

ABSTRACT

Title of thesis: EFFECT OF KINETIC DEGREES OF FREEDOM ON
MULTI-FINGER FORCE AND MOMENT
STABILIZING SYNERGIES

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The purpose of the present study was to test the principle of motor abundance as compared to motor redundancy, by investigating the changes in force stabilizing and moment stabilizing synergies for pressing tasks involving different number of fingers (IM, IR, IL, MR, ML, RL, IMR, IML, IRL, MRL, IMRL; where I=Index, M=Middle, R=Ring, L=Little). Twelve healthy right-handed subjects (6 males and 6 females, 27 ± 4.3 years) participated in the experiment. Subjects were explicitly provided a visual feedback of forces for a constant multi finger force production task. Since subjects were explicitly given a visual feedback of their performance for the force production task, strong force stabilizing synergies were expected (*Hypothesis 1*). Based on the principle of abundance, we hypothesized that the force stabilizing synergies would increase with the number of fingers (*Hypothesis 2*). Assuming that the precise moment stabilizing synergies are conditioned by everyday prehension experiences, we hypothesized that moment stabilizing synergies, if existing, would increase with the number of fingers, since everyday prehension and manipulation tasks require a precise control of moments (*Hypothesis 3*). Also, if both the synergies existed simultaneously, we hypothesized that those synergies would be more prominent when more fingers are involved in the task (*Hypothesis 4*). It was found that strong force stabilizing synergies existed for all the finger combinations. However, these force stabilizing synergies reduced with an increase in the number of task fingers. Moment destabilizing synergies were found for the two finger combinations and no moment synergies were present for the three finger combinations. However, moment stabilizing synergies existed for the four finger combinations. We interpret the findings as evidence for the principle of abundance for stabilization of moments during pressing tasks, regardless of the fact that only the visual feedback of forces was given to the subjects.

EFFECT OF KINETIC DEGREES OF FREEDOM ON MULTI-FINGER FORCE AND
MOMENT STABILIZING SYNERGIES

by

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INTRODUCTION

The mechanism by which the Central Nervous System (CNS) controls the voluntary movements of apparently redundant effectors in the human body is a major question in human motor control. The foremost challenge lies in discovering the framework within which the CNS chooses the combinations out of the numerous solutions available. This problem was first formulated by Bernstein and has also been referred to as the “degrees of freedom” problem in motor control literature (Bernstein, 1967).

Most of the theories to solve this problem suggest that the excessive degrees of freedom create a control problem for the CNS and hence, it tries to select an optimum solution by reducing the redundant degrees of freedom. However, excess degrees of freedom can also be perceived to be beneficial, and recently it has been suggested that within the redundant systems, the constituting elements behave in such a manner that some important task variables are stabilized (Schoner, 1995). Alternatively, the CNS actually uses the “abundant” solutions available, each solution depending upon the momentary perturbations and external constraints (Latash *et al.*, 2002a; Scholz & Schoner, 1999). Thus, the CNS need not compute a unique solution for redundant degrees of freedom but entire families of solutions fulfilling the task requirements. This has also been referred to as the *principle of abundance* (Gelfand & Latash, 1998), as compared to motor redundancy. These families of solutions can be considered as task specific synergies amongst various elements at the neuromotor level. Synergies can be defined as the task specific covariation of individual elements of a system to achieve a common goal (Li *et al.*, 1998b). However, the effect of changes in the degrees of freedom on the synergies pertaining to a particular motor task is still unknown.

The human hand is an excellent example of kinetic redundancy. For example, each finger of a hand can be considered as a force generator. If the task is to control a given pressing force by using two or more fingers, the system becomes redundant because that force can be achieved by a single finger only. Two important behavioral performance variables in multi finger force production tasks are the total force generated by the individual fingers and the total moment of forces around the longitudinal axis of the hand (Shim *et al.*, 2005a).

The purpose of this study is to examine the effect of changes in degrees of freedom on the force stabilizing and moment stabilizing synergies in a multi-finger pressing task, with only the visual feedback of forces given to the subjects. Synergies are quantified under the framework of Uncontrolled Manifold Hypothesis (UCM). Systematic variation of degrees of freedom would reveal the importance of these synergies from the perspective of neural control, and test the principle of abundance for both the force and moment synergies in multi-finger pressing tasks.

The thesis is divided into four chapters. The first chapter provides a literature review on different perspectives on the degrees of freedom problem and motor synergies. The second chapter explains the rationale behind this study and describes the methodology used in the study. The third chapter reviews the results of the study, and the fourth chapter discusses those results, and then suggests future research possibilities.

CHAPTER I

REVIEW OF LITERATURE

The Degree of Freedom Problem in Motor Control

Control of human movement requires one to incorporate different issues, such as the mechanical properties of limbs and muscles, the neuronal control structures for the individual limbs, the mechanics and neuronal control structures for the coordination between effectors, as well as central decisions that are based on external information and on internal states. Consider a simple act of reaching for an object. The object's description in space can be characterized by six descriptors— three describing its position, and the other three defining the motion about the three perpendicular axes passing through the object's centre of mass. The number of descriptors needed to characterize the object's position in space is the minimum number of mechanical degrees of freedom that characterize the human body. If only the joints in the human body are considered, there are about 100 degrees of freedom alone from the perspective of kinematics (Turvey, 1990). From a kinetic view point, there could be numerous combinations of muscle forces, which result in the same output force desired for a particular action (Ting & McKay, 2007) This is an example of a classic problem in human motor control – the *degrees of freedom* problem or the *motor redundancy* problem, popularly associated with the name of Nicholas Bernstein (Turvey, 1990).

The degree of freedom problem is encountered at different levels of human movement control. Consider, for example, the mechanism of voluntary force production by a muscle. Every muscle in the human body contains many fibers, innervated by the alpha-motorneurons. The number of motorneurons is less than the number of motor

fibers. When alpha motorneurons generate action potential, the signal is received by a group of muscle fibres, called motor units. The Central Nervous System (CNS) can modify the muscle force by modifying the number of alpha-motorneurons being recruited, by changing the frequency of action potentials being generated by individual motorneurons or by combining both of them together. Thus, the strategies for generating a particular amount of muscle force could be manifold, and at the microscopic level, the problem now becomes much more complex from the perspective of control, than it was at the level of kinematics.

Human Hand as a Tool to Investigate the Degree of Freedom Problem

The human hand is composed of many different bones, muscles, and ligaments that allow for a large amount of movement and dexterity. There are three major types of bones in the hand - phalanges, metacarpals and carpals (Figure 1.1). Phalanges are the 14 bones that are found in the fingers of each hand. Each finger has three phalanges (the distal, middle, and proximal) while the thumb only has two. Metacarpal bones are the five bones that compose the middle part of the hand. Carpal bones are the eight bones that create the wrist. The carpal bones are connected to two bones of the arm, the ulnar bone and the radius bone.

The movements of the human hand are accomplished by two sets of each of these tissues. They can be subdivided into two groups: the extrinsic and intrinsic muscle groups. The extrinsic muscle groups are the long flexors and extensors (Figure 1.2). They are called extrinsic because the muscle belly is located on the forearm.

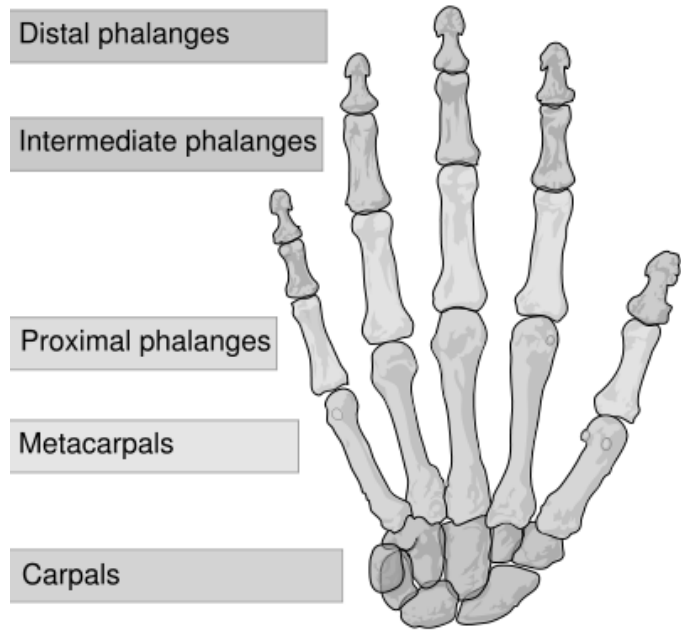


Figure 1.1 Bones of the human hand.

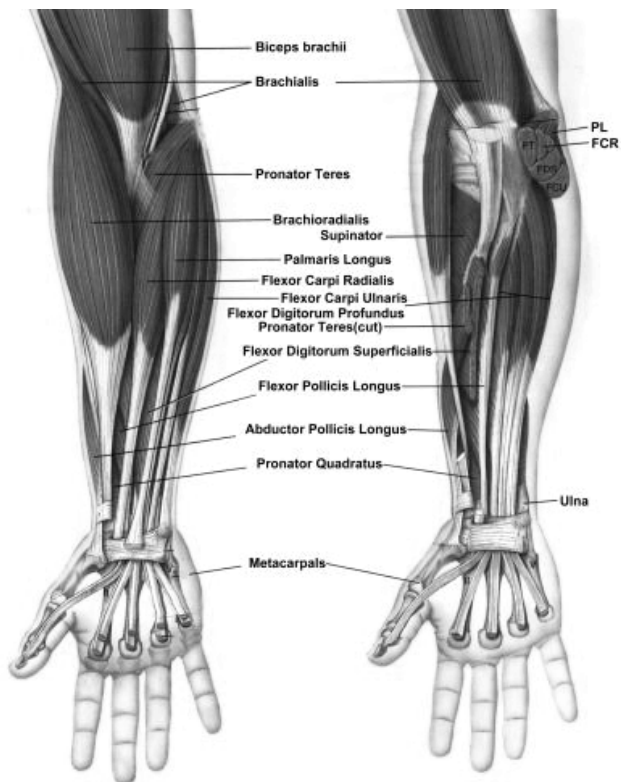


Figure 2.2. Extrinsic muscles of the hand, anterior and posterior view.

The intrinsic muscle groups are the thenar and hypothenar muscles (thenar referring to the thumb, hypothenar to the small finger), the interosseus muscles (between the metacarpal bones, four dorsally and three volarly) and the lumbrical muscles. These muscles arise from the deep flexor (and are special because they have no bony origin) and insert on the dorsal extensor hood mechanism.

In all, 27 bones in the human hand are controlled by 39 muscles (Loren *et al.*, 1996; Tubiana, 1981). There are many degrees of freedom available for hand motion, yet joint movements are not independent. Anatomical factors, such as inter-digit webbings, internal connections between various tendons (von Schroeder *et al.*, 1990) and multi-digit insertions of extrinsic finger muscles (Tubiana, 1981, 1986) result in mechanical coupling between various joints. Additionally, neuronal connections cause coupling. A single cortical motor neuron innervates multiple spinal motor neuron pools which in turn drive multiple tendons (Hamed *et al.*, 2007; Reilly *et al.*, 2008), and results in functional coupling between various muscles (Lang & Schieber, 2004). This remarkably complex structure of the hand makes it an apt tool to investigate the degree of freedom problem and probe the control strategies used by the CNS for controlling such a complex structure so efficiently.

Approaches to Solve the Degree of Freedom Problem

Most of the theories to solve the degrees of freedom problem assume that the excessive degrees of freedom pose a control problem for the CNS, and hence, the CNS tries to reduce them. In a nutshell, three different approaches to tackle the redundancy problem can be found in motor control literature – elimination, optimization and motor synergies (Latash *et al.*, 2007).

The earliest experiments of Bernstein suggested that the CNS tries to “freeze” or *eliminate* the extra degrees of freedom, in order to attain the task goals (Bernstein, 1969). Some later studies on the same lines invoked the same methodology to study human motor behavior (Newell & Carlton, 1988; Newell & Vaillancourt, 2001). These studies used variability of individual joints as well as the end effector, to measure the importance a particular joint is given from the perspective of control. Some studies suggest that the biomechanical coupling of effectors reduces the effective degrees of freedom, thus making the computations easier for the CNS (Heuer *et al.*, 1989; Turvey, 1990). Such interactions among body segments which are not directly connected from an anatomical standpoint are typical in many neonatal and post neonatal reflexes (Marinelli, 1983). However, it is can be argued that some of these reflexes are lost with motor development, and the CNS seems to have refined the use of extra degrees of freedom. This is also true for learning some new motor skills, like pistol shooting (Scholz *et al.*, 2000). Another argument against such theories is, that while it might be easier to control lesser number of effectors or muscles, it might not always be the most efficient methodology, considering the fact that involvement of large number of effectors or muscles for the same task would greatly reduce the effort required to perform that task and result in less fatigue.

Others approaches suggest that cost containment or *optimization* of some variable relevant to the tasks, is the strategy the CNS might consider. The heart to this approach is that the actor redefines the task until there is no ambiguity about how the task is to be performed (Bulas *et al.*, 1994; Winters *et al.*, 1988) There has been a wide argument on what cost functions the CNS considers for optimization. Claims are based on certain mechanical, engineering, psychological, or complex cost functions.

Most of the recent studies, however, point towards the utilization of *synergies* by the CNS to solve the degrees of freedom problem, and some of the newer and more sophisticated approaches, like the Optimal Feedback Control theory and Adaptive model theory (AMT), are also incorporated by some of the latest techniques to study the third approach, motor synergies (Bizzi *et al.*, 1991; Todorov & Jordan, 2002).

Motor Synergies –Definition and Quantification

The term synergy has been used to describe correlated outputs of muscles, joints or effectors in voluntary multijoint limb movements, force production tasks, quiet standing, locomotion, postural adjustments, quick reactions to perturbations, and other motor actions (Latash *et al.*, 2007). The literature tends to retain an anatomical perspective on synergy, in the sense of a fixed arrangement of agonists and antagonists. Traditionally, “synergists” are muscles having similar actions at a joint. However, there is much that argues against this tradition (Gelfand & Latash, 1998). From an alternative perspective, synergy is a label that conveys the notion of a collection of relatively independent degrees of freedom that behave as a single functional unit – meaning that the internal degrees of freedom take care of themselves, adjusting to their mutual fluctuations and to the fluctuations of the external force field, and do so in a way that preserves the functional integrity of the collection.

A more qualitative definition of synergy comprises of three essential parameters: *sharing*, *error compensation* to attain flexibility/stability in performing a task and *task dependence* (Latash *et al.*, 2007).

Sharing can be quantified as a percentage of contribution by a particular element to the required task, when a number of elements are involved in performing the task. Invariant sharing patterns have been described for many tasks including vertical posture,

locomotion, reaching, finger force production (Hsu *et al.*, 2007; Kelso & Tuller, 1984; Macpherson *et al.*, 1986; Santello *et al.*, 1998; Scholz *et al.*, 2002; Smith *et al.*, 1985; Wang & Stelmach, 1998). However, it is possible for a consistent sharing pattern to emerge without the presence of a central control. Another feature typical to synergies is that of error compensation amongst the participating elements. Error compensation has commonly been quantified in terms of the variability of individual elements, compared to the combined variability of all the elements. Small variability of all the elements combined together can be interpreted as a better task stability. Task dependence implies the ability of synergies to change and reform for different tasks, using the same elements, if required. It also implies that synergies are goal directed, and there has to be a task demand for a particular set of synergies to exist.

Most of the investigators have quantified synergies by measuring the motor variability of the individual elements involved in the task. Variability provides an attractive metric to quantify synergies, because an analysis of patterns of variability of individual elements can give a clear picture of the involvement and the importance of a particular element for a specific synergy. Analysis of variability has ranges from the simple comparison of elemental variabilities to the total task variabilities, to more sophisticated statistical analysis like the Principal Component Analysis and Factor Analysis, to some recent mathematical techniques like the Uncontrolled Manifold Analysis (UCM) and Point wise Dimension Estimation (PDE) (Clewley *et al.*, 2008; Scholz & Schoner, 1999).

Overview of Motor Synergies

Associated movements, postural adjustments and synergies are three motor concepts directly related to each other, although their historical developments have

followed relatively independent paths (Gahrey Y,1987). The concept of muscle synergies being laid down in the spinal cord, with the reflex arc being the basis of synergistic muscle grouping was first proposed by Sherrington (1935). This concept of synergies is linked to low-level neural processes, one level away from the muscles. Sherrington viewed movement as a consequence of alternating flexor and crossed extensor reflexes in the limbs. In contrast, Bernstein (1967) proposed a view of synergies, stressing the role of high-level neural processes and gave a more functional and operational definition of synergies. Accordingly, the CNS groups several variables into functional synergies, each synergy being controlled by a single central command. By doing this, the CNS reduces the computational effort of controlling each muscle independently. Although differing widely in implementation, these two perspectives on synergies have similar consequences at the muscular level.

Bernstein's view on synergies has been studied using various approaches, ranging from posture and dexterity in humans, to the coordination during swallowing in *Aplysia californica* (Latash *et al.*, 2005a; Latash *et al.*, 1998b; Ye *et al.*, 2006). He suggested that the movement functions which constitute activity are: the coordination of movement, the planning of movement, and the exploration of better, optimal ways to move (Bongaardt *et al.*, 2000).

Synergies have been analyzed both at the level of behavior, as well at the level of neurophysiologic correlates responsible for a particular behavior. The classical studies on the wiping reflex in frogs were first conducted in the nineteenth century. The spinal cords of the frogs were surgically separated from the brain. When a paper soaked in weak acid was wiped on the hind limb of the frog, it made a quick reflex to wipe it off (Berkinblit *et al.*, 1986; Richardson *et al.*, 2005). A typical wiping phase could be broken down into

fixed sequences of movements, each aiming to accomplish the task of wiping the acid, thus constituting synergies. Further, if one joint of the hind limb was blocked with a splint, the other joints modify their actions to accomplish the task of accurate wiping movements (reviewed in Latash, 2003).

Other experiments to study the effects of electrical simulation of spinal cord of the frogs on the hind limb endpoint action have revealed different effects on the position as well as the forces of hind limb, when different segments of the spinal cord are activated (Bizzi et al., 1991; Giszter *et al.*, 1993; Mussa-Ivaldi *et al.*, 1994). Similar studies on simulation of spinal cord at the cervical level of monkeys has shown that typically, many muscles are coactivated at the requisite current needed to produce movements (Moritz *et al.*, 2007). Another classical evidence pointing towards the generation of synergies at the level of spinal cord was demonstrated by Macpherson (Macpherson et al., 1986). The spinal cord of the cats was surgically removed from the brain, so that no afferent signals could be received. Ordinarily, the cat would have showed no signs of locomotion. However, when the cat's paws were placed on the treadmill, individual limbs were coordinated to produce a gait typical in walking. Changing the speed of the treadmill at a certain threshold resulted in a change in gait patten from walking to trotting. These experiments suggested that synergies with regard to locomotion have their neurophysiological correlates in the spinal cords. The presence of Central Pattern Generators (CPGs) in the spinal cord, and even in the limbs, are thought to be responsible for synergistic actions like locomotion (Schoner & Kelso, 1988). Studies on humans with severe spinal cord injuries have shown similar results (Shapkov Iu & Shapkova, 1998). The patients were able to produce involuntary stepping movements of their feet, when some portions of their spinal cord were electrically

excited. However, the patients were incapable of performing such movements voluntarily. Moreover, it was observed that when a particular joint was blocked, the other joints showed higher amplitude, to compensate for the change and attain the same goal of locomotion.

Many other similar experiments show that spinal cord is able to produce the neural patterns forming the basis of synergies pertaining to locomotion, hence displaying all the elements of motor synergies – sharing, error compensation and task specificity (Arshavskii Iu *et al.*, 1995; Grillner & Zangger, 1979; Shik *et al.*, 1966). However, it is to be noted that in all such studies, there was no voluntary control over the movements by the animals. This suggests that to ensure meaningful locomotion, apart from the spinal cord, synergies should also have their origin in the brain itself.

Studies among normal human populations, including voluntary movements, have described synergies for diverse tasks like posture, speech, locomotion, reaching, finger force production and pistol shooting (Hsu *et al.*, 2007; Kelso & Tuller, 1984; Macpherson *et al.*, 1986; Santello *et al.*, 1998; Scholz *et al.*, 2002; Smith *et al.*, 1985; Wang & Stelmach, 1998). A number of these experiments applied unexpected perturbations to an element of multi-element system during natural, complex movements.

Kinematic studies on posture point towards the existence of multi-joint and multi-muscle synergies to stabilize the position of head and trunk. These synergies are also found to be dependent on different sensory systems provided to the subjects, namely, vestibular, vision, touch, audition and graviceptors (Allison *et al.*, 2006; Jeka & Lackner, 1994; Johanssen *et al.*, 2007). Recent experiments employing a similar treadmill setup with cats having a *non severed* spinal cord have pointed towards the robustness of synergy organization across perturbation types and postures (Torres-Oviedo *et al.*, 2006;

Torres-Oviedo & Ting, 2007). These studies suggest that muscle synergies controlling task-variables are a general construct used by the CNS for balance control (Ting & McKay, 2007).

Experiments on reaching in dynamic force fields point towards the utilization of synergies as well (Malfait & Ostry, 2004; Shadmehr *et al.*, 1993; Yang *et al.*, 2007). In these experiments, subjects were asked to hold a robotic manipulandum and move the end effector in a plain, while allowing three joints to participate, making the system redundant. The robotic arm produced perturbations in the direction orthogonal to the end point trajectories. It was observed that with perturbations, the end point trajectory became curved, and the variability of end point increased as well. This pointed towards the fact the CNS was not adapted to moving the manipulandum in the force fields, and the participating synergies were still trying to move the end effector as if there was no force present. However, with practice, the errors reduced, pointing towards the flexibility amongst the elements to adapt to new forces.

The high redundancy in the human hand, added with its ability to perform a plethora of pressing, prehension and grasping tasks make it very attractive tool to study motor synergies. Kinematic studies on grasping have shown that static hand postures for mimed grasps can be described by a few basic postures (Mason *et al.*, 2001). Kinematic studies during reach to grasp task have shown synergies in the angular velocity profile of the MCP joint (Vinjamuri *et al.*, 2007). Only three different synergies were able to account for twenty eight different object grasps. Synergies during grasping are also known to be dependent on multisensory information – vision, audition, proprioception and even olfaction (Tubaldi *et al.*, 2008). Apart from the studies in which subjects were presented with a specific task, thus affecting the nature of synergies, a recent study

investigated the nature of hand synergies for an unconstrained haptic exploration task. The study found that most of the postures of the hand could be explained by seven basic postures.

Kinematic analysis of fingers in sequential tasks like typing has also revealed the presence of synergies in the time domain. Such synergies are also called temporal synergies. Subjects were asked to type lists of words, each word designed so that only one key would be pressed by a finger of one hand, the remaining letters being typed with the other hand. Changes in the lengths (flexion-extension) and orientation (abduction-adduction) of each finger were measured and the similarity of the motion of pairs of fingers was assessed by computing correlation coefficients. For each pair of fingers, the correlation coefficients were broadly distributed, but in most instances the mean was significantly greater than zero. Adjacent fingers showed a higher degree of correlation than did non-adjacent fingers. It was found that the fingers tended to move together most of the times, but were fairly capable of moving independently, if needed.

Analysis at the level of dynamics, both for pressing and prehension, has given further insights into the nature of synergies existing in human hand. Studies on the EMG activity of intrinsic and extrinsic muscles during force production in a precision grip have revealed the nature of muscle synergies both in spatial and temporal domains (Maier & Hepp-Reymond, 1995). It was found that synchronization was more frequent in pairs of muscles supplied by branches of the same peripheral nerve (46%) than in those innervated by different nerves (18%). Synergies in the amplitude domain were distributed in similar proportions across intrinsic, extrinsic, and combinations of both types of muscles, whereas synchronization mainly occurred in pairs of intrinsic muscles. Recent studies on EMG activity of the seven intrinsic muscles of the index finger in a tapping

task also points towards the presence of synergies among the muscles (Clewley et al., 2008).

Some of the earlier studies on multi-finger pressing pointed towards the presence of synergies. In particular, in one study, subjects were asked to produce ramp forces from zero to a level close to their maximal force (Li *et al.*, 1998b). They performed this task several times, and then variances of the total force and of individual finger forces were computed at the level close to peak force. In all subjects, the sum of the variances of individual finger forces was higher than the variance of the total force suggesting that fingers were not independent force generators. In another study subjects were asked to produce constant force with three fingers pressing in parallel, the index, the middle, and the ring finger (Latash *et al.*, 1998a). Then, they were asked to tap with one finger. During the first tap, the “tapping finger” lost contact with the sensor and stopped producing force. The other two fingers changed their forces out-of-phase with the tapping finger such that they compensated for close to 100% of the lost force.

Studies on lifting objects with unimanual and bimanual grasps with multi-digit grips have shown that the coordination of finger tip forces attempt to minimize fingertip forces while at the same time ensure that grasp stability is preserved (Flanagan *et al.*, 1999). Studies investigating finger forces in rectangular as well as circular object prehension have showed similar results as well (Shim *et al.*, 2004; Shim *et al.*, 2006). It was observed that individual finger forces were decoupled into two distinct groups: one group related to grasping stability control (normal force control) and the other group associated with rotational equilibrium control (tangential force control).

It is to be noted that most of the above studies used variability of individual elements to quantify synergies. However, some of the later studies further refined this

approach, by analyzing the components of variability in space, basing their analysis on the principle of abundance.

The Principle of Abundance

Some studies suggest that Bernstein's conception of change through the stages of learning is too narrow in its consideration of the degrees of freedom problem and the actual pathways of change evident in motor learning. It is shown that change in both the organization of the mechanical degrees of freedom and the dimension of the attractor dynamic organizing motor output can either increase or decrease, according to the confluence of constraints imposed on action (Newell & Vaillancourt, 2001).

Moving beyond Bernstein's original formulation, some investigators suggested that, within apparently redundant systems, all elements are always involved in solving a variety of motor tasks so that no degrees of freedom are eliminated (Gelfand *et al.*, 1963). The Uncontrolled Manifold hypothesis and the Optimal Feedback Control theory utilize this feature of redundancy (Latash *et al.*, 2002a; Scholz & Schoner, 1999; Todorov & Jordan, 2002). Redundancy in movement also allows for reduction of repetitiveness of individual muscle activities and thereby reduces fatigue and degenerative wear of organ components (Edelman & Gally, 2001; Tononi *et al.*, 1999). Alternatively, the CNS actually uses the “abundant” solutions available, each solution depending upon the momentary perturbations and external constraints. Thus, the CNS need not compute a unique solution for redundant degrees of freedom but entire families of solutions fulfilling the task requirements. This has also been referred to as the *principle of abundance* (Gelfand & Latash, 1998) as compared to motor redundancy. These families of solutions can be considered as task specific synergies amongst various elements (individual finger forces in the above example) at the neuromotor level. For the purpose

of this study, we *define synergies as the task specific covariation of individual elements of a system to achieve a common goal* (Li et al., 1998b).

The Uncontrolled Manifold (UCM) hypothesis is a mathematical tool to quantify the stability of a particular performance variable, which might be more important from the perspective of neural control than the other performance variables, when performing a specific task (Latash *et al.*, 2002b; Scholz *et al.*, 2002; Scholz & Schoner, 1999). According to the UCM approach, performing a task may be associated with selectively stabilizing some important task variables and the constituting elements of the system coordinate in such a manner that these important task variables are stabilized. The process may be viewed as selecting a lower dimensional vector sub space, within the state space of elements for each time instant. This manifold is such that the changes in the elements' state within the manifold have no effect on the performance variable. Thus, the elements can show higher variability within the manifold. Variability in the vector space orthogonal to the manifold will result in an error in task performance. Thus, for synergies to exist for a particular task, the variability within the manifold should be greater than the variability orthogonal to the manifold. By definition, orthogonal variability is the only component that affects variability of performance. So, a strong synergy may correspond to the same amount of orthogonal variability plus much more variability within the UCM, or a lower amount of orthogonal variability and the same amount of variability within the UCM. A separate manifold can be constructed for different performance variables which the CNS is hypothesized to be stabilizing. The amount of variability in the UCM can give an apt measure of the importance of that performance variable for the CNS.

Multi-finger force production is particularly attractive to test a hypothesis related to the coordination of multi-element systems because it is relatively easy to set different tasks and to record the outputs of individual elements (fingers). By manipulating the number of involved fingers and task constraints, one can also compare the system's performances when the number of constraints equals the number of fingers (a non-redundant system), and when the former number is smaller than the latter one (a redundant system). A number of studies have addressed the issue of finger coordination during pressing and grasping multi-finger tasks and showed that fingers can indeed compensate for each other's errors (Latash et al., 1998a; Li *et al.*, 1998a; Santello et al., 1998; Zhang *et al.*, 2006a).

The human hand has been commonly viewed as being controlled by (at least) a two-level hierarchy (Arbib, 1985). At the upper level of the hierarchy, the total force and the total moment of force produced on the hand-held object are distributed between the actions of the thumb and the virtual finger (VF, an imagined finger with the mechanical action equal to that of all the fingers of the hand (Arbib, 1985; Shim *et al.*, 2005c). At the lower level, the action of the VF is distributed among the four fingers of the hand.

Two important performance variables in pressing and prehension tasks are the total force being produced by the fingers and the total moments of forces about the longitudinal axis of the hand (called total moments from now on). Previous studies on kinetic redundancy of finger forces employing the UCM hypothesis have shown different results with respect to the stabilization of forces, depending upon the rate of change of force and the magnitude of the force (Latash *et al.*, 2001, 2002a; Scholz et al., 2002). It has been suggested that CNS is capable of utilizing the kinetic redundancy of multi-finger actions and stabilizing resultant force and/or resultant moment about the

longitudinal axis of the hand, during pressing tasks (Kang *et al.*, 2004; Shinohara *et al.*, 2004) as well as grasping tasks (Oliveira *et al.*, 2006; Shim, 2005; Shim *et al.*, 2004, 2005b), although these two performance variables require very different synergies, particularly if only two task fingers are involved. Some recent studies have shown that CNS is capable of simultaneously stabilizing both these performance variables in multi-finger pressing tasks, where the subjects were asked to produce time invariant, oscillating or ramp forces (Gorniak *et al.*, 2007; Latash *et al.*, 2005b). Specifically, subjects were given a visual feedback of total time varying resultant forces being produced by them in a multi finger pressing task. Surprisingly, despite the absence of any resultant moment feedback, the subjects stabilized the moments instead of forces for most part of the trials, thus suggesting that moment stabilizing synergies might be more important for the CNS in such tasks. This could be attributed to the fact that the CNS might be accustomed to day to day grasping tasks, which require a precise moment control, and normally such tasks employ all the four fingers. The subjects only stabilized the force and not the moments, when the force profile was time invariant (Latash *et al.*, 2002b; Slifkin & Newell, 1999) or quick force pulses were produced in a multi-finger pressing task (Goodman & Latash, 2006). Simultaneous stabilization of both the synergies in four finger pressing tasks, point towards the evidence of utilization of principle of abundance by the CNS. *However, so far, there have been no studies to investigate the relationship between the amount of kinetic redundancy and stabilization of total force and/or total moments in a multi finger pressing task.*

CHAPTER II

RESEARCH DESIGN

The purpose of the present study was to investigate the changes in force stabilizing and moment stabilizing synergies in a multi-finger pressing task. Kinetic degrees of freedom were manipulated by involving different number of fingers in the task (IM, IR, IL, MR, ML, RL, IMR, IML, IRL, MRL, IMRL; where I=Index finger, M=Middle finger, R=Ring finger, L=Little finger). Subjects were provided only with a visual feedback for the total forces being produced by them.

Since subjects were explicitly given a visual feedback of their performance for the force production task, strong force stabilizing synergies were expected (*Hypothesis 1*). Based on the principle of abundance, we hypothesized that the force stabilizing synergies would increase with the number of fingers (*Hypothesis 2*). Assuming that the precise moment stabilizing synergies are conditioned by everyday prehension experiences, we hypothesized that moment stabilizing synergies, if existing, would increase with the number of fingers, since all the four fingers are generally used for everyday prehension and manipulation tasks, which require a precise control of moments (*Hypothesis 3*). Also, if both the force and moment stabilizing synergies exist simultaneously, we hypothesized that those synergies would be more prominent when more fingers are involved in the task (*Hypothesis 4*). Such synergies would provide an evidence of principle of abundance in neural control of redundant motor systems.

Subjects

Twelve healthy volunteers (six males and six females), without any history of neurological disorders, participated in the experiments. All of them were right handed according to the criteria of Edinburgh test. The age of the subjects was 27 ± 4.3 years,

their weight was 64.2 ± 7 kg and their height was 1.69 ± 0.09 m. The right hand length was measured from the middle finger tip to the lunate of the wrist. The width was measured between the metacarpophalangeal (MCP) joints of the index and little fingers. The hand length was 18.2 ± 2.7 cm and the width was 8.2 ± 1.1 cm. All the subjects gave informed consent based on the procedures approved by the University of Maryland's Internal Review Board (IRB).

Experimental Setup

The experimental setup included four two-directional (tension and compression) force sensors (black rectangles in Fig. 1a) for four fingers (2nd–5th fingers) with amplifiers (Models 208 M182 and 484B, Piezotronics, Inc.). The sensors were supported by a customized aluminum frame (14.0x9.0x1.0 cm) along four slits. The slits allowed adjustments of the sensor positions along the longitudinal axis of fingers according to the individual hand and finger sizes of the subjects. Adjacent slits were separated medio-laterally by 20 mm. The frame was attached to a large aluminum panel (21.0x16.0x2.0 cm) with a vertical slit (14.0 cm), which allowed the frame two degrees of- freedom: one for vertical translation and the other for rotation about the z-axis. C-shaped aluminum thimbles were attached on the bottom of each sensor, and the subject rested pressed these thimbles, thus transmitting the forces to the sensors. The frame was tilted at 25° with respect to the anteroposterior axis (x-axis) such that all finger joints (distal inter-phalangeal, proximal inter-phalangeal, and MCP joints) were slightly flexed. The position was adjusted for individual subjects and, the frame was mechanically fixed to the panel using a nut–bolt structure. Signals from the sensors were conditioned, amplified, and digitized at 1,000 Hz with a 16-bit A/D board (PCI 6034E, National Instruments Corp.) and a custom software program made in LabVIEW (LabVIEW 7.1, National

Instruments Corp.). A desktop computer (Dimension 4700, Dell Inc.) with a 19 in. monitor was used for data acquisition. The task finger force applied on the sensors was displayed on the monitor screen online. MatLab (MatLAB 7, MathWorks, Inc.) programs were written for data processing and analysis.

Procedure

Subjects were asked to sit on a chair facing a computer screen, with the shoulder abducted 35° in the frontal plane and elbow flexed 45° in the sagittal plane such that the forearm was parallel to the aluminum frame (Figure 2.1 a). The forearm rested on the customized wrist-forearm brace (comprised of a piece of foam that was attached to a semi-circular plastic cylinder) fixed to a wooden panel (29.8 x8.8 x3.6 cm). Two Velcro straps, one near the wrist and other near the elbow, were used to avoid any wrist joint or forearm movements. The subjects were asked to rest the distal phalange of each finger in a thimble such that all joints were slightly flexed and formed a dome shape with the hand (Figure 2.1 b). The MCP joints were flexed at about 20° . In order to remove the gravitational effects of the fingers and any possible favor to finger flexion or extension due to passive stretching of the finger intrinsic and extrinsic muscles, the force signals for the initial 0.5 s were averaged for each finger and subtracted from the later signals. Thus, only the force signals due to active forces were shown on the computer monitor in real-time to the subjects.

Experiment 1-Maximum Voluntary Force

Subjects performed fifteen conditions of the MVF task in flexion: four conditions for single finger tasks(I, M, R and L), six for two finger tasks(IM,IR,IL,MR,ML and RL), four for three finger tasks (IMR,IML,IRL and MRL) and one for four finger task

(IMRL). One trial was performed for each condition, with a resting period of one minute between two conditions. The order of the conditions was balanced across subjects. No subject reported any fatigue. During each trial, all fingers were in the thimbles, and subjects were asked to produce maximum isometric force with a task finger(s) in flexion over a 3-s interval while watching the force feedback of the task finger(s) on the computer screen. The experimenter watched the subjects' right hand carefully for any joint movements. Trials with visible finger or wrist joint movements were rejected (~3% of the total number of trials) and performed again by the subjects. The subjects were instructed to concentrate on the task finger and not to pay attention to non-task fingers. However, they were instructed not to extend or lift any of the non task fingers from the sensors. The task finger/finger combination force produced was displayed on-line on the computer screen in front of the subject. At the beginning of each trial, the computer generated a 'get ready' sound, and the task finger force was shown graphically on the screen. The single finger MVF values were used to generate a linear estimate of finger Jacobians, giving the relation between changes in individual finger forces and in total force produced by all the involved fingers in a multi-finger task. The multi-finger MVF values were used to adjust the target force for constant flexion force task.

Experiment 2-Constant force production task

A target force line representing 0% of MVF for the first three seconds and 20% of MVF for the next twelve seconds for a particular subject was displayed on the computer screen. The summed force output of the task fingers was also shown with a different color. Subjects were asked to follow the target force lines. Following the 0% MVF line insured that the subjects were not applying any force initially. After hearing the beep from the computer, the subjects were asked to press the sensors with the force adequate

enough to trace the path of the MVF lines (Figure 2.1c). The subjects did not receive any information about the moments about the long axis of the hand. Twelve trials were done for each finger combination, with a resting period of one minute between each trial. No subject reported any fatigue.



Figure 2.1. Experimental Setting: (a) The experimental setting for the right hand: the wrists and the forearm of the subject were rested in a wrist-forearm brace and held by Velcro strap. The subject sat in a chair and watched the computer screen to perform a task. (b) The subject inserted the distal phalange of each finger in the thimbles. The sensor positions were adjusted along the aluminum frame.(c) Subjects were asked to follow the template shown on the computer screen (red line), and given a feedback of their performance (blue line).

Data Processing

For quantifying synergies, subsequent analysis was done under the framework of UCM hypothesis (Latash *et al.*, 2001; Schöner, 1995). When a voluntary command is given to produce force by the task finger, it leads to an involuntary force production by other fingers as well. This phenomenon is called finger force enslaving and can be written in the form of a 4x4 matrix $[E]$ for a four finger task (Shinohara *et al.*, 2003; Zatsiorsky *et al.*, 2000). The elements of the enslaving matrix were computed from regression analysis between finger forces during individual finger MVF tasks (Kang *et al.*, 2004). The diagonal and non-diagonal elements of the matrix were the task finger force changes and non-task finger force changes, normalized by the changes in total force of four fingers respectively. The four dimensional (i.e., four-finger) vector \mathbf{F} of mean free

finger force data was converted into finger force modes \mathbf{m} , the hypothetical commands by the CNS to the fingers to generate force (Danion *et al.*, 2003a; Danion *et al.*, 2003b) (Eq. 2). Thus, a four dimensional force mode space was generated for a four finger task, a three dimensional force mode space for a three finger tasks and a two dimensional force mode space for the two finger tasks.

$$\mathbf{m} = [\mathbf{E}]^{-1}\mathbf{F} \quad (1)$$

Change in performance variable ($d\mathbf{PV}$), expressed in terms of force modes can be written as (Eq. 2).

$$d\mathbf{PV} = [\mathbf{R}]^*[\mathbf{E}]^* \mathbf{m} \quad (2)$$

where the elements of 1x4 matrix $[\mathbf{R}]$ depends on the performance variable (PV): the elements are unity when the total force of four fingers is stabilized (“force stabilization hypothesis”) whereas the elements are the moment arms of each finger with respect to the functional longitudinal axis passing between the middle and the ring finger when the total moment of forces is stabilized (“moment stabilization hypothesis”). The functional longitudinal axis of the task fingers were located by taking half of the distance between the centers of the task finger sensors. Previous studies have shown that this approximation does not yield significantly different results from the calculating the instantaneous functional axis, because the lateral movements of the fingers on the sensors are negligibly small (Kang *et al.*, 2004; Zhang *et al.*, 2006a). The hypothesis was tested with respect to two performance variables, total force and total moment of finger forces. For a stable value of performance variable, $d\mathbf{PV} = 0$, and each manifold can be approximated linearly by the null space spanned by the basis vector \mathbf{e} (Eq. 3).

$$\mathbf{0} = [\mathbf{R}]^*[\mathbf{E}]^* \mathbf{e} \quad (3)$$

The total variance (V_{TOT}) at each time interval across all the trials was resolved into two components. The force mode vectors \mathbf{m} from each time interval was resolved into their projection on the null space, and perpendicular to it. The squared length of the deviation vector lying within the UCM per degree of freedom is called variability within the UCM (V_{UCM}). This component of total variability does not result in any change of the performance variable. The squared length of the deviation vector perpendicular to the UCM is called variability orthogonal (V_{ORTH}). This component of total variability resulted in the change of performance variable and is responsible for the errors. Since different subjects and tasks showed different magnitudes of variance, an index was computed by dividing the V_{UCM} by the dimension of UCM and normalized by the total variance per degree of freedom (Eq. 4).

$$\Delta V = [(V_{UCM}/(n-1) - V_{ORTH}/1)] / [(V_{UCM} + V_{ORTH})/n] \quad (4)$$

Where n = number of task fingers

The index ΔV has a normal distribution even for large differences between V_{UCM} and V_{ORTH} , in contrast to the ratio V_{UCM}/V_{ORTH} , which is not normal for low values of V_{ORTH} (Zhang et al., 2006b). Positive values of ΔV correspond to higher V_{UCM} than V_{ORTH} and would reflect the synergy between different force modes to stabilize a particular performance variable. On the other hand, negative values of ΔV would indicate the destabilization of the performance variable by the interactions between modes. A zero value of ΔV would represent no synergies at all. ΔV was calculated for force stabilization (ΔV_{force}) and moment stabilization (ΔV_{moment}) and was averaged between 5 to 8 seconds of the constant force production experiment and averaged across all twelve trials. This time was chosen in order to provide enough time to the subjects for adjusting to the task in the first 5 seconds, and preventing the change in control strategy among

fingers, which might occur due to the early lifting of fingers in anticipation of finishing the task (9-15 s in this case) (Shim et al, 2005).

Statistical Analysis

The changes in dependent variables with experimental conditions were analyzed using standard repeated measures ANOVA. Within factors of number of fingers with four levels (2f, 3f and 4f) were used with V_{UCM} , V_{ORTH} and ΔV as the dependent variables. The level of significance was set at 0.05 for all the comparisons. Data was checked for violation of sphericity across levels of a within subject factor. Pairwise comparisons were performed using the Bonferroni corrections, when needed.

CHAPTER III

RESULTS

For each finger combination, the subjects were able to follow the template without much difficulty. A typical performance for total task force in a single trial for IL, IRL and IMRL finger combinations is shown in figure 3.1 (a, b and c).

Typically, each subject deviated less from the template as the number of fingers increased and the output looked smoother. Numerical quantification of synergies was done using the Uncontrolled Manifold Analysis.

Uncontrolled Manifold Analysis (UCM)

A positive value of ΔV is associated with the presence of stronger synergies with respect to a particular performance variable, like the total force or the total moment of force. UCM analysis confirmed our first hypothesis that strong force stabilizing synergies would be present in the multi-finger pressing task we employed for this study. Figure 3.2 (a) and (b) show the values of ΔV_{force} for individual finger combinations and number of fingers involved, respectively. Although the values of ΔV_{force} were positive for all the multi finger combinations, the values significantly decreased from two finger to four finger combinations, thus suggesting stronger synergies for force stabilization in the two finger combinations. This is contrary to our second hypothesis, since we had expected ΔV_{force} to increase with the number of fingers. The results were supported by repeated measures ANOVA [F(2, 11), $p < 0.05 = 2.3$] with a significant effect of number of fingers. Pairwise comparisons revealed that ΔV_{force} for two finger combinations was significantly

greater than three finger combinations, and three finger combinations was significantly greater than the four finger combination.

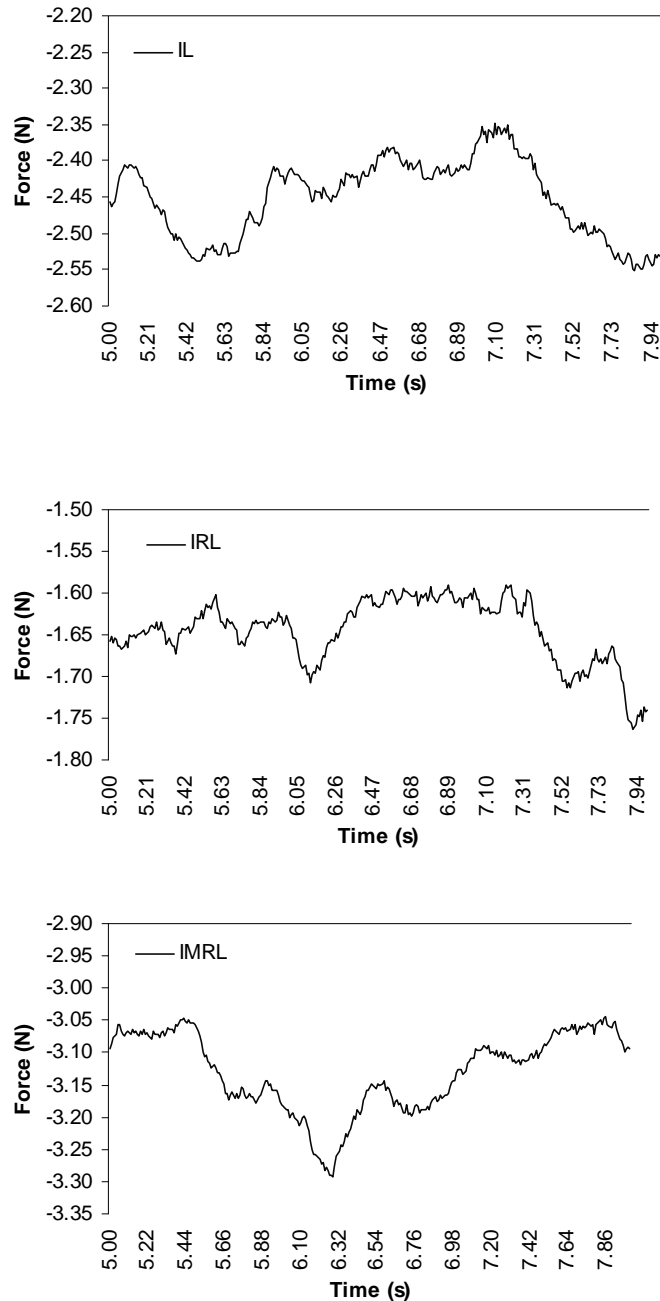


Figure 3.1 Profile for total force produced by the task fingers by a representative subject in a single trial. a. IL combination; b. IRL combination and c. IMRL combination. I, M, R, L stand for index, middle, ring and little fingers, respectively. Force profiles a are shown between 5-8 second interval.

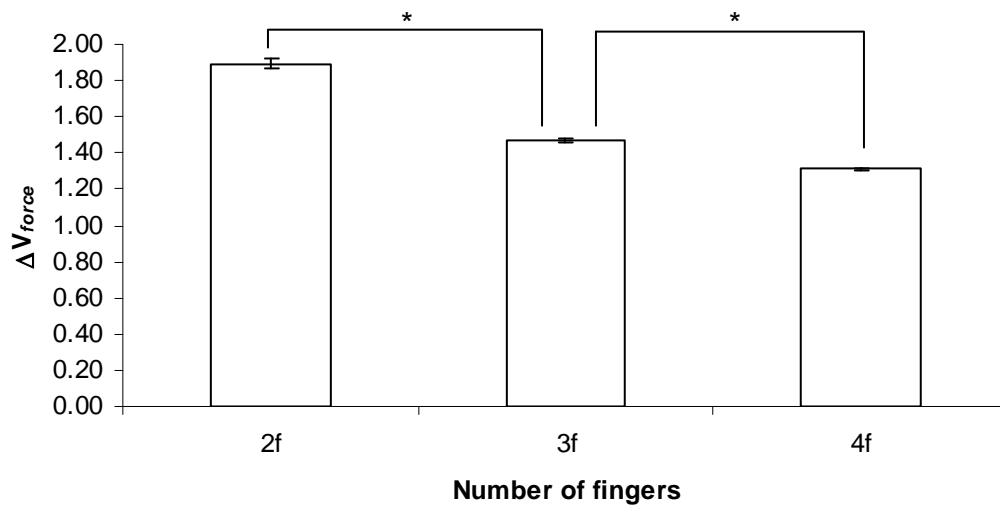
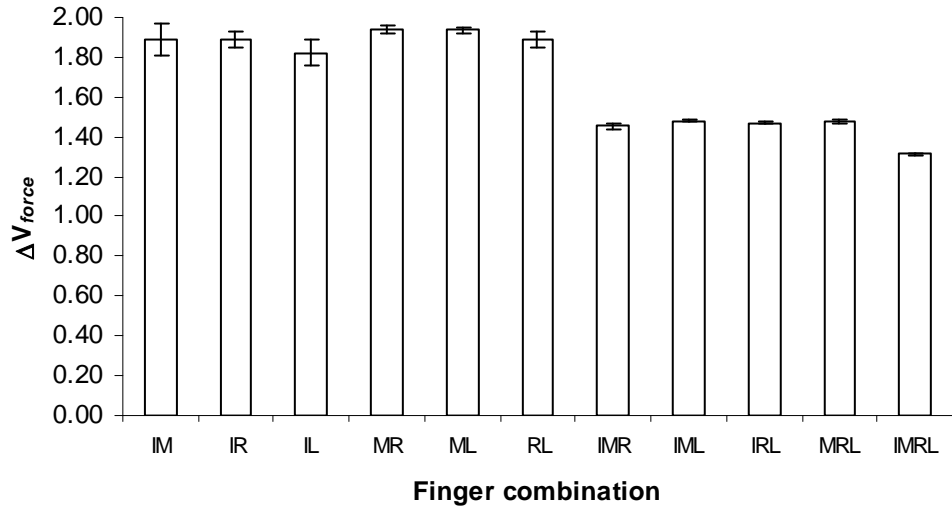


Figure 3.2 a. ΔV_{force} index computed for the total force for individual finger combinations; b. ΔV_{force} index averaged for two finger, three finger and four finger combinations respectively. I, M, R, L stand for index, middle, ring and little fingers, respectively. 2f, 3f and 4f stand for two finger, three finger and four finger combinations respectively. Means and standard errors are shown across 12 subjects. * $p < 0.05$.

Figure 3.3 (a) and (b) show the values of ΔV_{moment} for individual finger combinations and the number of fingers involved, respectively. The values of ΔV_{moment}

are negative for all the two finger combinations, nearly zero for three finger combinations and positive for the four finger combination. This suggests that there are no synergies for moment stabilization in the two finger combinations, very weak synergies or no synergies at all in the three finger combinations, while synergies controlling the total moments are present in the four finger combination. This supports our third hypothesis, since we expected that moment synergies, if present, would increase with the number of fingers. The results were supported by repeated measures ANOVA [$F_{[2, 11]} = 2.9, P < 0.01$], with a significant effect of number of fingers. Pairwise comparisons revealed that ΔV_{moment} for two finger combinations was significantly different than three finger and four finger combinations. It is to be noted that of all the three finger combinations, only the IMR finger combination has a positive ΔV_{moment} value comparable to the IMRL combination.

Analysis of components of ΔV_{force} showed a decrease in the variability within the UCM V_{UCM} from two finger combinations to four finger combinations [$F_{[2, 11]} = 2.79, P < 0.05$], with a significant effect of number of fingers. There was a corresponding significant decrease in the values of variability orthogonal to the UCM (V_{ORTH}) as well. These results are shown in Figure 3.4 (a) and (b) and Figure 3.5 (a) and (b).

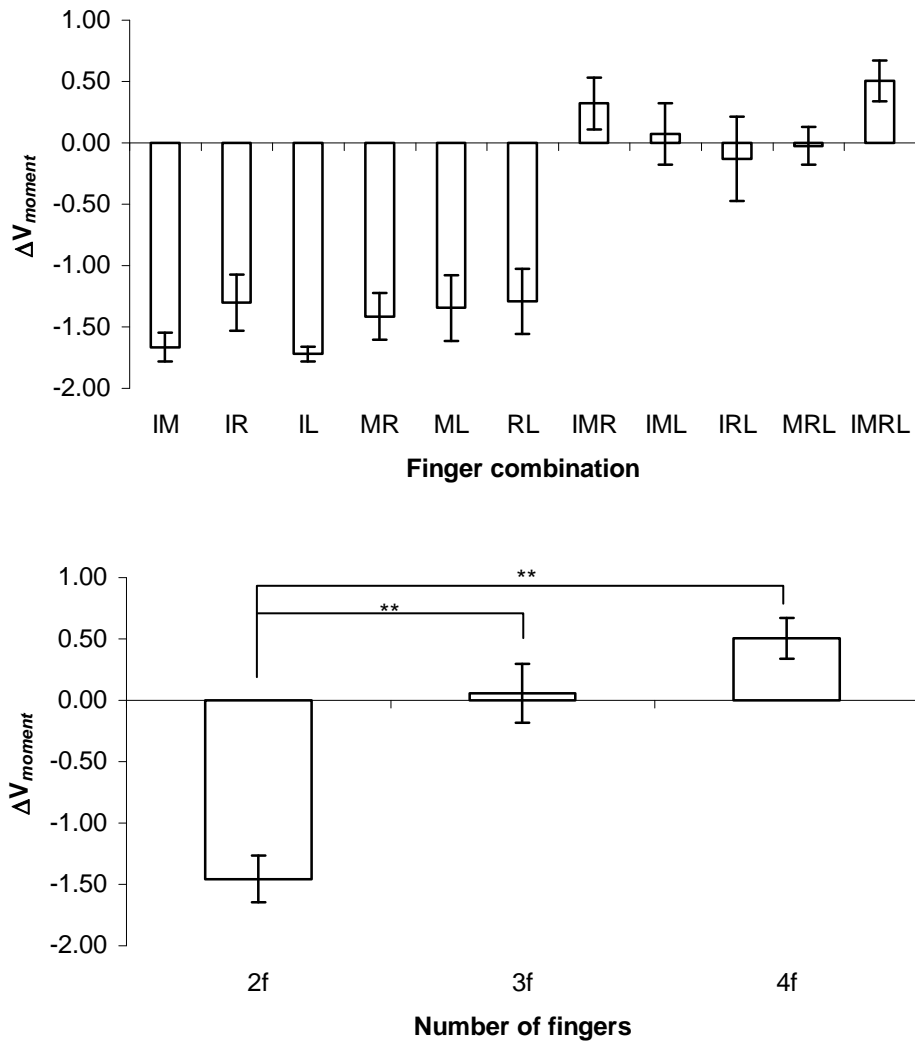


Figure 3.3 a. ΔV_{moment} index computed for the total force for individual finger combinations b. ΔV_{moment} index combined for two finger, three finger and four finger combinations respectively. I, M, R, L stand for index, middle, ring and little fingers, respectively. 2f, 3f and 4f stand for two finger, three finger and four finger combinations respectively. Means and standard errors are shown across 12 subjects. ** $p < 0.01$.

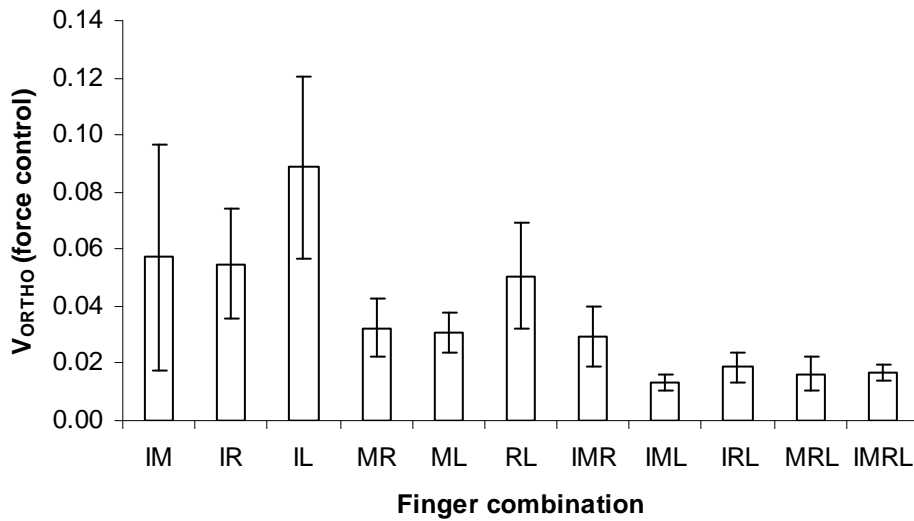
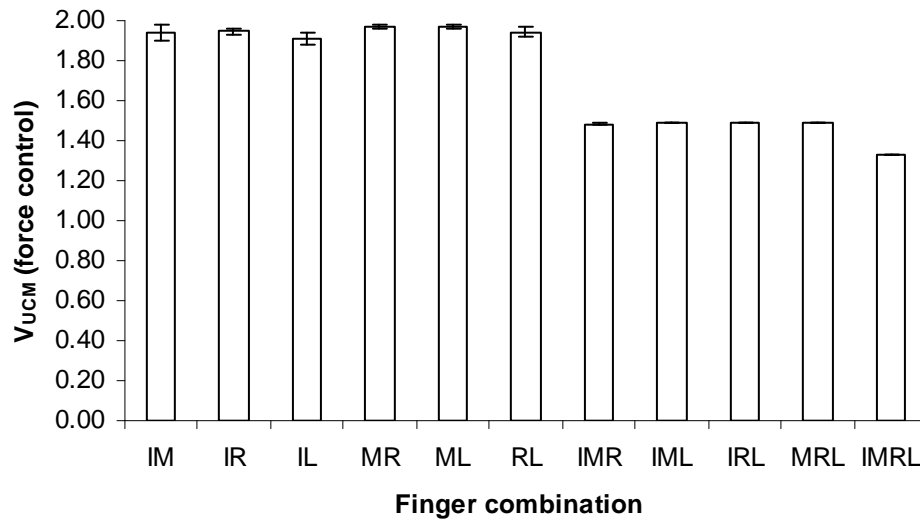


Figure 3.4 a. Components of the index ΔV_{force} a Variability within the UCM (V_{UCM}) for all the finger combinations; b. Variability orthogonal to the UCM (V_{ORTH}) for all the finger combinations. I, M, R, L stand for index, middle, ring and little fingers, respectively. Means and standard errors are shown for the data across 12 subjects.

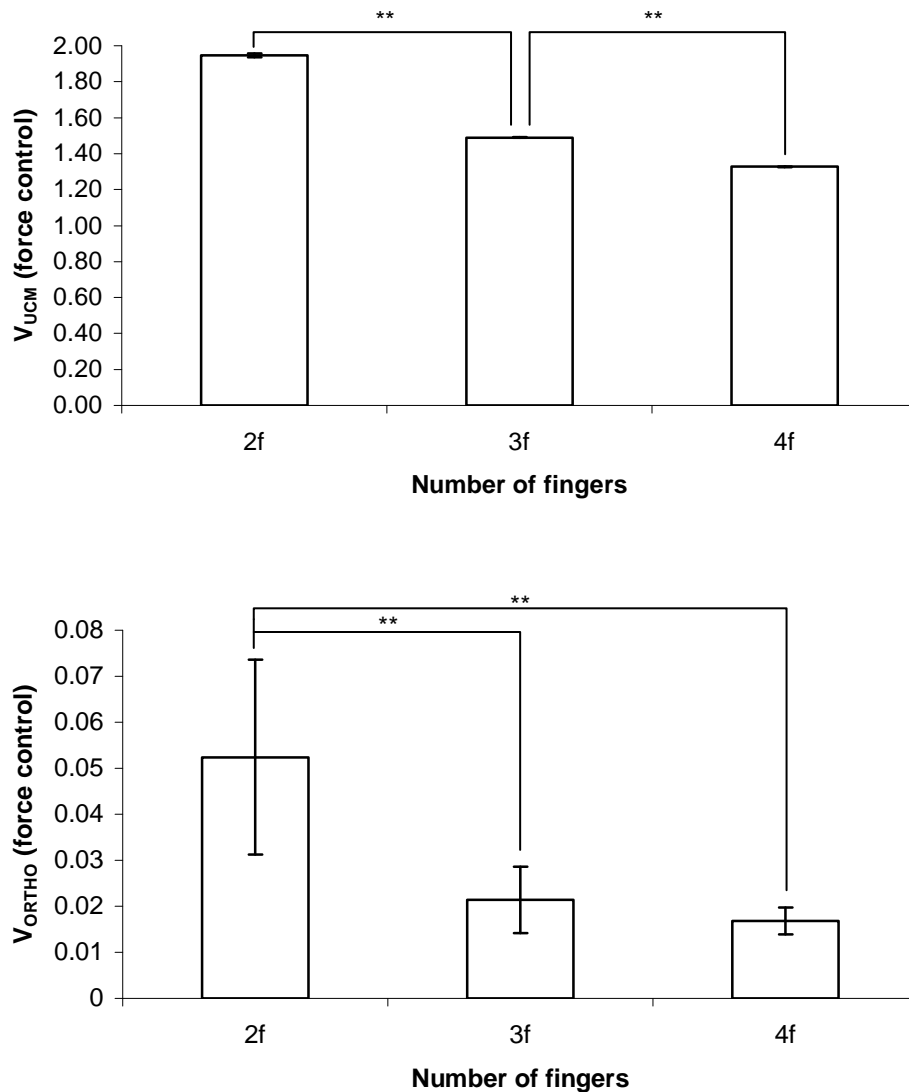


Figure 3.5 a. Components of the index ΔV_{force} a Variability within the UCM (V_{UCM}) for two, three and four finger combinations combined together; b. Variability orthogonal to the UCM (V_{ORTH}) for two, three and four finger combinations combined. 2f, 3f and 4f stand for two finger, three finger and four finger combinations respectively. Means and standard errors are shown for the data across 12 subjects. ** $p < 0.01$.

Interesting results emerged by analyzing the components of ΔV_{moment} . Although the V_{UCM} values for moment control hypothesis were positive for all the finger combinations, V_{ORTH} values were much higher for the two finger combinations, thus

yielding an overall negative value of ΔV_{moment} . The values of V_{ORTH} were the least for four finger combination, and the value of V_{UCM} was maximum for four finger combination. The results were supported by within factors ANOVA [$F_{[2,11]}=3.2$, $P < 0.05$ and $F_{[2,11]} = 3.6$, $P < 0.01$] and are shown in Figure 3.6 (a) and (b) and Figure 3.7 (a) and (b). It is to be noted that the order of magnitude of V_{ORTHO} for moment stabilization was the same as V_{UCM} , while it was ten times less in the case of force stabilization hypothesis. The results support our fourth hypothesis, that synergies would be more prominent when all the four fingers are utilized. It is to be noted, that although the force stabilization synergies decrease from two finger combinations to four finger combinations, there is a corresponding increase in the moment stabilization synergies as well. ΔV values for the four finger combination are positive for both the force stabilization and the moment stabilization hypothesis.

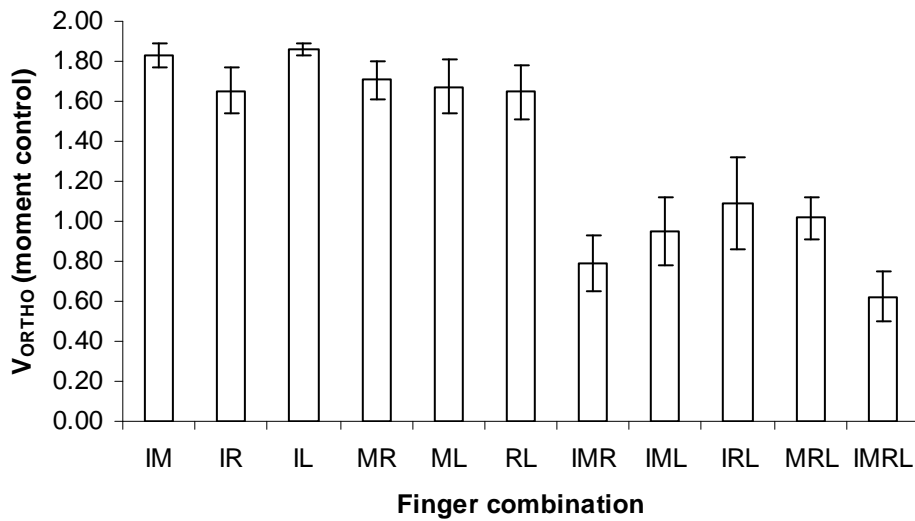
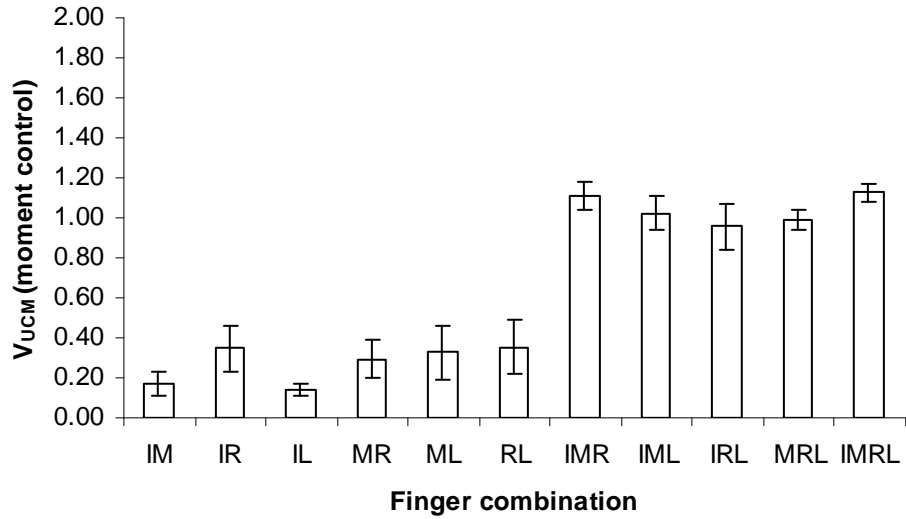


Figure 3.6 Components of the index ΔV_{moment} , computed for the moment stabilization hypothesis a. Variability within the UCM (V_{UCM}) for all the finger combinations; b. Variability orthogonal to the UCM (V_{ORTHO}) for all the finger combinations. . I, M, R, L stand for index, middle, ring and little fingers, respectively. Means and standard errors are shown for the data across 12 subjects.

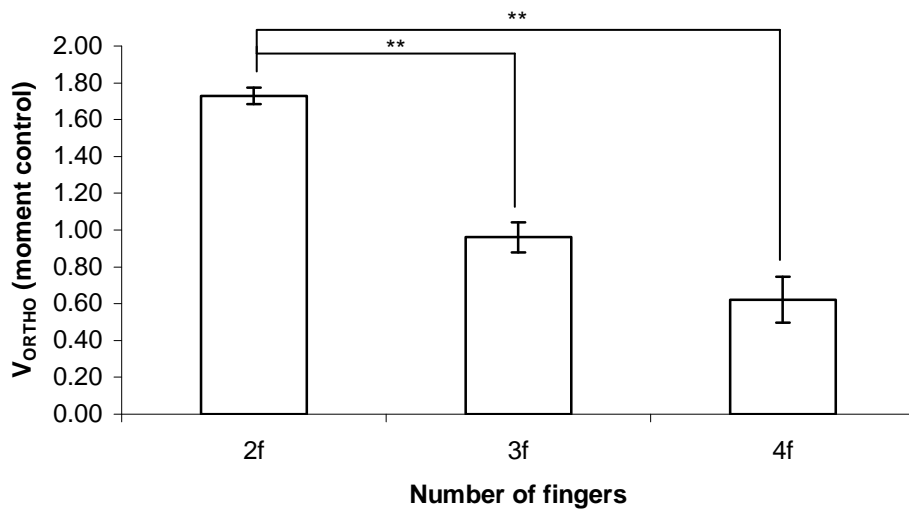
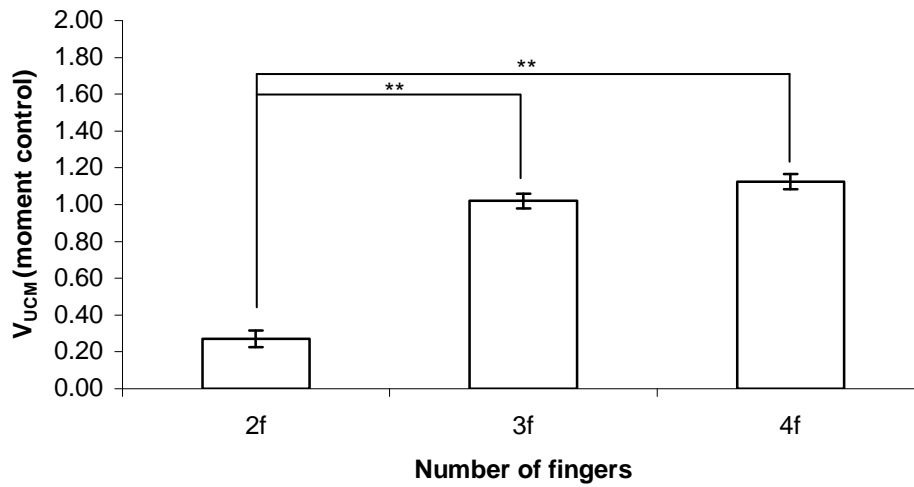


Figure 3.7 a. Components of the index ΔV_{moment} , computed for the moment stabilization hypothesis Variability within the UCM (V_{UCM}) for two, three and four finger combinations combined together; b Variability orthogonal to the UCM (V_{ORTH}) for two, three and four finger combinations combined. 2f, 3f and 4f stand for two finger, three finger and four finger combinations respectively. Means and standard errors are shown for the data across 12 subjects. ** $p < 0.01$.

CHAPTER IV

DISCUSSION

Effect of Number of Fingers on Total Force Stabilization

Results of this study indicated that for all the finger combinations, total force was stabilized. The distribution of the structure of variance of different finger combinations show that the stabilization of total pressing force was most effectively done in combinations involving two fingers i.e., the CNS ability to use flexible solutions (V_{UCM}) decreased with the increase in the number of fingers, for force stabilization hypothesis. It is noteworthy that orthogonal variability is the only component that affects variability of performance. So, a strong synergy may correspond to the same amount of orthogonal variability plus much more variability within the UCM. Notice that both components of variability had significantly higher values for the two finger combinations, than other multi-finger combinations. Thus, although there are greater synergies for the two fingers combination, looking at the error variability alone suggests that the other multi-finger combinations reduced the errors more efficiently. This decrease in the orthogonal component of variability is supported by some previous studies on steady-state tasks, in which a predominance of negative co-variation among finger forces produced by individual fingers was found (Shim et al., 2005c)

Some previous studies have found lower indices of force variability in multi-effector tasks simply because of the sharing of the total force among the effectors. In addition, in steady-state tasks, one could expect predominance of negative co-variation among finger forces produced by individual fingers (Latash et al., 2002a; Shim et al., 2005c). However, these studies did not consider the components of variability, nor did

they analyze the variability in the moment space. Stabilization of total force is contrary to the findings of some previous studies on oscillatory force production tasks, in which the subjects showed strong moment stabilization and force destabilization, even though they were not given any feedback of their performance on moment stabilization (Gorniak et al., 2007; Latash et al., 2001, 2002a).

Effect of Number of Fingers on Total Moment Stabilization

The values of ΔV_{moment} were found to be negative for two finger combinations, almost zero for three finger combinations and positive for the four finger combination. Analysis of the two components of variability revealed that a decrease in V_{UCM} for force stabilization resulted in a corresponding increase in V_{UCM} for the moment stabilization. Thus, we could not expect any moment synergies for the two finger combinations because force control and moment control are mutually exclusive for this case. However as the number of fingers increased, greater synergies with respect to moment stabilization were observed. This increase was due to the ability of CNS to use the flexible solutions (increase in V_{UCM}) as well as a better control of total moment as well (decrease in V_{ORTHO} with the number of fingers). It is noteworthy that the magnitude of variability orthogonal to the UCM decreased in this case as well, just like the force stabilization hypothesis.

Some previous studies have attributed a positive value of ΔV_{moment} to the fact that principle of minimization of secondary moments (Zatsiorsky *et al.*, 1998) is powerful enough to override explicit task demands (force stabilization in this case). According to this principle, total force is shared among the fingers such that the total moment with respect to the longitudinal axis of the forearm is minimal. This principle has been supported in a series of studies (Li et al., 1998b; Zatsiorsky & King, 1998; Zatsiorsky et

al., 2000), although its violations have also been reported (Danion et al., 2003b; Latash et al., 1998a). Our results seem to violate this principle as well, because for the two finger combination, subjects did not stabilize the moments at all.

Force and Moment Synergies in Two Finger Combinations

Two finger combination is a special case in terms of physical task constraints, because the force and moment stabilizing synergies are opposite to each other. A positive covariation among task fingers will result in stabilization of total moments, while a negative covariation would result in the stabilization of total force. Such a system has been call marginally redundant in previous studies (Latash et al., 2001).

Force stabilizing synergies were greater for two finger combinations than for the four finger combination. It is to be noted that the V_{ORTH} for the finger combinations involving the index finger in two finger combinations (IM, IR and IL) was higher than other combinations, while the V_{UCM} was the same for all the two finger combinations. This would imply that the CNS tries to stabilize the total force as efficiently as in the other two finger combinations, because a larger value of V_{UCM} implies more efficient control, but there is a greater error component in finger combinations involving the index finger. (Latash *et al.*, 2003). The reason for high values of V_{ORTHO} in two finger tasks involving index finger could be the use of index finger in all day to day activities (writing, holding a spoon etc), which compulsively require a precise moment control. It might be possible that the moment stabilization or stabilization of some other unknown variable at the behavioral level is more important for the CNS in tasks involving index finger, and hence there is a tradeoff between the task at hand (force stabilization) and the task which the CNS is used to performing more often (e.g. moment stabilization). For a two finger combination, force stabilizing synergies and moment stabilizing synergies are

mutually exclusive. Although the CNS is stabilizing the total force for all the two finger combinations, high values of V_{ORTH} in index finger combinations might be interpreted as the tendency of the CNS to stabilize total moments as well.

For all the two finger combinations in the moment stabilization hypothesis, the values of V_{UCM} were lower than V_{ORTHO} , thus resulting in a negative values of ΔV_{moment} . However, it is interesting to note that the positive V_{UCM} for force and moment stabilization hypothesis in case of two finger tasks suggest that the CNS tried to stabilize both of them simultaneously, but given the physical constraints, it could only stabilize the forces.

Evidence for the Principle of Abundance

Results of this study suggest that in all the finger combinations, the stabilization of total force was executed efficiently by the CNS. This is contrary to the findings of some previous studies on oscillatory force production tasks, in which the subjects showed strong moment stabilization and force destabilization, even though they were not given any feedback of their performance on moment stabilization (Latash et al, 2001). However, lesser synergies were found as the numbers of task fingers increased, thus suggesting that the principle of abundance might not be employed by the CNS for the given task. Analysis of moment stabilizing synergies however reveals a completely opposite picture. It seems that the subjects had a greater tendency to stabilize the moments, even though it was not explicitly demanded by the task. Increase in variability within the UCM and simultaneous decrease in variability orthogonal to it, with the number of fingers for the moment stabilization hypothesis clearly point towards the principle of abundance for the moment stabilization hypothesis. The choice of

performance variable at the behavioral level can depend on several factors, depending upon the task constraints as well as ecological bias, and the results of this study could be the consequence of any of those factors.

Factors Affecting the Choice of Performance Variable

For the four finger task, both, the moment and the force, were stabilized throughout the task period. This is consistent with the previous studies on ramp and oscillation tasks, as well as our recent study in which subjects performed the same task, but only with four fingers (Shim et al, in review). Stabilization of total forces in two finger tasks differs from the results of previous studies, and could be attributed to the fact that the oscillatory and ramp tasks require larger synergies between the fingers involved than the simple constant force production task. Moreover, previous studies have been conducted only on commonly used and more stable finger combinations (IM, IMR and IMRL) and how other uncommonly used finger combinations (ML, RL, IL, IRL etc) behave for ramp and oscillation tasks is a matter of further investigation. The anomaly, that moments are stabilized in four finger tasks can also be attributed to the fact that this combination is primarily used for normal day to day tasks like grasping or holding an object and these tasks require a precise moment control by the fingers with respect to the point of thumb contact. On the other hand, forces can vary between a wide range, above the slipping threshold and below the crushing force.

Synergies to stabilize a performance variable can broadly emerge at two hypothetical levels: by changing the force sharing pattern among the fingers called higher level synergies (Schöner, 1995), which may particularly change across trials in typical populations, like patients suffering with Down's syndrome (Scholz et al,2003) or by

covariation of forces between the fingers involved peripheral level synergies (Scholz et al, 2002). Also, peripheral level synergies can be hypothesized to occur in two ways. First, in which the increase in force of one finger results in the increase in force exerted by the other finger. This is also called the fork strategy and is well suited for moment control (Li et al, 1998a). The second strategy is co varying the forces of the different fingers in such a manner, that the output force remains the same. This is also called error compensation. In the steady force production task of this study, the CNS seems to employ the second strategy.

It has been shown before that the variability within UCM is affected by the rate of change of force production, as present in ramp and oscillation tasks (Latash et al, 2002). It has been suggested that at higher rates of force, error correction between task fingers involves a time delay that may be too long to allow an effective stabilization of total force. Thus, apart from the bias towards moment stabilization by the four finger combination, the rate of change of force also plays a role in the selection of the task variable to be stabilized.

The magnitude of force has also been found to affect the variance of total force. For higher magnitudes of forces, the component of variance orthogonal to the UCM increases, thus decreasing the stabilization of total force. In this study, low forces (20% of MVF) have been employed, so this factor does not come into play. The results of this study are consistent with previous studies performed in steady force production tasks (Silifkin and Newell 1999).

Recent studies on finger pressing tasks suggest that the presence of visual feedback, total time of force production and the magnitude of force are significant factors

affecting the variability of the task force. However, these factors were consistent in the present study across all the trials; hence they did not have any confounding effect.

Future Directions for This study

Decrease in force synergies with the increase in number of task fingers is an unexpected result. However, a corresponding increase in the moment stabilizing synergies account for the fact that total moments might be a more important performance variable at the behavioral level from the perspective of neural control. Analysis of components of variability within the UCM and orthogonal to it also suggests an anomalous behavior of tasks involving index finger. However, the systematic increase in moment stabilizing synergies with the number of fingers provides an evidence of principle of abundance for the moment stabilization hypothesis. Recent studies in which subjects were shown a time variant moment feedback have shown that subject stabilize moments for most part of the task(Zhang et al., 2006b, 2007). It would be interesting to see if any force stabilization occurs at all in a similar task when two finger combinations use and time invariant moments are used. Such a study would further clarify if the force stabilization results obtained for two finger combinations in the current study are due to task constraints, or if they occur as naturally as the moment synergies for four finger tasks.

The role of principle of minimization of secondary moments in a similar task needs to be investigated further for time varying tasks as well, in order to generalize the results. Also, it would be interesting to see if similar results can be found for more natural tasks like grasping. Most of the previous studies have been done on pressing tasks, and

the role of thumb and a mechanically different task demand in grasping with different number of digits might reveal some useful insights.

Some recent studies have explored multi-finger synergies in bimanual pressing tasks (Gornaik). Our recent study on similar tasks with children revealed significant amount of motor overflow from the contralateral to the ipsilateral limbs (Shim *et al*, 2008). Keeping in fact the interhemispheric transition of commands, it would be interesting to explore if the CNS employs a different control strategy for bimanual pressing tasks with systematically changing the degrees of freedom.

Another useful extension of this study could be the exploration of synergies in finger amputees. Previous studies have shown that the cortical plasticity an important role in the control of stump muscles after finger amputation (Reilly *et al.*, 2008). However, the effect of tactile feedback and remaining fingers on multi-finger synergies has not been studied, and can have useful implications in prosthetic design.

Conclusion

The results of this study support the principle of abundance with respect to the moment stabilization hypothesis, even though subjects were given a visual feedback of the forces they were asked to produce. We conclude that for a constant force production task, moment stabilization might be a more important variable from the perspective of neural control. There could be various factors favoring this control strategy, including task constraints, sensory feedback and principle of minimization of secondary moments. Further studies are needed to clarify the role of each of these factors on the choice of performance variable as well as the principle of abundance for multi-finger pressing tasks.

REFERENCES

- Allison, L. K., Kiemel, T., & Jeka, J. J. (2006). Multisensory reweighting of vision and touch is intact in healthy and fall-prone older adults. *Exp Brain Res*, 175(2), 342-352.
- Arbib, M. A. (1985). Brain theory and cooperative computation. *Hum Neurobiol*, 4(4), 201-218.
- Arshavskii Iu, I., Gel'fand, I. M., Deliagina, T. G., Orlovskii, G. N., Pavlova, G. A., Panchin Iu, V., et al. (1995). [principles controlling movement]. *Mol Biol (Mosk)*, 29(6), 1427-1435.
- Berkinblit, M. B., Gel'fand, I. M., & Fel'dman, A. G. (1986). [a model of control of the movement of the multiarticular extremity]. *Biofizika*, 31(1), 128-138.
- Bizzi, E., Mussa-Ivaldi, F. A., & Giszter, S. (1991). Computations underlying the execution of movement: A biological perspective. *Science*, 253(5017), 287-291.
- Bongaardt, R., Pickenhain, L., & Meijer, O. G. (2000). Bernstein's anti-reductionistic materialism: On the road towards a biology of activity (1965). *Motor Control*, 4(4), 377-406.
- Bulas, D. I., Stern, H. J., Rosenbaum, K. N., Fonda, J. A., Glass, R. B., & Tiffet, C. (1994). Variable prenatal appearance of osteogenesis imperfecta. *J Ultrasound Med*, 13(6), 419-427.
- Clewley, R. H., Guckenheimer, J. M., & Valero-Cuevas, F. J. (2008). Estimating effective degrees of freedom in motor systems. *IEEE Trans Biomed Eng*, 55(2), 430-442.
- Danion, F., Latash, M. L., & Li, S. (2003a). Finger interactions studied with transcranial magnetic stimulation during multi-finger force production tasks. *Clin Neurophysiol*, 114(8), 1445-1455.
- Danion, F., Schoner, G., Latash, M. L., Li, S., Scholz, J. P., & Zatsiorsky, V. M. (2003b). A mode hypothesis for finger interaction during multi-finger force-production tasks. *Biol Cybern*, 88(2), 91-98.
- Edelman, G. M., & Gally, J. A. (2001). Degeneracy and complexity in biological systems. *Proc Natl Acad Sci U S A*, 98(24), 13763-13768.
- Flanagan, J. R., Burstedt, M. K., & Johansson, R. S. (1999). Control of fingertip forces in multidigit manipulation. *J Neurophysiol*, 81(4), 1706-1717.
- Gelfand, I. M., Gurfinkel, V. S., IaM, K., Tsetlin, M. L., & Shik, M. L. (1963). [on the synchronization of motor units and its connection with the model representation.]. *Biofizika*, 8, 475-487.
- Gelfand, I. M., & Latash, M. L. (1998). On the problem of adequate language in motor control. *Motor Control*, 2(4), 306-313.
- Giszter, S. F., Mussa-Ivaldi, F. A., & Bizzi, E. (1993). Convergent force fields organized in the frog's spinal cord. *J Neurosci*, 13(2), 467-491.
- Goodman, S. R., & Latash, M. L. (2006). Feed-forward control of a redundant motor system. *Biol Cybern*, 95(3), 271-280.
- Gorniak, S. L., Zatsiorsky, V. M., & Latash, M. L. (2007). Hierarchies of synergies: An example of two-hand, multi-finger tasks. *Exp Brain Res*, 179(2), 167-180.

- Grillner, S., & Zangger, P. (1979). On the central generation of locomotion in the low spinal cat. *Exp Brain Res*, 34(2), 241-261.
- Hamed, S. B., Schieber, M. H., & Pouget, A. (2007). Decoding m1 neurons during multiple finger movements. *J Neurophysiol*, 98(1), 327-333.
- Heuer, H., Bruwer, M., & Wischmeyer, E. (1989). [additive hypotheses of the effect of head and eye movement on dark convergence]. *Z Exp Angew Psychol*, 36(3), 411-432.
- Hsu, W. L., Scholz, J. P., Schoner, G., Jeka, J. J., Kiemel, T., Scholz, J. P., et al. (2007). Control and estimation of posture during quiet stance depends on multijoint coordination
motor equivalent control of the center of mass in response to support surface perturbations. *J Neurophysiol*, 97(4), 3024-3035.
- Jeka, J. J., & Lackner, J. R. (1994). Fingertip contact influences human postural control. *Exp Brain Res*, 100(3), 495-502.
- Johannsen, L., Wing, A. M., & Hatzitaki, V. (2007). Effects of maintaining touch contact on predictive and reactive balance. *J Neurophysiol*, 97(4), 2686-2695.
- Kang, N., Shinohara, M., Zatsiorsky, V. M., & Latash, M. L. (2004). Learning multi-finger synergies: An uncontrolled manifold analysis. *Exp Brain Res*, 157(3), 336-350.
- Kelso, J. A., & Tuller, B. (1984). Converging evidence in support of common dynamical principles for speech and movement coordination. *Am J Physiol*, 246(6 Pt 2), R928-935.
- Lang, C. E., & Schieber, M. H. (2004). Human finger independence: Limitations due to passive mechanical coupling versus active neuromuscular control. *J Neurophysiol*, 92(5), 2802-2810.
- Latash, M. L., Danion, F., Scholz, J. F., Zatsiorsky, V. M., & Schoner, G. (2003). Approaches to analysis of handwriting as a task of coordinating a redundant motor system. *Hum Mov Sci*, 22(2), 153-171.
- Latash, M. L., Gelfand, I. M., Li, Z. M., & Zatsiorsky, V. M. (1998a). Changes in the force-sharing pattern induced by modifications of visual feedback during force production by a set of fingers. *Exp Brain Res*, 123(3), 255-262.
- Latash, M. L., Krishnamoorthy, V., Scholz, J. P., & Zatsiorsky, V. M. (2005a). Postural synergies and their development. *Neural Plast*, 12(2-3), 119-130; discussion 263-172.
- Latash, M. L., Li, Z. M., & Zatsiorsky, V. M. (1998b). A principle of error compensation studied within a task of force production by a redundant set of fingers. *Exp Brain Res*, 122(2), 131-138.
- Latash, M. L., Scholz, J. F., Danion, F., & Schoner, G. (2001). Structure of motor variability in marginally redundant multifinger force production tasks. *Exp Brain Res*, 141(2), 153-165.
- Latash, M. L., Scholz, J. F., Danion, F., & Schoner, G. (2002a). Finger coordination during discrete and oscillatory force production tasks. *Exp Brain Res*, 146(4), 419-432.
- Latash, M. L., Scholz, J. P., & Schoner, G. (2002b). Motor control strategies revealed in the structure of motor variability. *Exerc Sport Sci Rev*, 30(1), 26-31.
- Latash, M. L., Scholz, J. P., & Schoner, G. (2007). Toward a new theory of motor synergies. *Motor Control*, 11(3), 276-308.

- Latash, M. L., Shim, J. K., Smilga, A. V., & Zatsiorsky, V. M. (2005b). A central back-coupling hypothesis on the organization of motor synergies: A physical metaphor and a neural model. *Biol Cybern*, 92(3), 186-191.
- Li, Z. M., Latash, M. L., Newell, K. M., & Zatsiorsky, V. M. (1998a). Motor redundancy during maximal voluntary contraction in four-finger tasks. *Exp Brain Res*, 122(1), 71-78.
- Li, Z. M., Latash, M. L., & Zatsiorsky, V. M. (1998b). Force sharing among fingers as a model of the redundancy problem. *Exp Brain Res*, 119(3), 276-286.
- Loren, G. J., Shoemaker, S. D., Burkholder, T. J., Jacobson, M. D., Friden, J., & Lieber, R. L. (1996). Human wrist motors: Biomechanical design and application to tendon transfers. *J Biomech*, 29(3), 331-342.
- Macpherson, J. M., Rushmer, D. S., & Dunbar, D. C. (1986). Postural responses in the cat to unexpected rotations of the supporting surface: Evidence for a centrally generated synergic organization. *Exp Brain Res*, 62(1), 152-160.
- Maier, M. A., & Hepp-Reymond, M. C. (1995). Emg activation patterns during force production in precision grip. II. Muscular synergies in the spatial and temporal domain. *Exp Brain Res*, 103(1), 123-136.
- Malfait, N., & Ostry, D. J. (2004). Is interlimb transfer of force-field adaptation a cognitive response to the sudden introduction of load? *J Neurosci*, 24(37), 8084-8089.
- Marinelli, P. V. (1983). The asymmetric tonic neck reflex. Its presence and significance in the newborn. *Clin Pediatr (Phila)*, 22(8), 544-546.
- Mason, C. R., Gomez, J. E., & Ebner, T. J. (2001). Hand synergies during reach-to-grasp. *J Neurophysiol*, 86(6), 2896-2910.
- Moritz, C. T., Lucas, T. H., Perlmutter, S. I., & Fetz, E. E. (2007). Forelimb movements and muscle responses evoked by microstimulation of cervical spinal cord in sedated monkeys. *J Neurophysiol*, 97(1), 110-120.
- Mussa-Ivaldi, F. A., Giszter, S. F., & Bizzi, E. (1994). Linear combinations of primitives in vertebrate motor control. *Proc Natl Acad Sci U S A*, 91(16), 7534-7538.
- Newell, K. M., & Carlton, L. G. (1988). Force variability in isometric responses. *J Exp Psychol Hum Percept Perform*, 14(1), 37-44.
- Newell, K. M., & Vaillancourt, D. E. (2001). Dimensional change in motor learning. *Hum Mov Sci*, 20(4-5), 695-715.
- Oliveira, M. A., Shim, J. K., Loss, J. F., Petersen, R. D., & Clark, J. E. (2006). Effect of kinetic redundancy on hand digit control in children with dcd. *Neurosci Lett*, 410(1), 42-46.
- Reilly, K. T., Schieber, M. H., & McNulty, P. A. (2008). Selectivity of voluntary finger flexion during ischemic nerve block of the hand. *Exp Brain Res*.
- Richardson, A. G., Slotine, J. J., Bizzi, E., & Tresch, M. C. (2005). Intrinsic musculoskeletal properties stabilize wiping movements in the spinalized frog. *J Neurosci*, 25(12), 3181-3191.
- Santello, M., Flanders, M., & Soechting, J. F. (1998). Postural hand synergies for tool use. *J Neurosci*, 18(23), 10105-10115.
- Scholz, J. P., Danion, F., Latash, M. L., & Schoner, G. (2002). Understanding finger coordination through analysis of the structure of force variability. *Biol Cybern*, 86(1), 29-39.
- Scholz, J. P., & Schoner, G. (1999). The uncontrolled manifold concept: Identifying control variables for a functional task. *Exp Brain Res*, 126(3), 289-306.

- Scholz, J. P., Schoner, G., & Latash, M. L. (2000). Identifying the control structure of multijoint coordination during pistol shooting. *Exp Brain Res*, 135(3), 382-404.
- Schöner, G. (1995). Recent developments and problems in human movement science and their conceptual implications. *Ecological Psychology*, 7(4), 291-314.
- Schoner, G., & Kelso, J. A. (1988). Dynamic pattern generation in behavioral and neural systems. *Science*, 239(4847), 1513-1520.
- Shadmehr, R., Mussa-Ivaldi, F. A., & Bizzi, E. (1993). Postural force fields of the human arm and their role in generating multijoint movements. *J Neurosci*, 13(1), 45-62.
- Shapkov Iu, T., & Shapkova, E. (1998). [spinal locomotor generators in humans: Problems in assessing effectiveness of stimulations]. *Med Tekh*(4), 24-27.
- Shik, M. L., Orlovskii, G. N., & Severin, F. V. (1966). [organization of locomotor synergism]. *Biofizika*, 11(5), 879-886.
- Shim, J. K. (2005). *Rotational equilibrium control in multi-digit human prehension*. The Pennsylvania State University, University Park.
- Shim, J. K., Latash, M. L., & Zatsiorsky, V. M. (2004). Prehension synergies in three dimensions. *J Neurophysiol*, 93, 766-776.
- Shim, J. K., Latash, M. L., & Zatsiorsky, V. M. (2005a). Prehension synergies: Trial-to-trial variability and principle of superposition during static prehension in three dimensions. *J Neurophysiol*, 93(6), 3649-3658.
- Shim, J. K., Latash, M. L., & Zatsiorsky, V. M. (2005b). Prehension synergies: Trial-to-trial variability and principle of superposition during static prehension in three dimensions. *J Neurophysiol*, 93(6), 3649-3658.
- Shim, J. K., Olafsdottir, H., Zatsiorsky, V. M., & Latash, M. L. (2005c). The emergence and disappearance of multi-digit synergies during force-production tasks. *Exp Brain Res*, 164(2), 260-270.
- Shim, J. K., Oliveira, M. A., Hsu, J., Huang, J., Park, J., & Clark, J. E. (2006). Hand digit control in children: Age-related changes in hand digit force interactions during maximum flexion and extension force production tasks. *Exp Brain Res*.
- Shinohara, M., Li, S., Kang, N., Zatsiorsky, V. M., & Latash, M. L. (2003). Effects of age and gender on finger coordination in mvc and submaximal force-matching tasks. *J Appl Physiol*, 94(1), 259-270.
- Shinohara, M., Scholz, J. P., Zatsiorsky, V. M., & Latash, M. L. (2004). Finger interaction during accurate multi-finger force production tasks in young and elderly persons. *Exp Brain Res*, 156(3), 282-292.
- Slifkin, A. B., & Newell, K. M. (1999). Noise, information transmission, and force variability. *J Exp Psychol Hum Percept Perform*, 25(3), 837-851.
- Smith, J. L., Hoy, M. G., Koshland, G. F., Phillips, D. M., & Zernicke, R. F. (1985). Intralimb coordination of the paw-shake response: A novel mixed synergy. *J Neurophysiol*, 54(5), 1271-1281.
- Ting, L. H., & McKay, J. L. (2007). Neuromechanics of muscle synergies for posture and movement. *Curr Opin Neurobiol*, 17(6), 622-628.
- Todorov, E., & Jordan, M. I. (2002). Optimal feedback control as a theory of motor coordination. *Nat Neurosci*, 5(11), 1226-1235.
- Tononi, G., Sporns, O., & Edelman, G. M. (1999). Measures of degeneracy and redundancy in biological networks. *Proc Natl Acad Sci U S A*, 96(6), 3257-3262.
- Torres-Oviedo, G., Macpherson, J. M., & Ting, L. H. (2006). Muscle synergy organization is robust across a variety of postural perturbations. *J Neurophysiol*, 96(3), 1530-1546.

- Torres-Oviedo, G., & Ting, L. H. (2007). Muscle synergies characterizing human postural responses. *J Neurophysiol*, 98(4), 2144-2156.
- Tubaldi, F., Ansuini, C., Tirindelli, R., & Castiello, U. (2008). The grasping side of odours. *PLoS ONE*, 3(3), e1795.
- Tubiana, R. (1981). [about the surgical treatment of fractures of the metacarpals and phalanges (author's transl)]. *Ann Chir*, 35(9 Pt 2), 757-758.
- Tubiana, R. (1986). Injuries to the digital extensors. *Hand Clin*, 2(1), 149-156.
- Turvey, M. T. (1990). Coordination. *Am Psychol*, 45(8), 938-953.
- Vinjamuri, R., Mao, Z. H., Sclabassi, R., & Sun, M. (2007). Time-varying synergies in velocity profiles of finger joints of the hand during reach and grasp. *Conf Proc IEEE Eng Med Biol Soc, 2007*, 4846-4849.
- von Schroeder, H. P., Botte, M. J., & Gellman, H. (1990). Anatomy of the juncturae tendinum of the hand. *J Hand Surg [Am]*, 15(4), 595-602.
- Wang, J., & Stelmach, G. E. (1998). Coordination among the body segments during reach-to-grasp action involving the trunk. *Exp Brain Res*, 123(3), 346-350.
- Winters, J., Stark, L., & Seif-Naraghi, A. H. (1988). An analysis of the sources of musculoskeletal system impedance. *J Biomech*, 21(12), 1011-1025.
- Yang, J. F., Scholz, J. P., & Latash, M. L. (2007). The role of kinematic redundancy in adaptation of reaching. *Exp Brain Res*, 176(1), 54-69.
- Ye, H., Morton, D. W., & Chiel, H. J. (2006). Neuromechanics of coordination during swallowing in *aplysia californica*. *J Neurosci*, 26(5), 1470-1485.
- Zatsiorsky, V. M., & King, D. L. (1998). An algorithm for determining gravity line location from posturographic recordings. *J Biomech*, 31(2), 161-164.
- Zatsiorsky, V. M., Li, Z. M., & Latash, M. L. (1998). Coordinated force production in multi-finger tasks: Finger interaction and neural network modeling. *Biol Cybern*, 79(2), 139-150.
- Zatsiorsky, V. M., Li, Z. M., & Latash, M. L. (2000). Enslaving effects in multi-finger force production. *Exp Brain Res*, 131(2), 187-195.
- Zhang, W., Sainburg, R. L., Zatsiorsky, V. M., & Latash, M. L. (2006a). Hand dominance and multi-finger synergies. *Neurosci Lett*, 409(3), 200-204.
- Zhang, W., Zatsiorsky, V. M., & Latash, M. L. (2006b). Accurate production of time-varying patterns of the moment of force in multi-finger tasks. *Exp Brain Res*, 175(1), 68-82.
- Zhang, W., Zatsiorsky, V. M., & Latash, M. L. (2007). Finger synergies during multi-finger cyclic production of moment of force. *Exp Brain Res*, 177(2), 243-254.