadprog} function from Optimization Toolbox of Matlab (Matlab 7.4.0, Mathworks, Inc, Natick, MA). If the function converged to a solution within 1,000 iterations the plane was accepted as feasible, otherwise it was discarded. We used this procedure to generate 10,000 feasible planes for each subject.

\textbf{G.2 Tests}

The feasible planes were used to estimate the probability that a random experimental plane could be explained by a cost function additive with respect to the forces. To achieve this, for each feasible plane we took the vectors \([F]^i\) as experimental data points and applied ANIO to them. The D-angle and the coefficients of the cost function corresponding to the plane were determined. We computed the percentage of the feasible planes for which two conditions were satisfied at the same time: 1) the D-angle was below 5°, 2) all second order coefficients were positive. The percentage was estimated for each subject and yielded \(10.3\pm6.2\%\) across the group. The same planes were used to estimate the probability that the same data set can be explained by a cost function additive with respect to the forces and by a cost function additive with respect to the NCs. For that we computed the NCs corresponding to the forces \([F]^i\), applied ANIO method to both data sets and computed the percentage of the planes for which the same conditions as before were met both for the forces and for the NCs. The resultant percentage was \(5.0\pm1.3\%\) across all subjects.
APPENDIX H

Abbreviations Used in Studies

This appendix complements Chapters 3-7.

H.1 Study #1 - Effects of the Index Finger Position and Force Production on
the FDS Moment Arms at the MCP Joints - an MRI Study
CNS: central nervous system
DIP: distal interphalangeal
FDP: flexor digitorum profundus
FDS: flexor digitorum superficialis
MA: moment arm
MCP: metacarpal phalangeal
MRI: magnetic resonance imaging
MVC: maximum voluntary contraction
PIP: proximal interphalangeal

H.2 Study #2 - Stabilization of the Total Force in Multi-finger Pressing Tasks
Studied with the ‘Inverse Piano’ Technique
I: index finger
IP: inverse piano
L: little finger
M: middle finger
MVC: maximum voluntary contraction
R: ring finger
UCM: uncontrolled manifold

H.3 Study #3 - Multi-finger Interaction during Involuntary and Voluntary Single
Finger Force Changes
CNS: central nervous system
COMP%: compensation percentage
DIP: distal interphalangeal
EMG: electromyography
F: force
I-Piano: inverse piano
I: index finger
Invol: involuntary
L: little finger
L_i: moment arm of \( i \)th finger
M: middle finger
MCP: metacarpal phalangeal
MD: mode
MVC: maximum voluntary contraction
NL: neutral line
PIP: proximal interphalangeal
R: ring finger
Vol: voluntary

**H.4 Study #4 - Comparison of Inter-Finger Connection Matrix Computation Techniques**

*Abbreviations*
ANIO: analytical inverse optimization
CNS: central nervous system
DIP: distal interphalangeal
\( F_{TOT} \): total force
I: index finger
L: little finger
M: middle finger
MCP: metacarpophalangeal
\( M_{TOT} \): total moment
MVC: maximal voluntary contraction
NC: neural command
NN: neural network
PC: principal component
PCA: principal component analysis
PIP: proximal interphalangeal
PR: pronation
R: ring finger
RM: repeated measure
SU: supination

Mathematical symbols

$[F]$: $4 \times 1$ vector of finger forces
$G$: gain factor that is inversely proportional to the number of fingers
$[IFC]$: $4 \times 4$ inter-finger connection matrix
$N$: number of fingers involved in task
$[NC]$: $4 \times 1$ vector of the hypothetical neural commands
$[v]$: $4 \times 4$ diagonal matrix
$[w]$: $4 \times 4$ matrix of connection weights between the fingers

H.5 Study #5 - Does the Brain Optimize and Stabilize the Motor Behavior in the Same Space of Elemental Variables? Evidence From a Finger Pressing Study

Abbreviations

ANIO: analytical inverse optimization
CBC: central back-coupling
CNS: central nervous system
D-angle: dihedral angle between experimental data and optimal solutions
DIP: distal interphalangeal
EV: elemental variable
$F_{TOT}$: total force produced by fingers
I: index finger
L: little finger
M: middle finger
NC: neural command
MCP: metacarpophalangeal
$M_{\text{Target}}$: target total moment to be produced by fingers
$M_{\text{TOT}}$: total moment produced by fingers
MVC: maximum voluntary contraction
MVC$_j$: maximum voluntary contraction of finger $j$
NN: neural network
PCA: principal component analysis
PC: principal component
PV: performance variable
PIP: proximal interphalangeal
PR: pronation effort
R: ring finger
RM ANOVA: repeated measure analysis of variance
RMSE: root mean square error
SU: supination effort
U-angle: angle between the uncontrolled manifold and plane of optimal solutions
UCM: uncontrolled manifold
$V_{\text{UCM}}$: variance within the uncontrolled manifold
$V_{\text{ORT}}$: variance orthogonal to the uncontrolled manifold
$\Delta V$: index to describe the relative variance in the uncontrolled manifold

Mathematical symbols
$[B]$: vector of target values of the total force and total moment of force
$[NC]$: 4 × 1 vector of the hypothetical neural commands
$[C]$: matrix of constraints on the total force (first row) and total moment of force (second row)
$d_j$: moment arm of finger $j$
$F_j$: force of finger $j$
$[F]$: 4 × 1 vector of finger forces
$[IFC]$: 4 × 4 inter-finger connection matrix
$J$: cost function
$J_F$: cost function additive with respect to forces

$J_{NC}$: cost function additive with respect to motor commands

$k_i$: second-order coefficient of cost function

$S_f$: moment scaling factor

$w_j$: first-order coefficient of cost function
Curriculum Vitae

Education:

The Pennsylvania State University – University Park, PA
   Ph.D., Kinesiology, (ABD; expected graduation: August 2012)
   M.S. Mechanical Engineering, May 2012
   M.S. Kinesiology, August 2009

State University of New York at Binghamton – Binghamton, NY
   B.S., Mechanical Engineering, May 2007

Peer-Reviewed Publications:


Scholarly Activity:

- 8 Conference Presentations (6 posters, 1 podium, 1 demonstration)
- Transcranial Magnetic Stimulation Course – University of Southern California, August 2009.
- Medical Imaging Workshop – “Frontiers of Biomedical Imaging Science”, Vanderbilt University, June 2011.
- Volunteer Biomechanist for USA Track & Field – Ongoing.