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STABILITY OF MULTI-FINGER ACTION IN DIFFERENT STATE SPACES

A Thesis in

Kinesiology

by

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ABSTRACT

This thesis investigates the task-specific stability of action by the human hand during isometric accurate force production tasks. These tasks were performed using different numbers of instructed fingers, a subset of which were subjected to transient spatial perturbations. Subjects utilized visual feedback to produce a constant target force with index, index and middle, index, middle, and ring, and all four fingers; after reaching this target force, the visual feedback was removed and the subjects were instructed “do not interfere” while their index fingers (and, in some conditions, ring fingers) were perturbed by the “inverse piano” apparatus. Results were analyzed in the space of finger forces as well as hypothetical finger commands (modes), which reflect the inter-dependence of force production by each digit (enslaving). The main results were: (1) Inter-trial variance during steady states, in the space of modes and forces, was higher in directions which did not affect total force production (within the uncontrolled manifold or UCM); (2) Perturbations resulted in large deviations of finger forces and modes within the UCM (i.e. large motor equivalent, or ME, displacements were observed); (3) Deviations in forces and modes resulting from the perturbation showed larger variances within the UCM. Strikingly, no significant effect of the number of fingers involved was seen for any condition, including the single-finger condition, despite the apparent differences in system redundancy in each condition. Together, these results suggest that *all* tasks carried out with the whole hand are effectively four-finger tasks with only quantitative differences in the involvement of instructed and non-instructed fingers. Additionally, high volatility of enslaving was observed as a result of transient perturbations, which led to significantly higher enslaving in certain conditions. These results are considered in the framework of the UCM hypothesis and control with hierarchically organized referent body configurations which ensure task-specific stability of the system by means of synergic interactions.

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LIST OF ABBREVIATIONS AND SYMBOLS

CNS	central nervous system
DIP	distal interphalangeal joint
DoF	degree(s) of freedom
E	enslaving matrix (4×4)
EN	index of enslaving
EP	equilibrium point
F	magnitude of force
F	force vector (4×1)
FDP	flexor digitorum profundus
FDS	flexor digitorum superficialis
I	index finger
L	little finger
M	middle finger
m	mode vector (1×4)
MCP	metacarpophalangeal joint
ME	motor equivalent
MVC	maximum voluntary contraction
N	newtons
nME	non-motor equivalent
PIP	proximal interphalangeal joint
R	ring finger
RC	referent configuration

ROM	range of motion
TSR	tonic stretch reflex
UCM	uncontrolled manifold
V_{UCM}	inter-trial variance within the uncontrolled manifold
V_{ORT}	inter-trial variance orthogonal to the uncontrolled manifold
ΔV	index of synergy
λ	activation threshold of the tonic stretch reflex

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CHAPTER 1

Introduction

1.1 Problem Statement

In recent studies, stability of actions by abundant sets of elements has been explored using three main approaches. First, analysis of the structure of inter-trial variance during multiple repetitions of a given task assumes that each trial begins from a slightly different internal state, and that variance along less stable directions will be larger. This approach has been developed within the framework of the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999). Within this analysis, inter-trial variance in the space of elemental variables is partitioned into two components: variance within the UCM (V_{UCM}), which does not affect a task-specific performance variable, and variance orthogonal to the UCM (V_{ORT}), which does affect the performance variable. Task-specific stability can be characterized by an inequality $V_{UCM} > V_{ORT}$.

Second, if a small, transient perturbation is applied during the execution of a steady-state task, inter-trial variance of the difference in elemental variables between initial and final conditions is expected to be larger in directions of relatively low stability. As such, perturbations are expected - and have been experimentally shown - to lead to a higher inter-trial variance in elemental variables along directions that kept the task-related salient performance variable unchanged (Wilhelm et al. 2013) than in directions that led to changes in that variable.

Third, net displacements between an initial and final steady state caused by a transient perturbation may be analyzed. These displacements are expected to be large in directions within the corresponding UCM (addressed as motor equivalent, ME; Mattos et al. 2011). While there is no obligatory connection between the three methods, they may be expected to lead to consistent results reflecting task-specific stability of the system. To our knowledge, so far, no study has used all three methods applied to a single data set.

The present study was primarily motivated by an earlier experiment (Wilhelm et al. 2013) that used the “inverse piano” device (Martin et al. 2011; also see Methods) to produce a transient perturbation of a finger during accurate four-finger force production tasks. That study explored the structure of inter-trial variance in the finger force changes induced by the perturbation and showed that most variance was within the UCM. Here we used this method across tasks with different numbers of explicitly involved fingers (one, two, three, and four) in the spaces of both finger forces and hypothetical finger *modes* (Zatsiorsky et al. 1998; Latash et al. 2001; Danion et al. 2003). A finger mode is a hypothetical neural command to a finger that leads to force changes in all the fingers of the hand due to the phenomenon of enslaving (Kilbreath and Gandevia 1994; Schieber 2001; Zatsiorsky et al. 1998). We used all three aforementioned methods to quantify indices of task-specific stability. Increasing the number of instructed fingers for tasks with only one task-specific performance variable (total force) affords the system more ways to vary without affecting the task performance, while varying the number of fingers involved affects the redundancy of the task, or degrees of freedom (DoF) available to the motor system.

1.2 Goals of the Study

There are two main contrasts to be made in this study: the first is between a theoretically non-redundant system and a redundant one. The second is between redundant systems with different numbers of elements and consequently different degrees of redundancy. The specific hypotheses relating to each of these contrasts were formulated:

1.2.1 Contrasting Redundant and Non-Redundant Systems

1. Both before and after application of a transient perturbation, total force would be stabilized ($V_{UCM} > V_{ORT}$) between steady states in the redundant state spaces (finger forces in one- and two-finger tasks; finger modes in the two-finger tasks), but not in the non-redundant state space of finger modes during the one-finger task.
2. When an instructed finger was perturbed, total force would also be stabilized ($V_{UCM} > V_{ORT}$) for *changes* between pre- and post-perturbation steady states only in redundant state spaces.
3. When a non-instructed finger was perturbed, no particular structure of variance was expected in either one- or two-finger tasks in mode space, while $V_{UCM} > V_{ORT}$ was expected in force space. This is because the modes for non-instructed fingers are, by definition, zero – so perturbations to these zero modes are not expected to affect other modes.

1.2.2 Contrasting Systems with Different Levels of Redundancy

4. The signature of inter-trial indices of variance $V_{UCM} > V_{ORT}$ at steady states would hold for all redundant systems; the difference between V_{UCM} and V_{ORT} would increase as the number of elements explicitly involved in the system increased.
5. The signature of inter-trial indices of variance $V_{UCM} > V_{ORT}$ in the *differences* between initial and final steady states would hold for all redundant systems; the difference between V_{UCM} and V_{ORT} would increase as the number of elements explicitly involved in the system increased.
6. The ME component of system displacement would increase as the number of elements explicitly involved in the system increased.

1.3 Related Publications

The procedures and data in this thesis have been described in two journal articles. The contrast between redundant and non-redundant systems is published in *Journal of Neurophysiology* 112 under the title “Stability of Multi-Finger Action in Different State Spaces” by Sasha Reschechtko, Vladimir M. Zatsiorsky, and Mark L. Latash. The investigation into different degrees of redundancy is published in *Journal of Motor Behavior* under the title “Task-Specific Stability of Multi-Finger Steady-State Actions” by Sasha Reschechtko, Vladimir M. Zatsiorsky, and Mark L. Latash.

CHAPTER 2

Literature Review

2.1 Motor Redundancy

Since the conception of the field – and arguably even before – a fundamental problem in motor control has been that of *redundancy*. Formulated by Bernstein (1967), the problem arises in typical motor tasks because, at any level at which we choose to describe the system which brings movement production to fruition, the number of elements which can contribute to this movement (and their outputs, *elemental variables*) is larger than the number of constraints imposed upon the movement to be produced. As such, positing a scheme by which a given motor task is actualized in any single particular way (as it must be when an action is performed) becomes difficult.

A classical approach to this problem held that the central nervous system (CNS) eliminated the redundant degrees of freedom (DoF) available at the elemental level and thereby rendered motor tasks *non-redundant*, at which point the problem of redundancy should cease to exist. This approach has been criticized, however, because the elimination of redundant DoF is generally attributed to physiologically unfeasible control schemes which require complex calculations carried out at a central level and explicit instruction to all body structures to be involved in the action. Additionally, this approach is susceptible to a difficulty of infinite regress: the problem of redundancy is applicable at *all* levels of description of the motor system, potentially ranging from whole-body involvement to recruitment of individual motor units. While the elimination of DoF may be psychologically feasible at a macroscopic level (for example, choosing the limb with which to perform a task), it becomes increasingly unfeasible as the level of description becomes more microscopic, resulting in a huge increase in the number of potentially involved (and redundant) DoF, for example defining a combination of synaptic inputs to a neuron corresponding to its desired frequency of generation of action potentials.

One response to these difficulties has been to take a cue from robotic control and ascribe certain computational *optimization* principles to neural controllers (reviewed in Prilutsky & Zatsiorsky 2002). By assuming that the controller uses some optimality criteria for choosing between apparently redundant solutions, this scheme poses a means for the system to avoid a problem of motor redundancy without explicitly deciding upon a reduction of DoF. Despite a lack of agreement regarding the optimization criteria which the motor system may use, this approach continues to be popular in the field. Recent developments of optimal control theory include optimal feedback control (Todorov & Jordan 2002). A related approach, Analytical Inverse Optimization (ANIO, Terekhov et al 2010; Niu et al 2011) has been proposed to determine an optimality function which can model data recorded, thereby requiring fewer assumptions to be made by the experimenters.

Optimization approaches have yielded some criteria which nicely model certain observed behavior – particularly in activities in which the applicable cost functions seem relatively straightforward, like energetic efficiency at various gaits and preferred gait parameters at various speeds (Anderson & Pandy 2001; Kuo 2001). While many of these insights are valuable and have inspired productive research, the notion of the motor system as an optimal controller has been criticized for being *physiologically* unclear. Even when costs appear straightforward, additional concerns may arise in certain situations (cf. stability in inclined walking: Hunter et al.

2010), which serve to complicate the matter of deciphering a particular set of optimality criteria for a given task. Further, as movements produced by the motor system become more "trivial" – have less obvious associated costs – the choice of optimality criterion to investigate seems to become more arbitrary and the position that the motor system has access to metrics of such costs becomes more tenuous. Choosing optimization criteria for the motor system in the endeavor of *motor control* (rather than description of motor behavior) still requires the basic assumption that the motor system is actually an optimal controller, and it is not at all obvious what kinds of observations ought to be taken as evidence for this hypothesis, since the notion of optimal control is not necessarily specific enough to generate consistently testable and falsifiable hypotheses (Diedrichsen et al. 2010). The feasibility of such a control paradigm residing in a biological system (especially as a lone control paradigm) is, at least, controversial and in need of further elucidation.

In contrast to the optimality approach, the problem of motor redundancy has been recontextualized as a “principle of motor *abundance*” (Gelfand & Latash, 1998; Latash 2012). In contrast to the previously described approaches, the principle of motor abundance provides a means by which the CNS can take advantage of the full array of DoF at its disposal in order to ensure the stability of the motor actions which it directs. When the principle of motor abundance is integrated with the notion of hierarchical control of motor actions (Latash 2010), the CNS is conceptualized as only setting a relatively small number of neural variables corresponding to task constraints. From these few neural variables, it is envisioned that a series of few-to-many mappings engages relevant structures in the periphery to carry out the task specified. In contrast to the classical model of DoF reduction, these few-to-many mappings engage relevant DoF by means of interactions with the external environment rather than any particular explicit specification by a controller.

2.2 The Equilibrium Point Hypothesis

At first blush, the motor system seems ill-suited for the array of tasks it accomplishes. The muscles exhibit force- and velocity-dependent force-generation characteristics which, if the motor system were wholly envisioned as a conventional servo controller, would make them nearly impossible to control predictably without perfect knowledge of the instantaneous state of each muscle. In addition, muscles contract in response to neuronal activity, but neurons are threshold units: they can only encode “instructions” by means of changing their rate of firing. The finely coordinated movements of the human body, which belie well graded changes in force production, appear to be at odds with the control mechanisms available to the human motor system.

A proposed mechanism for control by threshold elements like neurons, the equilibrium-point (EP) hypothesis proposes that the basic variable controlled in the motor system is the threshold length for activation of the tonic stretch reflex (TSR). TSR is a reflex mechanism which leads to a dependence of a muscle’s active force on its length. When a muscle lengthens, length-sensitive muscle spindle endings within the muscle increase their firing rate; these impulses travel to the alpha-motoneuronal pool via an unknown loop, likely polysynaptic, which innervates the muscle whose length is increasing. As a result, the muscle’s activation level and resistance to this lengthening are increased.

According to the EP-hypothesis, the threshold length of the TSR for a given muscle (λ) is the control variable which the central nervous system encodes. The TSR has the effect of holding

a given muscle's force dependence on its length relatively invariant. Since the body is always subject to interactions with external forces (due to at least the mass of the body in the gravitational field of Earth), specifying a length at which a muscle's active force production is equal to external forces and is in an *equilibrium state*, where it is held by the external forces and TSR working in concert. By changing λ , then, the CNS can specify the length of a muscle given the external forces which it experiences.

Figure 1 illustrates the characteristic force/length relationship resulting from the TSR with the curved lines originating from λ_1 and λ_2 on the x-axis. At an initial state, the “equilibrium point” EP_1 , the force produced by the muscle given TSR at a given muscle length and λ combination (L_1, λ_1) is equal to a certain load. This force equilibrium, $F_{\text{muscle}}(L_1, \lambda_1) = F_{\text{load}}$ lends its name to the equilibrium point. When the CNS shifts the coordinate of the TSR threshold along the x-axis from λ_1 to λ_2 , the characteristic force/length relationship of the muscle does not change (that is: the shapes of the lines from λ_1 and λ_2 are the same), but the amount of force produced at a given length does change. As such, a new equilibrium point, EP_2 is established where $F_{\text{muscle}}(L_2, \lambda_2) = F_{\text{load}}$. Note that, while $F_{\text{muscle}}(L_1, \lambda_1)$ and $F_{\text{muscle}}(L_2, \lambda_2)$ are equal (to F_{load}), the lengths L_1 and L_2 are not equal, nor are TSR threshold lengths λ_1 and λ_2 . As such, when the CNS moves the TSR threshold from λ_1 to λ_2 , this has the effect of changing muscle length if the external forces stay constant. A change in λ can, therefore, effectively change the configuration of the body by changing muscle length. Similarly, if F_{load} is altered and λ_1 remains constant, the muscle will lengthen until $F_{\text{muscle}}(L_3, \lambda_1) = F_{\text{load}2}$.

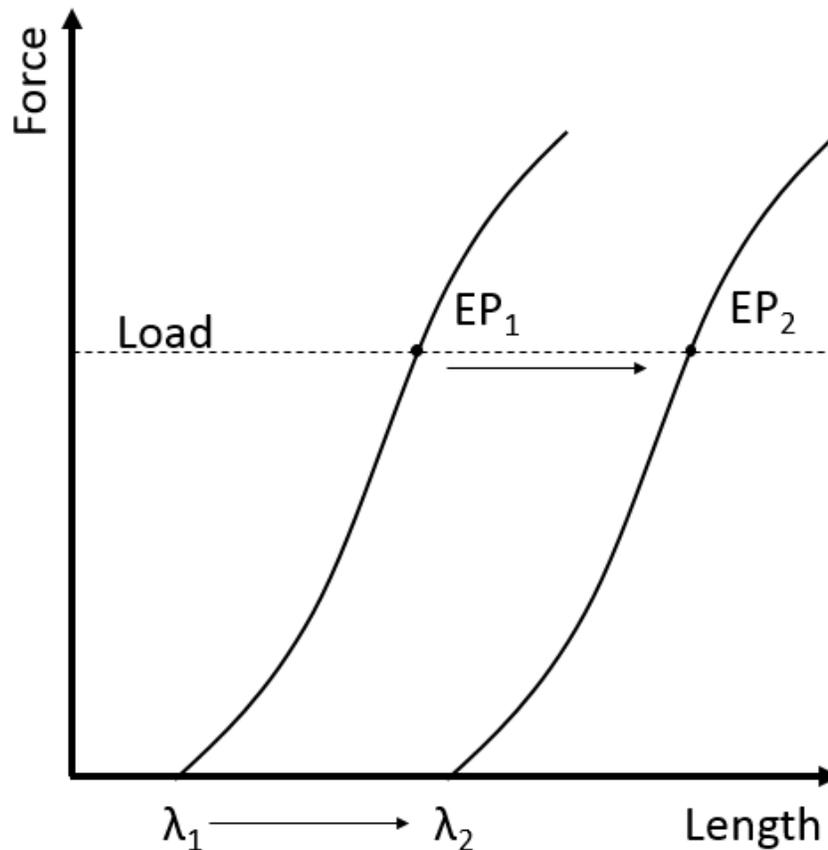


Figure 1: The effect of shifting the activation threshold of the TSR, λ , under constant external force. Muscle length is shown on the x-axis and muscle force due to TSR is on the y-axis.

2.3 Referent Configurations and Equifinality

The Referent Configuration (RC) Hypothesis (Feldman 2009) can be viewed as a generalization of the EP hypothesis from a single muscle up to an arbitrarily large muscle-actuated system engaged in intentional movement. The RC hypothesis conceptualizes the aforementioned high-level neural variables set by the motor system as relating to referent body configurations which are task-specific (RC_{TASK}). The few-to-many mappings lead to other RCs at lower levels, down to that of individual alpha-motoneuronal pools, where the relevant RC is equivalent to the threshold of the tonic stretch reflex, as in Feldman's lambda-model (1986).

Since actualization of the RC will lead either to movement toward the RC or force production (if movement toward the RC is blocked), both movement and force production are outcomes of the same neural processes. As such, the RC hypothesis predicts that, so long as the RC is held constant (the subject of this experiment is instructed "not to interfere voluntarily with effects of perturbations"), a system will come back to its initial state after being subject to a *transient* force perturbation. This tendency to return to the initial state upon conclusion of the perturbation is called *equifinality*. A large body of work in the field motor control has sought to strengthen RC hypothesis by observing equifinality (Bizzi et al. 1976; Kelso & Holt 1980; Latash & Gottlieb 1990; Schmidt & McGown 1980) or disprove it by observing violations of equifinality (in a centrifuge DiZio & Lackner 1995; Lackner & DiZio 1994, or velocity-dependent "negative damping" forcefield in Hinder & Milner 2003). A recent group studies (Ambike et al 2014a; Ambike et al 2014b; Wilhelm et al 2013; Zhou et al 2014b), including this one, have observed systematic violations of equifinality that point toward the utility of an addition to the RC Hypothesis according to the notion of "RC back-coupling," (Reschechtko et al 2014; more in Discussion) a phenomenon in which the Referent Configuration seems to move toward the body's actual configuration.

2.4 The UCM Hypothesis, Synergies, and Task-Specific Stability

When an investigator chooses a level of analysis for his or her experimental observations of the human motor system during task performance, the potential for contribution of elemental variables (the outputs of the elements relevant at the chosen level of analysis) to the task variable(s) is specified. When the motor task investigated is redundant, this process can be thought of as the projection of a high-dimensional space (of elemental variables) onto the lower dimensional *task* space (of output variables). A natural result of this dimension reduction is that the changes in elemental variables will lead to more or less change in the task variable depending upon where they occur in the high-dimensional task space. In particular, for a given point in the task space, there will be a *family* of combinations of elemental variables which result in the same magnitude(s) of task variable(s).

The Uncontrolled Manifold (UCM) Hypothesis (Sholz & Schöner 1999) is a formalization of this fact. For an N -dimensional space of elemental variables and a P -dimensional space of task constraints such that $P < N$, the family of values which elemental variables can take without resulting in a change in the task space will be a hypersurface – or *manifold* – of the dimension of $(N - P)$. Whenever the values of elemental variables contemporaneously fall on this surface, task performance is preserved. However, note that the position of the motor system is only *partially* specified by this constraint: while the elemental variables must lie along the UCM to ensure perfect performance, they may lie anywhere on this

surface. As such, the system is free to vary *along* the UCM: in directions which *do not* affect task performance. In this sense, the motor system does not need to “control” elemental variables within the UCM, thereby lending this particular manifold its “uncontrolled” moniker. *Figure 2* illustrates a two-element force-production system which is maintaining total force at two levels: 10N, the solution manifold of which is UCM₁, and 8N, with relevant solution manifold UCM₂.

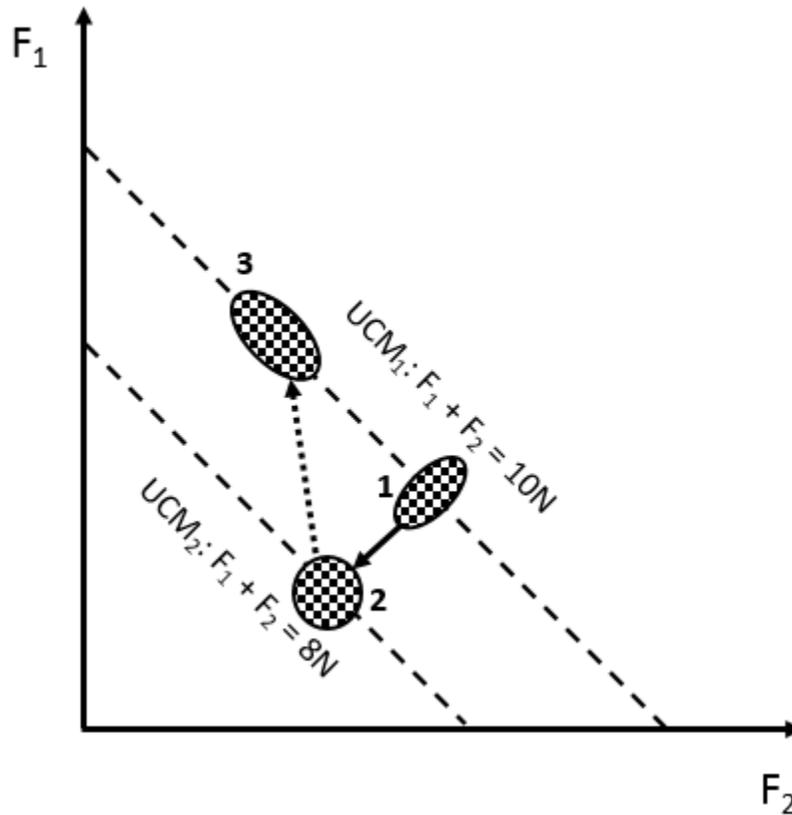


Figure 2: A two-element system and relevant UCMs at 10N and 8N. The ellipses at points 1, 2, and 3 represent various possible distributions of inter-trial variance ($V_{ORT} > V_{UCM}$, $V_{UCM} = V_{ORT}$, and $V_{UCM} > V_{ORT}$ respectively). The arrow between ellipses 1 and 2 is a path between UCM₁ and UCM₂ with only nME displacement, whereas the arrow between 2 and 3 has both ME and nME displacement.

The UCM hypothesis is primarily used to partition the inter-trial variability of the motor system according to whether it is in directions which affect or do not affect the task. Since variance in directions orthogonal to the UCM (this subspace orthogonal to the UCM is subsequently referred to as ORT, and variance within it is V_{ORT}) is incompatible with perfect task performance, it is possible that the motor system would tolerate less variance in this direction than it would tolerate within the UCM (variance within the UCM is V_{UCM}). Reasonably expecting *stability* to be reflected in reduction in inter-trial variance, when a system exhibits *task-specific stability* (Schöner 1995), it is *preferentially* stable in directions which do affect the task as compared to directions which do not affect the task. This relation can also be described with the inequality of inter-trial variance $V_{UCM} > V_{ORT}$. A third term, *synergy*, is unhelpfully ascribed various meanings in other contexts. Clinically, “synergy” often refers to stereotypical muscle activation patterns which interfere with voluntary movement which are often

symptomatic of stroke (Bobath 1978; DeWald et al. 1995). In motor control, “synergy” is most commonly used to describe a group of variables which scale together over the execution of a task across variations in that task’s parameters (d’Avela et al. 2003; Ivaneko et al. 2004; Ting & Mcpherson 2005; Tresch & Jarc 2009). In this case, however, the term “synergy” is used to describe a system in which the elements co-vary so as to preserve task variable; this result goes hand-in-hand with the $V_{UCM} > V_{ORT}$ variance signature. The ellipses in *Figure 2* illustrate possible synergic (3) and non-synergic (1 and 2) distributions of inter-trial variance with respect to the task of accurate total force production.

Recently, another metric has been used to describe a potential consequence of task-specific stability (Mattos et al, 2011). The notion of *motor equivalent* (ME) displacement refers to the resultant of the movement of a system on the UCM (ME) and in the ORT direction(s) (non-motor equivalent; nME) between predefined epochs during a single trial. Since ME and nME are defined as differences in the state of the system between two time points, ME is a displacement rather than a path length. While large ME displacement is a potential outcome of task-specific stability and certainly compatible with $V_{UCM} > V_{ORT}$, it is not the case that the $ME > nME$ is a necessary consequence of the synergic variance signature; indeed, the ME/nME and V_{UCM}/V_{ORT} are not directly related. *Figure 2* illustrates this fact by showing a no particular relationship between inter-trial variance at points 1, 2, and 3, and the direction of the displacement vector between points 1 and 2 and points 2 and 3. It should be explicitly noted that V_{ORT} and V_{UCM} are inter-trial measurements, while ME and nME system displacements may be computed for a single trial.

In the experiment described in this thesis, the space of elemental variables is considered four-dimensional in force space, and usually considered four-dimensional in mode space as well, although lower dimensionality was considered in preliminary investigation), while the task space is one-dimensional (total force output). As such, the UCM subspace is three-dimensional and its orthogonal complement, ORT, is one-dimensional.

2.5 The Human Hand

Compared to the entire human body, or even a single upper limb, the human hand provides a convenient model in which to explore redundant motor action. While the hand is responsible for many complex actions, in isometric force production tasks like those presented here it provides a system with only limited redundancy. In isometric tasks, the hand can basically be thought of as a parallel chain of four effectors: the index, middle, ring, and little fingers. Increasing the complexity of the system, however, is the fact that each finger is itself a serial chain of three segments, and each finger is articulated by means of multiple muscles which reside within and outside of the hand. The following sections describe the anatomy of the human hand as well as considerations which must be made when investigating finger force production as a result of these anatomical (and additional neural) features.

2.5.1 Anatomy of the Human Hand

This subsection is divided according to the skeletal, muscular, and neural anatomical properties of the human hand.

2.5.1.1 Skeletal Anatomy of the Hand

There are 29 bones in the forearm, wrist, and fingers of the human hand.

The distal aspects of the radius and ulna, as well as the eight carpal bones (two rows of four bones) form the wrist. The wrist permits movement in two planes: flexion/extension (range of motion: 70°-90° of flexion and 65°-85° of extension) and abduction/adduction (15°-25°/25°-45° respectively). Both of these movements occur between the distal aspect of the radius and the proximal row of carpal bones.

Each finger has three joints. From proximal to distal these joints are the: metacarpalphalangeal (MCP), proximal interphalangeal (PIP), and distal interphalangeal (DIP) joints. The MCPs allow movement in two planes: flexion/extension (85°-100°/0-40° respectively) and abduction/adduction. As MCP joints deviate from neutral position in one plane of motion, their range of motion (ROM) in the other plane of motion decreases (Schultz et al 1987). In contrast to the two planes of motion afforded by the MCPs, the PIPs and DIPs can only flex and extend plane; PIPs can move from full extension to 90°-120° of flexion while DIPs can move from full extension to 80°-90° of flexion.

The thumb, being irrelevant to the studies presented here, is omitted from this description. The preceding information is summarized from Napier (1980).

2.5.1.2 Musculature of the Hand

The muscles of the hand are classified according to their function and where they are located. *Extrinsic* muscles originate outside of the hand and insert inside of it; *intrinsic* muscles originate and insert within the hand. While the intrinsic muscles are responsible for precise movements of fingers, the extrinsic muscles produce the more powerful, gross movements (Freivalds, 2004).

The extrinsic muscles of the hand can be differentiated according to anterior and posterior musculature. The anterior muscles are finger flexors and the posterior muscles are finger extensors. The experimental task presented here explicitly concerns finger flexion only. The extrinsic flexors are flexor digitorum profundus (FDP) and flexor digitorum superficialis (FDS). The muscle bellies of FDP and FDS do not reside in the hand but rather insert into the digits by means of long tendons; this method of connection reduces the bulk of the hand. FDP tendons are connected to the distal phalanges and can be used to flex the fingers without loading, while FDS tendons insert into the medial phalanges and are generally recruited for tasks which require additional force production. Additionally, the FDP is composed of two divisions: radial and ulnar. Disregarding the thumb, the index finger is the most independent of the four fingers; some of the independence of the index finger can be attributed to the fact that the radial FDP connects only to it, while the ulnar division of the FDP connects to the middle, ring, and little fingers.

The intrinsic muscles of the hand are grouped topologically according to the digits they move: thenar muscles for extension, ab- and adduction of the thumb; hypothenar for little finger flexion and adduction; and midpalmar muscles for MCP flexion and ab- and adduction. Each of these groups is composed of multiple muscles for each individual digit.

2.5.1.3 Innervation and Sensation of the Hand

Specialized receptors reside in skin, muscle, tendons, and joints can transduce mechanical stimuli into neural signals. A single hand has approximately 17,000 cutaneous mechanoreceptors (Vallbo & Johansson, 1984). Additional receptors in the tendons, muscles, and joints contribute to proprioception. The task which subjects performed in the presented experiment are largely in isometric conditions, so it is expected that cutaneous and tendon receptors (golgi tendon organs) – encoding skin deformation and muscle loading, loading, respectively – were most active during steady-state tasks, while muscle spindle fibers and joint receptors – transducing muscle length and joint rotation – may have been more active during perturbations while the digits were actually moving.

2.5.2 Considerations Regarding the Interdependence of Finger Forces

It is well known that, when a finger of the hand produces force intentionally, the other fingers of the hand also produce some (unintended) amount of force. This phenomenon of interdependence of finger forces is called *enslaving* (Li et al. 1998; Zatsiorsky et al. 2000). Enslaving results from the anatomy of the human hand: shared musculature, as well as friction between connective tissues, is partially responsible for this unintentional force production. In addition, there are neural reasons for enslaving: the cortical representation of the digits are not completely differentiated.

While enslaving has been shown to change over long time periods with training (Slobonov et al. 2002), healthy aging (Shinohara et al. 2003, 2004), and with onset of neurological disorder (Park et al. 2012), enslaving has generally been assumed to be stable over short periods of time. Based upon this assumption, a definition of *finger modes* (Zatsiorsky et al. 2008; Danion et al. 2003) was introduced to present a hypothetical elemental variable which reflects the motor system's *intended* finger force recruitment, rather than the actual peripheral output of the system which reflects enslaving. Analyses in this thesis are carried in two elemental state spaces, finger forces and finger modes, and some of the results cast doubt upon the robustness of finger modes in perturbation tasks.

CHAPTER 3

Methodology

3.1 Subjects

Eight self-reported right-handed subjects were recruited for this study. Subjects' ages ranged from 23-36 years; they included four men and four women. Subjects were healthy, had no history of hand injury, and did not participate professionally in activities likely to significantly alter their dexterity. All subjects provided informed consent in accordance with procedures approved by the Office of Research Protections at The Pennsylvania State University.

3.2 Apparatus

Data were recorded and perturbations were applied by means of the "inverse piano" apparatus (Martin et al. 2011). This custom-built piece of equipment uses four PCB 208C01 single-axis piezoelectric force transducers (PCB Piezotronics, Depew, NY) to record finger forces from four fingers. The force sensors are mounted on individual Linmot PS01-23×80 linear actuators (Linmot, Spreitenbach, Switzerland) and are controlled by a Linmot E400AT four-channel servo drive such that each sensor can move vertically with a finger during experimental procedures. Force data were sent from each transducer to its respective PCB 484B11 signal conditioner (one per sensor); the analog data were then digitized at 300 Hz using a 16-bit PCI-6052E analog-to-digital card (National Instruments Corp., Austin, Tx). Before each trial, sensor readings were zeroed while the subjects' fingers rested on the sensors, ensuring that the weight of the fingers was not included in force measurements. Visual feedback to the subjects was provided by means of a 19" monitor placed 0.8 m from the subject. Data collection, actuator control, and visual feedback to the subject and experimenter were all managed by means of a customized program running in a National Instruments LabVIEW environment. Although subjects were asked to press with varying numbers of fingers during the procedure, they were always presented with feedback on the total force they produced with all four fingers regardless of the number of fingers they were instructed to use. *Figure 3* illustrates the Inverse Piano apparatus.

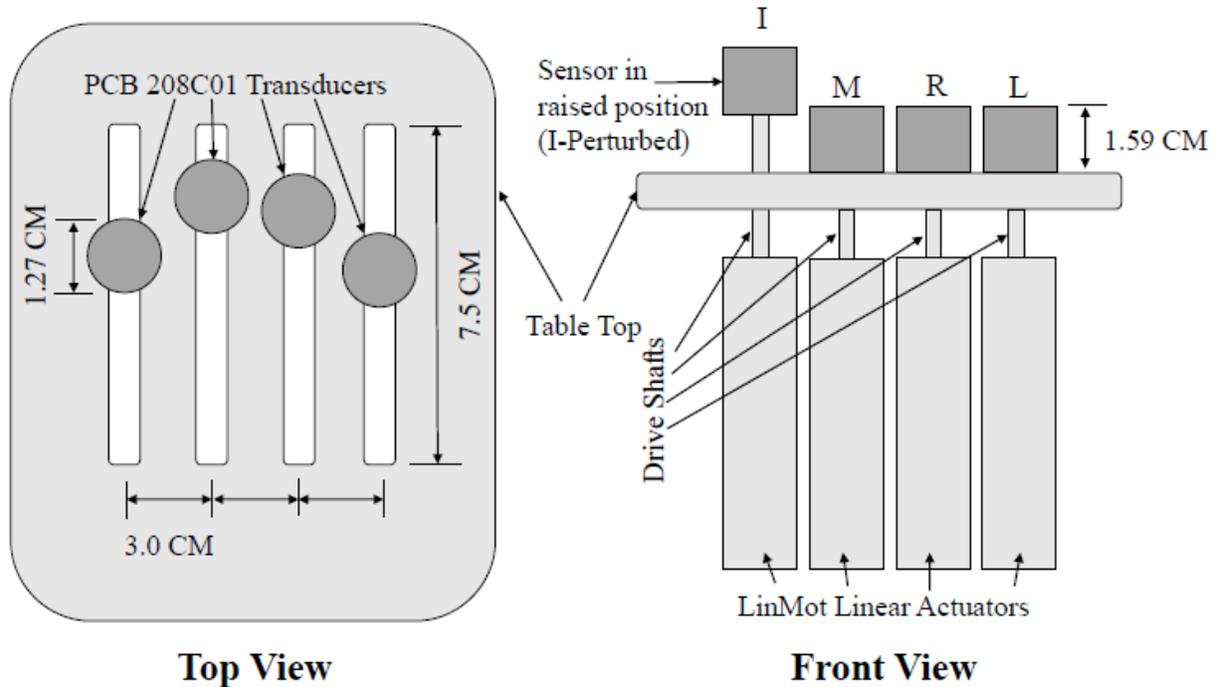


Figure 3: the Inverse Piano

3.3 Experimental Procedure

The full experimental procedure comprised of three main tasks. In the first task, each subject was instructed to press as hard as possible on each sensor in order for the experimenter to measure the subject's maximal voluntary contraction (MVC) force. The collection of the MVC force allowed the force levels for subsequent tasks to be adjusted according to the subjects' capacities for force production. In each MVC trial, subjects were given 6 s to produce MVC in a smoothly increasing manner. Each subject repeated the MVC task two times and was required to rest for 30 s in between trials.

In the second task, subjects produced force ramps with individual fingers. Subjects were instructed to produce force using a specific (instructed) finger and follow a target force trajectory. The subject always received feedback on total force produced by all four fingers. The target force corresponded to 5% of the instructed finger's contribution to the 4-finger MVC for 2 s, a smooth increase from 5% to 45% of the instructed finger's MVC contribution over 6 s, and finally 2 s at 45% of the instructed finger's MVC contribution. This task involved four repetitions so that each finger was the task finger for one trial. The data from these trials were used to calculate enslaving matrices (Zatsiorsky et al. 2000).

The third task was the main experimental task for this study. Each trial in this task lasted for 12 s and had the same basic form: for the first 6 s, the subject was provided with visual feedback on total force (F_{TOT}) and instructed to reach and maintain a target force level. After the first 6 s, visual feedback on F_{TOT} was removed, so the subject could only see the line, which corresponded to the target force level. There were four combinations of fingers with which subjects were instructed to press (instructed fingers): Index only (I), Index and Middle (IM),

Index, Middle, and Ring (IMR), and all fingers (IMRL). While data were collected for the I-pressing condition, they are not presented here. The task force was always set to 20% of the instructed fingers' contribution to the 4-finger MVC; for example, for the IM task, F_{TOT} was set at 20% of the sum of the forces of the I and M fingers at the time of peak F_{TOT} in the four-finger MVC task. No subjects reported fatigue during the course of the procedure.

Contemporaneously with the disappearance of visual feedback on their force production, in most trials, one of the subject's fingers was perturbed by being raised by 1.0 cm at 2.0 cm/s, held in place for 1.5 s, and then lowered to its initial position at -2.0 cm/s. The first three trials in each finger-pressing condition were controls: visual feedback on F_{TOT} was removed, but no finger was moved. After those initial trials, trials with perturbations were performed. Across all conditions, the perturbation was applied to the I finger. In addition, in the I and IM conditions, R finger was also perturbed. These data will be considered in the comparison of redundant (IM-pressing) and non-redundant (I-pressing), but not in the comparison of systems with varying degrees of redundancy (IM, IMR, and IMRL). Subjects paced themselves through each series of 24 perturbation trials and were required to rest for 30 s after each series. Finger-pressing conditions were randomized. *Table 1* illustrates this sequence of experimental conditions.

Task		Total Trials
1.	MVC Trials IMRL	2
2.	Single-Finger Ramps 1 per finger	4
3 - 6. Order of Blocks Randomly Assigned	Experimental Trials	
	I-Pressing; I and R perturbed 24 Trials per perturbation + 3 control	51
	IM-Pressing; I and R perturbed 24 Trials per perturbation + 3 control	51
	IMR-Pressing; I perturbed 24 Trials per perturbation + 3 control	27
	IMRL-Pressing; I Perturbed 24 Trials per perturbation + 3 control	27

Table 1: sequence of experimental conditions.

3.4 Data Processing

In the MVC trials, the forces produced by individual fingers were recorded when the total four-finger force was at its peak magnitude. Although fairly infrequent, sometimes recording errors corrupted the data we collected; these trials needed to be excluded from our results. The largest number of corrupted trials for a single subject was two. In order to maintain a balanced number of observations for each subject, when a subject had fewer than two corrupt trials, we rejected the one or two trials with largest deviations from that subject's mean performance per condition. As a result, each subject's performance over 22 accepted trials was analyzed. For the main trials, all accepted trials for a given condition were time-aligned.

3.5 Calculation of the Enslaving Matrix and Finger Modes

Even when a person attempts to produce force with only one finger, the rest of the fingers of his or her hand also produce force; this phenomenon is called enslaving or lack of finger individuation (Kilbreath & Gandevia 1994; Li et al. 1998, Zatsiorsky et al. 2000; Schieber & Santello 2004). We quantified enslaving individually for each subject by constructing a 4×4 enslaving matrix $[E]$ using the data collected from each of the force production ramp tasks. In each of these tasks, the force produced by all four fingers increased even though only one finger was instructed to produce force. Linear regression was used to quantify the contribution of each finger's force to F_{TOT} :

$$F_{i,j} = F_i^0 + k_{i,j} \times F_{TOT,j} \quad (1)$$

where $i, j = \{I, M, R, L\}$, $F_{TOT,j}$ is the total force produced by all fingers when j is the instructed finger, and $F_{i,j}$ is the force produced by finger i when j is the instructed finger. The constants $k_{i,j}$ were taken as representing partial derivatives of total force with respect to individual finger forces and arranged into $[E]$. F_i^0 is the intercept calculated from each regression; it may be thought of as the initial force level for a given enslaved finger in the ramp trial when the total force is zero; values of F_i^0 were very close to zero and they do not appear in $[E]$, which is composed only of the regression slopes. Subsequently, we used $[E]$ to calculate modes, which are hypothetical commands to fingers, which can be modified by the central nervous system one at a time (Latash et al. 2001; Danion et al. 2003):

$$\mathbf{m} = [E]^{-1} \mathbf{F} \quad (2)$$

where \mathbf{m} is a 4×1 vector of mode values and \mathbf{F} is a 4×1 vector of force values. It should be noted that, according to this methodology, finger modes are expressed in newtons, and the sum of finger modes at a given time point will be identical to the sum of finger forces at the same point; the mode analysis re-apportions total force to each finger mode according to the observed interdependence of digits during ramp trials.

Analysis of multi-finger actions can be performed in both force and mode spaces. Within this study, all the methods of analysis of the main task compared finger force changes and variances in different directions within the space of elemental variables, forces or modes. We have assumed that enslaving is a robust phenomenon seen across tasks and force ranges (Li et al. 1998; Danion et al. 2003). It is expected to lead to finger force inter-dependence and, hence, to unequal magnitudes of force changes and variances in different directions in the finger force space. This could potentially lead to false positive or false negative conclusions depending on the selected performance variable with respect to which analysis is performed. Using finger modes is expected to eliminate the inter-dependence among the elemental variables and alleviate or even remove this potential problem.

3.5 Analysis of the Main Task

Over the course of the experimental trials - which required subjects to accurately produce and maintain a given amount of force - subjects displayed relatively consistent behavior. Panels A and B of *Figure 4* show a typical subject's performance for the I- (Panel A) and IM-pressing

(Panel B) tasks during control (thin dotted line), I-perturbed (thick solid line), and R-perturbed (thin solid line) trials.

We chose three 250-ms phases during which to analyze subjects' behavior: phase-1 was defined to be well before the perturbation in order to define a pre-perturbation steady state and was therefore set from 3.00-3.25 s from perturbation onset. Next, phase-2 was defined to occur during the middle of the time the perturbed finger was lifted (7.23-7.48 s); note that it is not midway between the onset of the perturbation, but is rather midway between the end of the upward perturbation (when the sensor stopped moving) and when the sensor began to move downward again. Finally, phase-3 was a post-perturbation steady state (8.92-9.17 s). These phases, as well as their relations to force changes induced by the perturbations, can be seen in *Figure 4*.

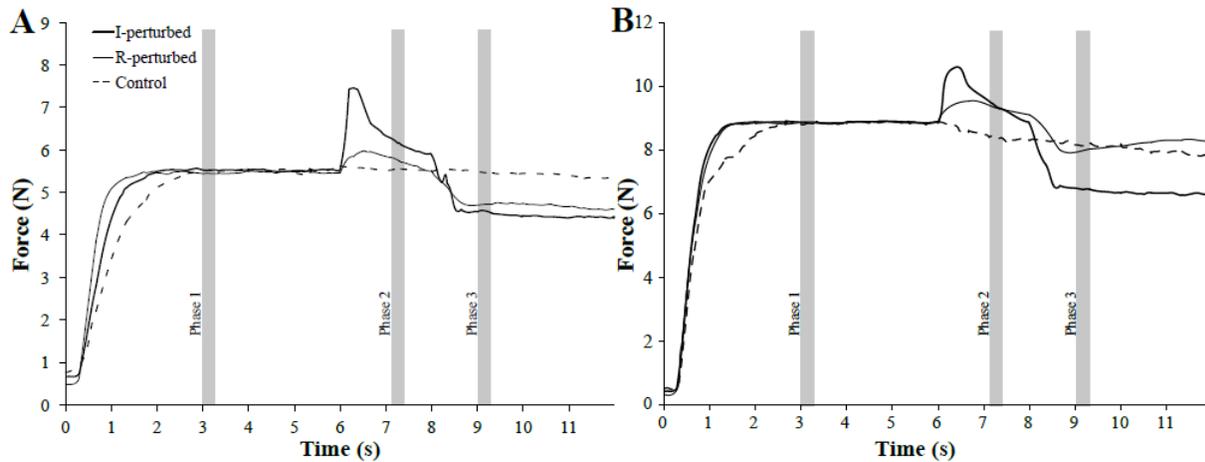


Figure 4: A representative subject's performance in I- and IM-pressing tasks while experiencing various perturbations. The shaded Phases represent the 250-ms epochs between which we analyzed subjects' average behavior.

3.7 Analysis of Force Change

For each condition, the difference between F_{TOT} produced in phase-3 and phase-1 (ΔF_{TOT}) was calculated for each subject. Since ΔF_{TOT} has been shown to depend on the initial force level (Vaillancourt & Russell 2002; Ambike et al. 2014b), we also calculated ΔF_{TOT} as a percentage of task force.

3.8 Analysis of Variance of Finger Forces and Modes

Inter-trial variance in two spaces of elemental variables, those of finger forces (F) and finger modes (m), was analyzed for each subject within the framework of the UCM hypothesis (Scholz & Schöner 1999). According to this hypothesis, the neural control results in different stability properties in different directions within the multi-dimensional space of elemental variables. In particular, relatively high stability (reflected in low across-trials variance) is expected in directions that lead to changes in a potentially important performance variable, while relatively low stability (high variance) is expected in directions that lead to changes in this performance variable. This analysis was performed using the individual finger F (m) data averaged over each of the three phases in each trial. We also applied this analysis to the

differences in the forces (modes) between phase-3 and phase-1 computed for each trial separately. This analysis quantifies variance in two spaces, the UCM (where F_{TOT} is constant) and the space orthogonal to the UCM (ORT, where F_{TOT} changes). We will refer to these two variance components as V_{UCM} and V_{ORT} .

For analysis in the force space, the two variance components will be referred to as $V_{UCM,F}$ and $V_{ORT,F}$; for analysis in the mode space, $V_{UCM,m}$ and $V_{ORT,m}$ will be used. Analysis of the differences in forces (modes) between phase-3 and phase-1 resulted in variance indices $V_{UCM,\Delta F}$ and $V_{ORT,\Delta F}$ in the force space, and $V_{UCM,\Delta m}$ and $V_{ORT,\Delta m}$ in the mode space.

An index of multi-finger synergy (ΔV) was computed reflecting the difference between V_{UCM} and V_{ORT} after normalization of each of these indices by the dimensionality of the corresponding spaces (3 for V_{UCM} , 1 for V_{ORT}). To compare these indices across subjects, they were normalized by total variance (V_{TOT}), also computed per dimension:

$$\Delta V = (V_{UCM}/3 - V_{ORT}/1)/(V_{TOT}/4) \quad (3)$$

For parametric statistical analysis, ΔV was log-transformed using Fisher's transformation adjusted for its computational limits ($-4 \leq \Delta V \leq 1.33$). This resulted in the transformed indices of synergy, ΔV_{ZF} and ΔV_{Zm} , in force and mode spaces, respectively.

3.9 Analysis of Motor Equivalence

This analysis quantified the force and mode difference vectors (ΔF and Δm) between phase-3 and phase-1. These vectors were projected onto the UCM and ORT spaces. The vector component within the UCM does not affect F_{TOT} and is therefore called the Motor Equivalent (ME) component. Conversely, the component within ORT does affect F_{TOT} and is called the non-Motor Equivalence (nME) component (Mattos et al. 2011). As with the described analysis of variance, high deviations are expected in directions of low stability (ME). ME and nME components were computed using the across-trial average values of the ΔF and Δm vectors in each experimental condition. The ME and nME components were normalized by the square root of the dimensionality of their respective spaces.

3.10 Statistics

Unless otherwise stated, data are presented as means \pm standard errors. Two-way ANOVAs with repeated measures were used to test the effects of Condition (three levels, IM, IMR, and IMRL) and Phase (three levels, phase-1, phase-2, and phase-3) on the main outcome variables such as variance components (V_{UCM} and V_{ORT}), synergy index (ΔV), and ME and nME components of force (mode) changes between phase-3 and phase-1. Statistical tests were run in SAS 9.3 (SAS Institute Inc, Cary, NC) using linear mixed models with compound symmetrical covariance structure. When necessary, data were transformed according to statistical assumptions of normality. The Kenward-Roger method was used to adjust test degrees of freedom when necessary. Statistical significance was set at $p < 0.05$.

CHAPTER 4

Experimental Results

Results are presented in two sections. Section 4.1 presents results contrasting I and-IM pressing and including data from both I- and R-perturbed conditions. Section 4.2 presents results contrasting IM, IMR, and IMRL-pressing with I-perturbation only.

4.1 Redundant Systems and Non-Redundant Systems

We tested three hypotheses in our comparisons of redundant systems (IM-pressing in force and mode space and I-pressing in force space) and non-redundant (I-pressing in mode space) systems. Our first hypothesis was that we would see a synergic structure of inter-trial variance ($V_{UCM} > V_{ORT}$) during all steady states in redundant state spaces, but not in non-redundant state space. Second, we hypothesized that the *changes* in forces and modes from the initial (pre-perturbation) steady states to final (post-perturbation) steady states would also show a synergic structure of variance in redundant state spaces but not in non-redundant state space. Finally, our third hypothesis was that, when the ring finger – which was not explicitly involved in the task – was perturbed, we would observe a synergic structure of inter-trial variance during steady states in force space, but not in mode space.

Results relating to all three of the specific hypotheses above are presented in section 4.1.2 (Analysis of the Structure of Variance). In addition to the hypothesis tests, we decided to explore two observed phenomena regarding which we formulated no explicit hypotheses. In section 4.1.1, we describe and analyze the changes in force observed over the course of the experimental trials, specifically as they relate to observed *violations of equifinality* and *changes in enslaving*. In section 4.1.3, we analyze the displacement of the system between initial and final states in the framework of motor equivalence (Mattos et al. 2011).

4.1.1 General Patterns of Force Change

Across both perturbation (I, R) and finger pressing (I, IM) conditions, the perturbation resulted in the lifted finger increasing its force. This force decreased while the finger remained raised, and then decreased further when the finger was lowered to its original position, often dropping below the level it had produced before the perturbation. The other fingers of the hand typically showed force changes in the opposite direction to those of the perturbed finger: a force drop when the perturbed finger was raised and an increase in force when the perturbed finger was lowered. Changes in total force were dominated by the changes in the perturbed finger force. *Figure 5* shows total force profiles for a typical subject during both I-perturbation (master finger perturbation) and R-perturbation (enslaved finger perturbation) applied during the I-condition (A) and the IM-condition (B).

In the unperturbed (control) trials, the total force decreased (ΔF_{TOT}) modestly after the feedback removal between Phase-1 and Phase-3, on average by 0.2 ± 0.06 N and 0.5 ± 0.1 N for the I- and IM-conditions, respectively. The magnitude of ΔF_{TOT} was larger in trials with perturbations. In the I-condition, F_{TOT} decreased by 0.4 ± 0.26 N for I-perturbation and 0.36 ± 0.15 N for R-perturbation. In the IM-condition, force decreased by 1.3 ± 0.36 N for I-perturbation and 1.1 ± 0.15 N for R-perturbation.

The two-way repeated measures ANOVA on ΔF with factors *Condition* and *Finger-Perturbed* showed significant main effects for *Condition* ($F_{1,35} = 20.95$; $p < 0.001$) and *Finger-Perturbed* ($F_{2,35} = 4.36$; $p < 0.05$). Tukey-Kramer adjusted post-hoc analysis on *Finger-Perturbed* showed that during control trials, ΔF was significantly smaller than in I-perturbed and R-perturbed trials, but that I-perturbed and R-perturbed conditions were not significantly different from one another. This means that perturbations applied to the instructed and non-instructed fingers led to similar results in the single-finger and two-finger tasks. *Figure 5* illustrates the ΔF data with associated significance indicated.

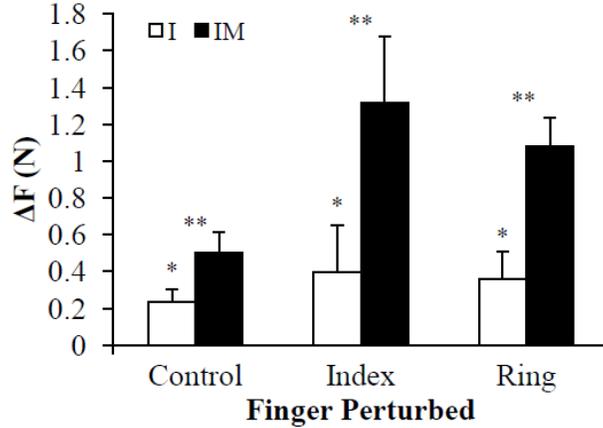


Figure 5: Magnitude of decrease of force between Phase 1 and Phase 3. Positive magnitudes indicate that total force at Phase 3 was lower than it was at Phase 1. * indicates significant differences in ΔF in I-pressing and IM-pressing conditions. ** indicates significant differences in magnitude of ΔF between no perturbation, index perturbation, and ring perturbation conditions.

The amount of force produced by non-instructed fingers changed between Phase-1 and Phase-3. We quantified the phenomenon of enslaving with an index of enslaving (EN) calculated as the percentage of total force produced by fingers, which were not instructed to produce force (see Methods). Typically, this index showed no changes during the control trials; the average change in EN, ΔEN was $-0.3 \pm 2.4\%$ and $0.1 \pm 0.96\%$ for the I- and IM-conditions, respectively. In contrast, trials with perturbations resulted in an increase in EN from Phase-1 to Phase-3 (*Figure 6*). In the I-condition, ΔEN was $8.6 \pm 2.0\%$ for I-perturbation and $7.4 \pm 2.1\%$ for R-perturbation; in the IM-condition, ΔEN was $1.9 \pm 0.90\%$ for I-perturbation and $5.3 \pm 1.7\%$ for R-perturbation. Single-group t-tests confirmed that ΔEN was not different from zero for the control trials and for the I-perturbation during the IM condition. However, ΔEN was significantly different from zero in the other three conditions illustrated in *Figure 6*. A two-way ANOVA confirmed significant effects of both factors, *Condition* ($F_{1,35} = 4.14$; $p < 0.05$) and *Finger-Perturbed* ($F_{2,35} = 8.43$; $p < 0.001$) without a significant interaction.

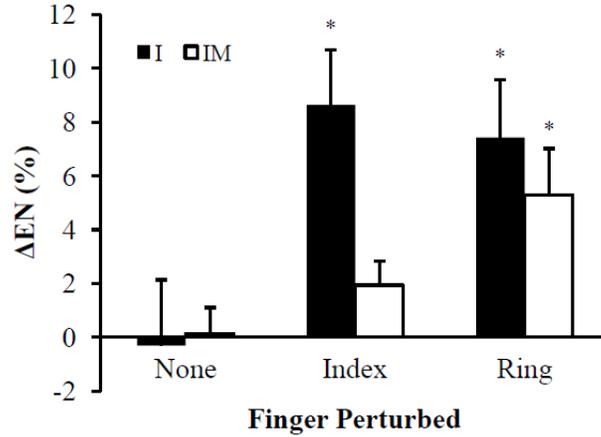


Figure 6: Change in the index of enslaving between Phase 1 and Phase 3. Units are % of force produced by enslaved fingers. * indicates values which are significantly different from 0.

Mode profiles showed similar trends to force profiles. Some subjects showed mode values for non-instructed fingers that had negative magnitudes. Since, in this situation, modes are hypothetical variables which reflect a subject's intention to press with a given finger, negative modes may be interpreted as subjects' efforts to unload a particular finger. *Table 2* shows the number of subjects who produced a negative mode in each experimental condition with non-instructed modes in boldface.

<i>Finger(s) Pressing</i> <i>Finger Perturbed</i>		<i>Index</i>			<i>Index + Middle</i>		
		<i>Control</i>	<i>Index</i>	<i>Ring</i>	<i>Control</i>	<i>Index</i>	<i>Ring</i>
<i>Phase 1</i>	Index	0	0	0	0	0	0
	Middle	3	1	1	0	0	0
	Ring	2	2	1	2	2	1
	Little	1	0	0	0	1	1
<i>Phase 3</i>	Index	0	0	0	0	0	0
	Middle	2	0	2	0	0	0
	Ring	2	1	2	1	1	3
	Little	2	0	0	1	2	0

Table 2. The number of subjects is shown who produced a negative mode value during a particular *Finger-Pressing x Finger-Perturbed* condition for the initial steady state (Phase 1) and final steady state (Phase 3). Non-instructed modes are in bold.

4.1.2 Analysis of the Structure of Variance

To test our first and third hypotheses, the structure of inter-trial variance was analyzed within the framework of the UCM hypothesis (see Methods). These analyses were carried out in both force space and mode space. Overall, when inter-trial variance was analyzed within each subject and each condition, ΔV was positive for all pressing and perturbation combinations in all

three phases, reflecting $V_{UCM} > V_{ORT}$ (both indices normalized per dimension, see Methods) in both force-based and mode-based analyses. Even in single-finger tasks, the inequality $V_{UCM} > V_{ORT}$ was confirmed across all phases with the perturbation applied to the task finger (I) and to a non-task finger (R).

The index of synergy, ΔV , showed the highest values in Phase-1 and dropped across the three phases in all conditions. *Figure 7* illustrates these results over individual phases in mode space (A, $\Delta V_{Z,m}$) and force space (B, $\Delta V_{Z,F}$). Three-way ANOVAs with factors *Condition*, *Finger-Perturbed* and *Phase* (1, 2, 3) on ΔV_Z confirmed a significant main effect of *Phase* in both mode space ($F_{2,77} = 84.62$; $p < 0.001$) and force space ($F_{2,77} = 77.31$; $p < 0.001$), without other effects. Tukey-Kramer adjusted post-hoc comparisons showed that each phase was significantly different from all other phases in both force space and mode space.

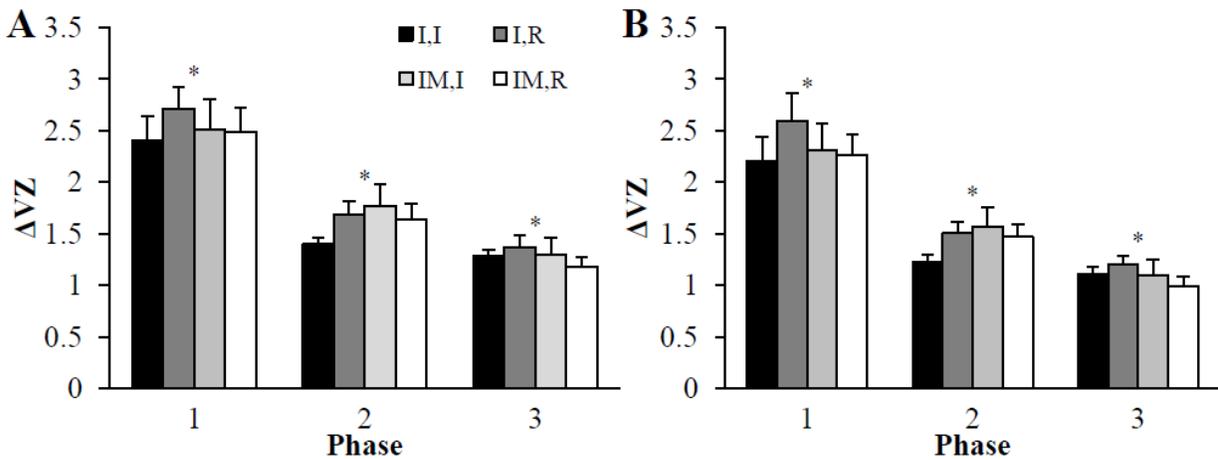


Figure 7: The z-transformed index of synergy, ΔV_Z , at Phases 1, 2, and 3 for each finger pressing/finger perturbed combination. * indicates significantly different magnitude of ΔV_Z between each phase. There were no significant differences in ΔV_Z between conditions within a phase.

To test our second hypothesis, the changes in finger forces and modes between Phase-3 and Phase-1 were analyzed. This analysis showed that most of inter-trial variance once again was confined to the UCM. This is illustrated in *Figure 8* for the analyses in both mode and force space. Again, even in one-finger tasks, transient perturbations resulted in changes in the finger force and finger mode spaces such that there was more variance in directions that did not affect total force; this occurred both for perturbations applied to the task finger (I) and those applied to a non-task finger (R).

These results were confirmed by three-way ANOVAs with factors *Condition*, *Finger-Perturbed* and *Variance* performed in both force and mode spaces. Variance was log-transformed for normality before statistical analysis. In both force and mode space, there were significant main effects for *Variance* ($F_{1,49} = 18.13$; $p < 0.001$) reflecting $V_{UCM} > V_{ORT}$ and for *Finger-Perturbed* ($F_{1,49} = 16.94$; $p < 0.001$) reflecting larger variance in the I-perturbed trials, but the effect of *Condition* ($F_{1,49} = 1.76$; $p = 0.19$) was not significant. The *Finger-Perturbed* \times *Variance* interaction was significant for the mode space analysis ($F_{1,49} = 4.99$; $p < 0.05$) and was just under the significance level for the force-space analysis ($F_{1,49} = 3.89$; $p = 0.054$). Tukey-

Kramer analysis on the interaction showed that V_{UCM} was significantly greater than V_{ORT} in I-perturbed trials, and that V_{UCM} in I-perturbed trials was significantly greater than V_{UCM} and V_{ORT} in R-perturbed trials.

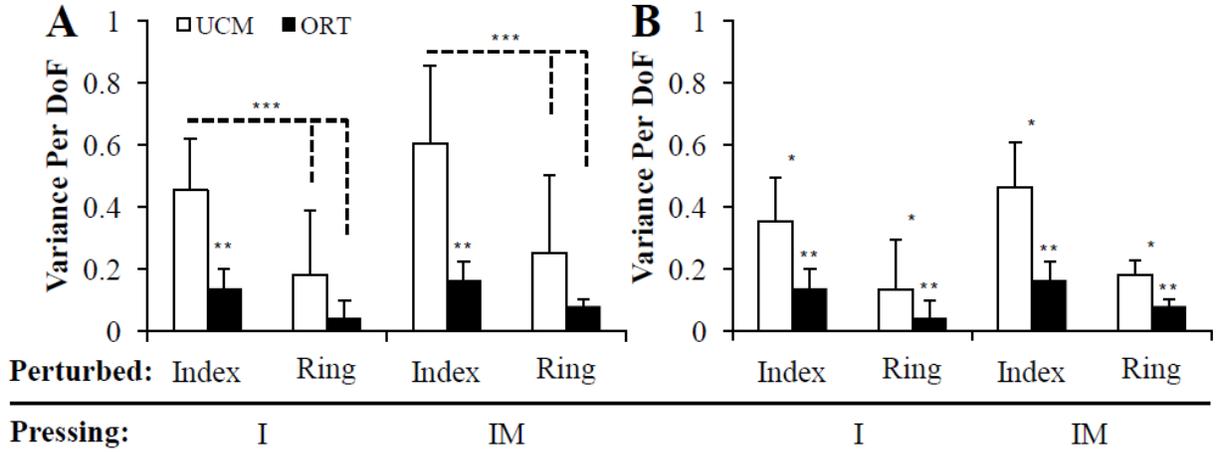


Figure 8: Variance within and orthogonal to the UCM (normalized by the dimensionality of the respective subspaces) between Phase 1 and Phase 3, in mode space (Panel A) and force space (Panel B). * indicates a significant difference in variances between index- and ring-perturbed conditions; ** indicates V_{UCM} significantly greater than V_{ORT} ; *** indicates a significant difference in magnitude between V_{UCM} during index-perturbed conditions and V_{UCM} and V_{ORT} during ring-perturbed conditions.

4.1.3 Analysis of Motor Equivalence

We explored the magnitude of the two components of changes in the force and mode vectors ($\Delta\mathbf{F}$ and $\Delta\mathbf{m}$) from Phase-1 to Phase-3, one component that did not lead to total force change (*motor equivalent*, ME), and the other component that did (*not motor equivalent*, nME). For this purpose, in each trial $\Delta\mathbf{F}$ and $\Delta\mathbf{m}$ vectors were projected onto the UCM and the subspace orthogonal to it (ORT). For quantitative comparison, the length of the projections was normalized by square root of the corresponding dimensionality (cf. Mattos et al. 2011).

Mean magnitudes of ME projections were larger than those for nME projections in both force space and mode space for all pressing and perturbation conditions. *Figure 9* illustrates the relative magnitudes of ME (black bars) and nME (open bars) projections in mode space (A) and force space (B). Note that the ME projections were consistently larger than the nME ones.

Three-way ANOVAs with factors *Condition*, *Finger-Perturbed* (Control, I-perturbed, and R-perturbed), and *Component* (ME and nME) were run in both mode space and force space. In both cases, ME and nME magnitudes were log-transformed for normality (reflecting their lower bound at 0). In force space, *Condition*, *Finger-Perturbed*, and *Component* all showed significant main effects without interactions (respectively: $F_{1,77} = 57.82$; $p < 0.001$; $F_{2,77} = 45.69$; $p < 0.001$; $F_{1,77} = 4.33$; $p < 0.05$). Post-hoc comparisons using the Tukey-Kramer method showed that all three levels (control, I-perturbed, and R-perturbed) were significantly different from one another. These results were consistent in the mode space analysis.

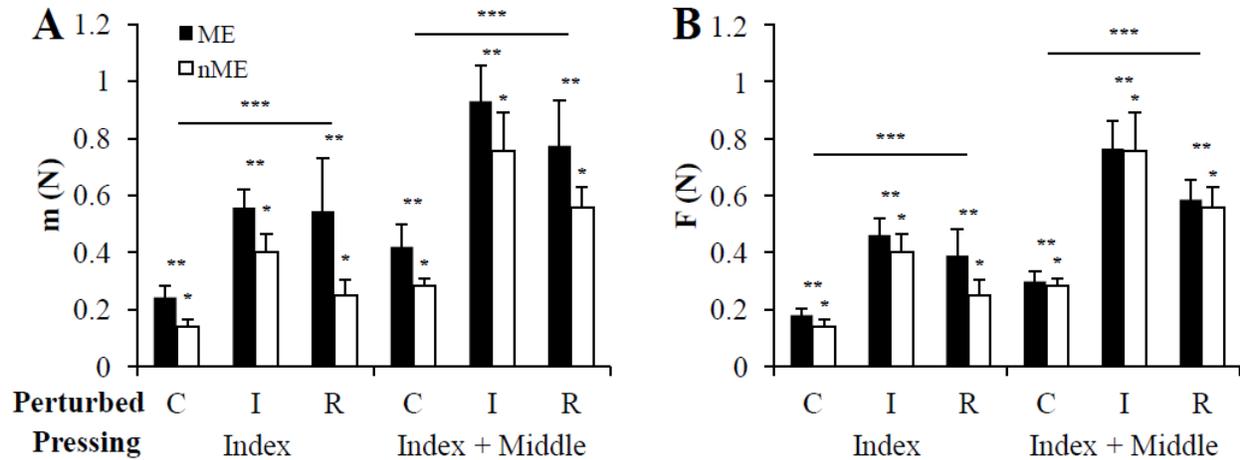


Figure 9: The magnitudes of motor equivalent (ME) and non-motor equivalent (nME) components of the change in mode (A) and force vectors (B) between Phase-1 and Phase-3 for each perturbation type and in each pressing condition. * denotes the significant effect of component; ** denotes significant effect of finger-perturbed, and *** the significant effect of condition.

4.2 Redundant Systems with Varying Degrees of Redundancy

Three hypotheses were also tested in the comparison of redundant systems with varying degrees of redundancy. While we expected to observe synergic structures of inter-trial variance ($V_{UCM} > V_{ORT}$) during steady states in all systems because they were all redundant, we hypothesized (Hypothesis 4) that the difference between V_{UCM} and V_{ORT} would increase as additional elements were added. In addition, we hypothesized this relationship between the $V_{UCM} - V_{ORT}$ difference and the number of involved elements would hold for inter-trial variance of the *difference* in forces and modes between the initial and final steady states (Hypothesis 5). Finally, we hypothesized that the motor equivalent component of the within-trial displacement between initial and final steady states would be greater than the non-motor equivalent component, and that this difference would also increase as the number of involved elements increased.

In addition to testing the aforementioned hypotheses in sections 4.2.2 and 4.2.3, we present further description and analysis of the observed changes in forces and modes (and resultant violations of equifinality) in 4.2.1.

4.2.1 General Patterns of Force Change

Across all three (IM, IMR, IMRL) finger pressing conditions, lifting the index (I) finger resulted in an increase of its force. As the I finger remained in the raised position, the force it produced decreased; when the finger was lowered to its initial position, this force decreased further. Usually, after the raising-and-lowering sequence (in phase-3), the I-finger force was lower than before the perturbation (in phase-1). The fingers, which were not perturbed, showed a drop in their forces when the I finger was raised and an increase in their forces when the I finger was lowered. In general, however, changes in total force (F_{TOT}) were dominated by the I-finger force changes. In particular, F_{TOT} at the end of trials (phase-3) was usually lower than at the

beginning of trial; this decrease in F_{TOT} can be seen in *Figure 10B*. During control trials, F_{TOT} also decreased from phase-1 to phase-3 (*Figure 10A*), but this force drop was smaller than in trials with perturbations.

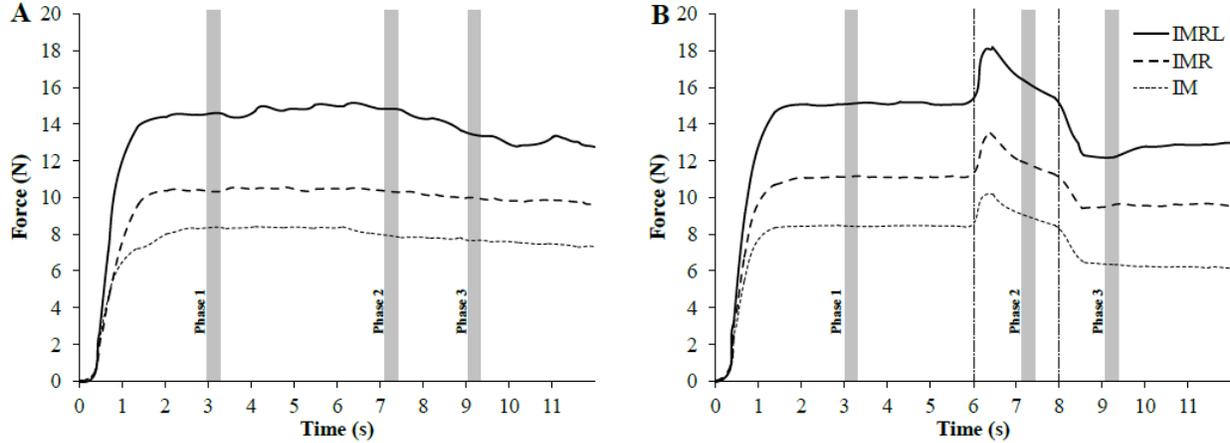


Figure 10: A representative subject’s average performance during the unperturbed (Panel A) and perturbed (Panel B) tasks. The shaded regions denote phases of data comparison chosen to correspond to pre, mid, and post-perturbation steady states. The hashed vertical lines in Panel B correspond to when the index sensor began to raise and when it began to lower.

The F_{TOT} change (ΔF_{TOT}) was larger as the number of fingers pressing increased: for trials with perturbations, the average magnitude of ΔF_{TOT} was -1.32 ± 0.36 N, -1.90 ± 0.28 N, and -2.37 ± 0.31 N for the IM, IMR, and IMRL conditions, respectively. In control trials, the magnitudes of force changes were smaller: -0.50 ± 0.11 N, -0.55 ± 0.22 N, and -0.76 ± 0.11 N for the IM, IMR, and IMRL conditions, respectively. Two-way ANOVAs with repeated measures, using factors *Condition* (3 levels) and *Perturbation* (2 levels), showed significant effects of both *Condition* ($F_{2,35} = 5.67$; $p < 0.01$) and *Perturbation* ($F_{1,35} = 62.7$; $p < 0.001$) with no significant interaction. Tukey-Kramer adjusted mean comparisons on *Condition* showed that only IMRL was significantly different from IM ($p < 0.05$).

After force changes between phase-3 and phase-1 were normalized by the initial force level ($\Delta F_{TOT,\%}$), the two-way ANOVA showed a significant main effect of *Perturbation* ($F_{1,35} = 38.4$; $p < 0.001$), but no effect of *Condition* ($F_{2,35} = 0.13$; $p > 0.8$). *Figure 11* shows ΔF_{TOT} (A) and $\Delta F_{TOT,\%}$ (B) for perturbed trials (closed bars) and unperturbed trials (open bars) with associated significance.

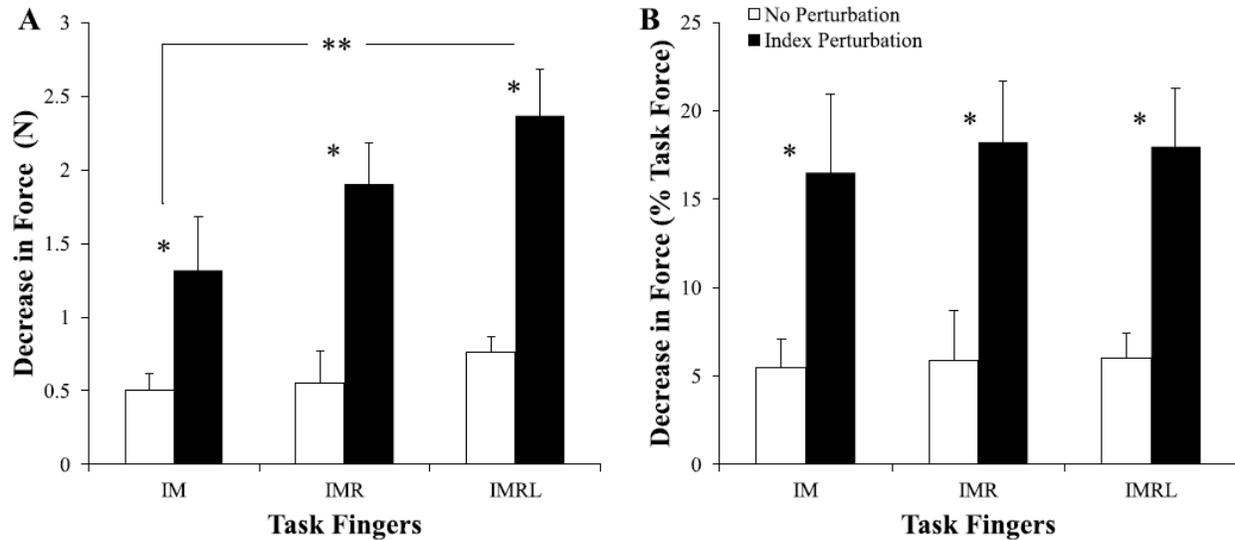


Figure 11: The decrease in total force between Phase 1 and Phase 3 in newtons (Panel A) and normalized units (Panel B). * Indicates a significant difference between perturbed and unperturbed trials; ** indicates a significant difference between magnitude of force decrease in perturbed trials.

4.2.2 Analysis of the Structure of Variance

To test the effect of explicitly involved fingers on variance of elements within and orthogonal to the UCM (Hypothesis-4), we analyzed the structure of inter-trial variance using both finger forces and finger modes as elemental variables at all three data collection phases. V_{UCM} was of larger magnitude than V_{ORT} during at all phases and for all pressing conditions during both perturbed and unperturbed trials. V_{ORT} was especially small during phase-1; this is unsurprising because subjects had visual feedback by which they could correct deviation in the ORT direction during phase-1. In contrast, V_{UCM} had similar values across the phases and condition.

Figure 12 illustrates the structure of variance in force space (A) and mode space (B) with V_{ORT} on the left half of each panel and V_{UCM} on the right half. Finger pressing conditions are represented by open bars (IM), shaded bars (IMR), and filled bars (IMRL). In order to provide cross-subject comparison, each subject's V_{UCM} and V_{ORT} values were normalized by the square of each his or her target force for the associated task before these values were averaged across all subjects. The only consistent differences were between the V_{ORT} values in phase-1 compared to phases-2 and -3.

To test Hypothesis-4 statistically at each steady state, three-way ANOVAs with repeated measures with factors *Condition* (3 levels: IM, IMR, IMRL), *Phase* (3 levels: 1, 2, 3), and *Variance* (2 levels: UCM, ORT) were run on log-transformed data in both force and mode space. In force space, there was a significant *Phase* \times *Variance* interaction ($F_{2,119} = 5.50$; $p < 0.01$) but no significant main effect or interaction with *Condition*. Tukey-Kramer comparisons confirmed that $V_{UCM} > V_{ORT}$ for all phases. Additionally, V_{ORT} at phase-1 was significantly smaller than V_{ORT} at phase-2 and phase-3, while V_{ORT} was not significantly different between phase-2 and phase-3. There were no significant differences in V_{UCM} across the phases. These results were consistent in mode space.

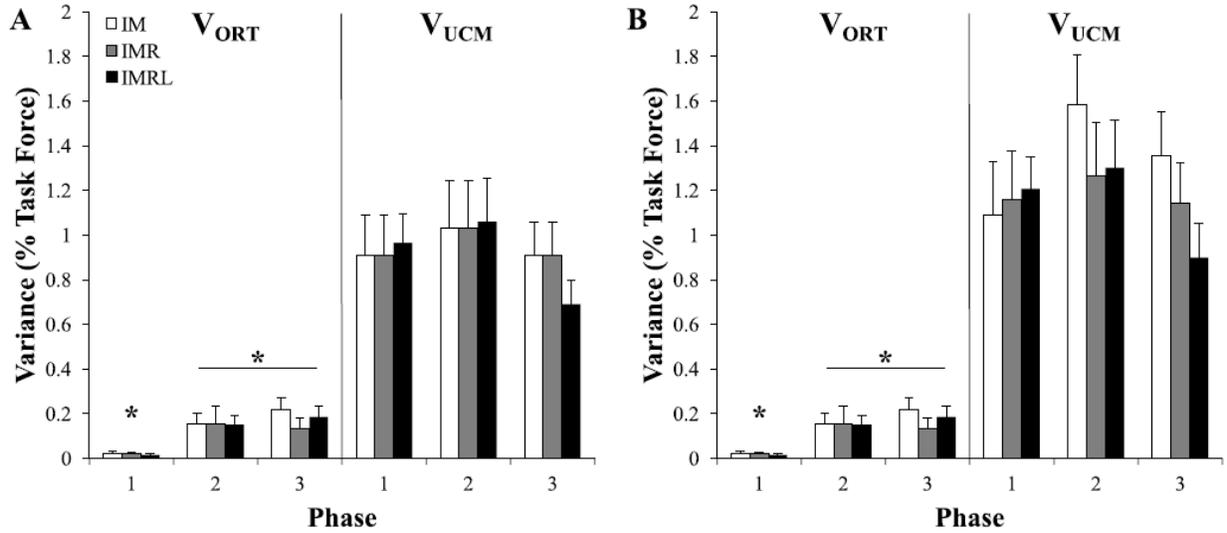


Figure 12: Structure of variance at each of the three phases of data analysis in force space (Panel A) and mode space (Panel B). * Indicates significant differences between V_{ORT} at Phase 1 and V_{ORT} at Phases 2 and 3.

An index of synergy (ΔV) was calculated separately for each subject at each of the three phases. We observed $\Delta V > 0$ for all phases and finger-pressing conditions, reflecting the inequality $V_{UCM} > V_{ORT}$ described previously. *Figure 13* shows ΔV_Z , the z-transformed index of synergy, for each condition (with the same shading scheme as in *Figure 12*) during each phase in force space (A) and mode space (B). In force space, a two-way ANOVA with repeated measures, using factors *Condition* and *Phase*, showed a significant main effect of *Phase* ($F_{2,56} = 52.97$; $p < 0.001$) without other effects. Since there was no significant effect of *Condition*, Hypothesis-1 was falsified: the number of explicitly instructed fingers did not significantly affect the difference between the magnitudes of V_{UCM} and V_{ORT} . Mean comparisons with Tukey-Kramer adjustment showed that all three levels of *Phase* were significantly different from one another. These results were consistent in both force and mode spaces.

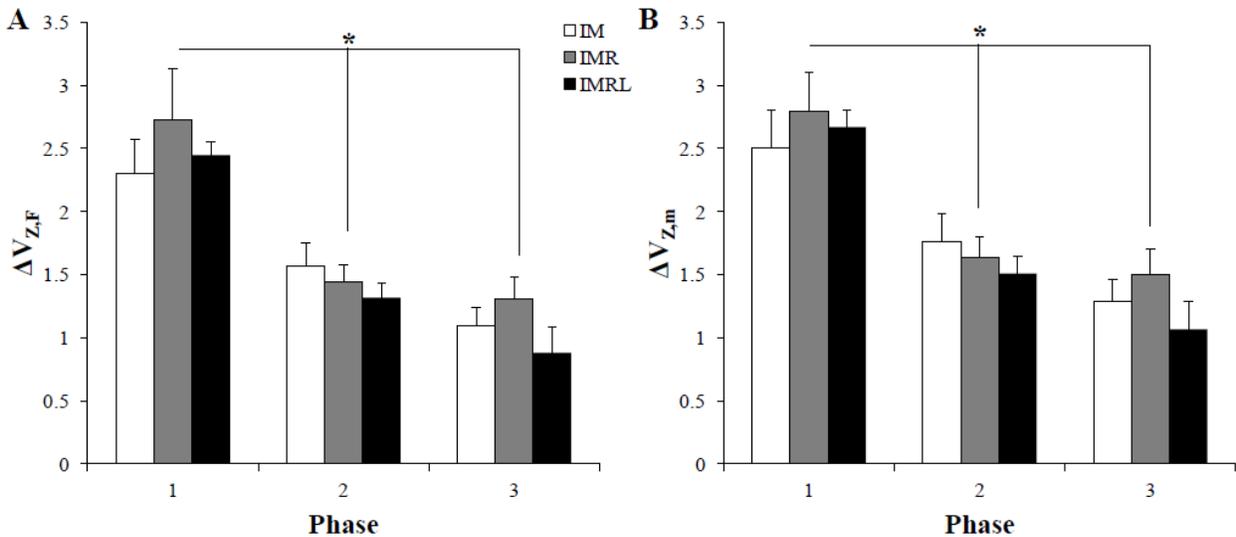


Figure 13: The Z-transformed index of synergy, ΔV_Z , in force space (Panel A) and mode space (Panel B) at each phase for each finger pressing combination. * Indicates a significant difference in the magnitude of ΔV_Z between Phases 1, 2, and 3.

We also analyzed inter-trial variance of the difference vector between forces (and modes) produced in phase-3 and phase-1, denoted by $V_{UCM,\Delta F}$ and $V_{ORT,\Delta F}$ in force space, and $V_{UCM,\Delta m}$ and $V_{ORT,\Delta m}$ in mode space. These results speak to the veracity of Hypothesis-5. Again, in order to make the cross-subject comparison, these data were normalized by the associated target force squared. *Figure 14* shows V_{UCM} (filled bars) and V_{ORT} (open bars) for the force-based (panel A) and mode-based analysis (panel B) for the three finger-pressing condition. The inequality $V_{UCM} > V_{ORT}$ was observed across conditions and analyses, with no obvious difference among finger-pressing conditions (effect of *Variance* in two-way ANOVA with no other effects, $F_{1,35} = 98.8$; $p < 0.001$). These results were consistent in mode space. The lack of a significant effect of *Condition* falsifies Hypothesis-5.

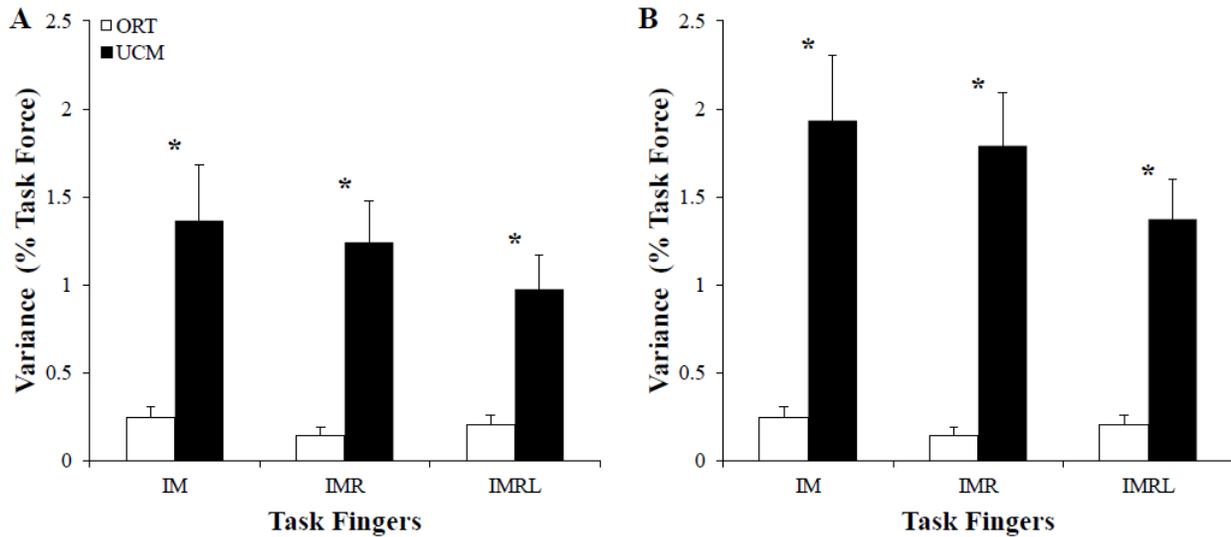


Figure 14: Variance within and orthogonal to the UCM for the difference in forces (Panel A) and modes (Panel B) between Phase 1 and Phase 3.

4.2.3 Analysis of Motor Equivalence

To test Hypothesis-6, two components of system displacement, motor equivalent (ME, leading to no F_{TOT} changes) and non-motor equivalent (nME) were computed for the differences in finger forces (and modes) between phase-3 and phase-1. Both ME and nME were normalized by the target force before their averages were computed across subjects. During trials with perturbations, the magnitude of nME changed very little across the finger-pressing condition, whereas the magnitude of ME decreased somewhat as the number of task fingers increased. In contrast, when no perturbation was applied, ME increased with the number of task fingers while nME stayed approximately consistent. Both ME and nME were larger during perturbed trials than control trials. *Figure 15* shows, in both force space (A) and mode space (B), the mean magnitudes of both ME (closed bars) and nME (open bars) for each finger-pressing condition during trials with (left) and without perturbation (right).

A 3-way ANOVA with repeated measures utilizing the factors *Condition*, *Perturbation*, and *Component* (2 levels: ME, nME) was used in both force and mode spaces. Data were log-transformed for normality. In force space, the *Perturbation* \times *Component* interaction was significant ($F_{1,77} = 5.42$; $p < 0.05$), while neither the main effect of *Condition* nor any

interactions including it were significant. Tukey-Kramer mean of the *Perturbation* \times *Component* interaction showed that magnitudes of ME and nME were significantly different during the I-perturbed trials from their respective values during the control trials, but nME and ME were not significantly different from one another. These results were similar in mode space, except that the ME component of system displacement was significantly greater than the nME component in the control trials. As in the other tests of our specific hypotheses, the lack of a significant *Condition* effect falsified Hypothesis-6 because no significant difference in the magnitude of ME displacement was observed as a function of the number of explicitly involved fingers.

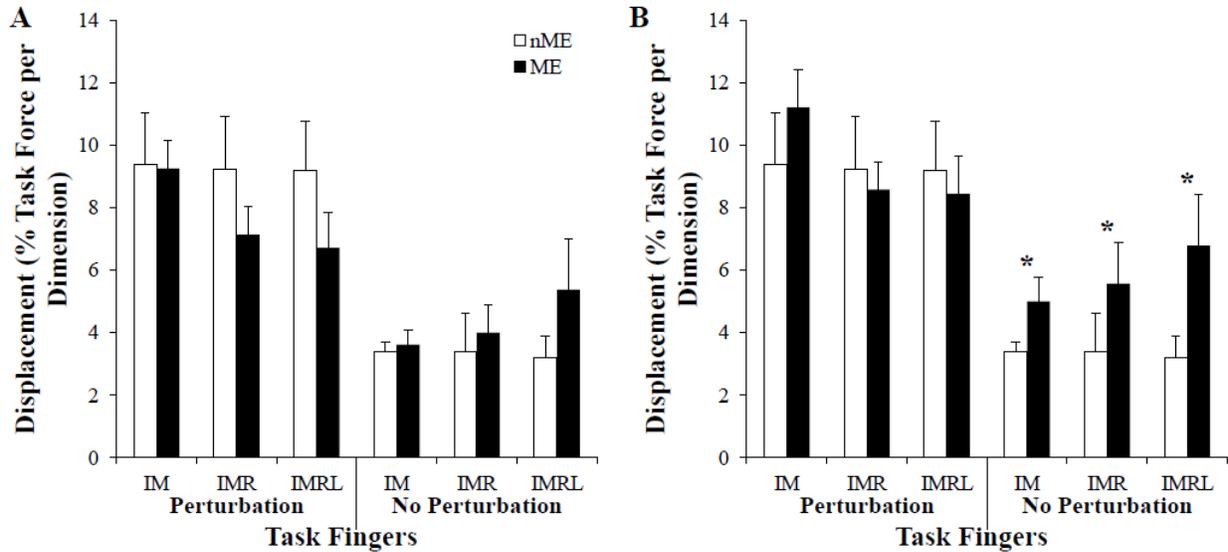


Figure 15: Motor equivalent and non-motor equivalent components of system displacement between Phase 1 and Phase 3 in force space (Panel A) and mode space (Panel B).

CHAPTER 5

Discussion

The study presented here tested six specific hypotheses, three relating to comparison of I- and IM-pressing tasks and three comparing IM-, IMR-, and IMRL-pressing tasks. In the former group, Hypothesis-1 predicted synergic inter-trial variance in all steady states only in redundant state spaces; Hypothesis-2 predicted synergic inter-trial variance in the difference in elemental variables between initial and final steady states only in redundant state spaces, and Hypothesis-3 predicted that perturbing a non-task finger would result in synergic inter-trial variance in differences of elemental variables only in force space. In the comparison of systems with varying levels of redundancy, Hypothesis-4 predicted synergic inter-trial variance and that the difference between V_{UCM} and V_{ORT} would increase with the number of elements involved; Hypothesis-5 predicted the same result in analysis of inter-trial variance of differences in forces and modes between initial and final steady states, and Hypothesis-6 predicted that motor equivalent (ME) component of within-trial displacement would be greater than the non-motor equivalent (nME) component of displacement, and that this difference would also increase as the number of involved elements increased. None of these specific hypotheses were completely correct, and some of them were completely incorrect.

In the contrast of apparently single finger system with the two-finger system, the single-finger task still displayed significantly more variance within the UCM (computed for the total force) than orthogonal to it ($V_{UCM} > V_{ORT}$). This was true for the analysis in each of the three phases: prior to the perturbation (Phase-1), in-between the lifting and lowering phases of the perturbation (Phase-2), and after the perturbation (Phase-3). Hypothesis 1 predicted this result only in the space of finger forces, but the experiment showed that the inequality $V_{UCM} > V_{ORT}$ was true for analysis in the space of finger modes (*Figure 7*) as well, even though a single-finger task is supposed to be non-redundant in mode space, which would imply V_{UCM} must be zero (cf. Scholz and Schöner 1999; Hsu et al. 2007). This result suggests that the subjects were using more than one mode even though they were instructed to press with only one finger.

V_{UCM} was also greater than V_{ORT} when the *differences* in the finger forces (and modes) between Phase-1 and Phase-3 were the subjects of analysis (*Figure 8*). Based on a previous study (Wilhelm et al. 2013), we expected $V_{UCM} > V_{ORT}$ only when a redundant set of elemental variables was involved in the action. In contrast to this expectation, this inequality was observed in analyses of I-condition in both finger force space and finger mode space. We therefore conclude that relative equifinality in the task variable (low V_{ORT} , reflecting low variance of total force) following a transient perturbation was accompanied by non-equifinality in both the redundant (force) and apparently non-redundant (mode) spaces of elemental variables (reflected in the high V_{UCM}). So, there was no qualitative difference in all the variance characteristics between the 1-finger and 2-finger tasks despite the fact that the latter were redundant in the mode space while the former were not.

We also predicted (Hypothesis 3) that a perturbation to a non-instructed finger would not lead to the $V_{UCM} > V_{ORT}$ signature in the finger mode space, while the inequality was expected in the force space. This hypothesis was also rejected because both force and mode analysis showed similar results. Indeed, across conditions, in trials with perturbation applied to the ring finger (a non-task finger), total force was stabilized by co-variation of finger forces and finger modes in

all three analyzed phases of the movement. Further, the changes in both finger forces and modes co-varied in a way that resulted in relative equifinality of total force.

Similarly, across the perturbation and finger-pressing conditions studied in redundant systems, the component of inter-trial variance that did not affect total force (V_{UCM}) was consistently larger than the component that affected total force (V_{ORT}). The inequality $V_{UCM} > V_{ORT}$ held for both phases and differences between phases; it was true for analyses in both force and mode spaces. Overall, these results confirm previous observations from the application of transient perturbations to the four-finger system (Wilhelm et al. 2013). Additionally, when two components of the displacements over the trial duration in the space of finger forces (modes) were quantified, motor equivalent (ME) and non-motor equivalent (nME), the ME component was consistently large: either larger than nME (in mode space for control trials), or statistically indistinguishable from nME displacement (for other analyses). These observations are similar to those reported in earlier studies of multi-joint reaching tasks quantified in the spaces of joint configurations and muscle activations (Mattos et al. 2011, 2013).

While the main result of Wilhelm and colleagues was duplicated in tasks with different numbers of instructed fingers, our specific hypotheses relating to the contrast of systems with varying levels of redundancy were largely falsified. Increasing the number of instructed fingers involved in the task did not significantly affect distribution of inter-trial variance between V_{UCM} and V_{ORT} as reflected in the magnitude of ΔV computed over steady states (Hypothesis-4) and for the difference between phase 3 and phase 1 (Hypothesis-5), while the magnitude of the ME component also did not vary across conditions with different numbers of task fingers (Hypothesis-6).

Taken together, these unexpected results force us to reconsider behavior of humans under the instructions to use any subset of fingers of a hand. These results also suggest that the phenomenon of enslaving is not as stable as previously thought - and that finger interactions may change within a few seconds under the action of an external perturbation, even if a person is trying not to change commands to the fingers.

5.1 Task Specific Stability and its Behavioral Consequences

The idea of task-specific stability (Schöner 1995) is tightly linked to the problem of motor redundancy (Bernstein 1967). This is because the central nervous system (CNS) can only prioritize stability in some directions over others when it has a redundant set of elemental variables at its disposal. One consequence of task-specific stability is the so-called *synergic* structure of inter-trial variance. The word "synergy" takes on various meanings in the motor control literature (see Latash 2008 for a review), and is often taken to mean a group of variables, which scale together during a task or across tasks (d'Avela et al. 2003; Ivanenko et al. 2004; Ting & Mcpherson 2005; Tresch & Jarc 2009). This definition of synergy follows from Bernstein's (1967) hypothesis that the central nervous system must somehow reduce the number of elemental variables in redundant systems to a manageable number for control purposes. Within the theoretical framework provided by the principle of motor abundance and the UCM hypothesis (Scholz & Schöner 1999; Latash et al. 2007; Latash 2012), however, *synergy* refers to co-variation in a relatively high-dimensional space of elemental variables such that the relatively high variance in this space is associated with relatively low variance of a salient performance variable. This characteristic of synergy is evident in the data presented: the magnitude of V_{UCM} was far greater than that of V_{ORT} for all finger-pressing conditions, with and without

perturbations, even in minimally redundant (two-finger, and – to some extent – single-finger) tasks (cf. Latash et al. 2001).

When a redundant system is subject to a perturbation, it is expected to deviate primarily along the directions of low stability, i.e. along the UCM. Our analysis of the differences between forces and modes in phase-1 and phase-3 confirm these predictions: inter-trial variance of deviations over the time course of each trial also displayed the signature of synergic organization: $V_{UCM} > V_{ORT}$. While this observation supports earlier results of studies with perturbations applied during multi-finger and multi-joint tasks (Wilhelm et al. 2013; Zhou et al. 2014a), it also extends these observations to tasks with different numbers of explicitly involved elements. While redundancy is theoretically essential for the inequality $V_{UCM} > V_{ORT}$ to exist (in non-redundant tasks, V_{UCM} is zero by definition), our study shows that changes in the number of explicitly involved elements has no effects on the structure of inter-trial variance (reflected in particular in the synergy index ΔV , *Figure 13*). Indeed, it appears that even apparently “non-redundant” systems, it seems that the human motor system does not act accordingly: in the I-pressing task, this synergistic signature of variance was also observed (*Figure 7*), an impossibility in a truly non-redundant task.

A system with task-specific stability may also be expected to show large drift within the UCM both spontaneously and under the action of transient perturbations. This characteristic has been observed in terms of the large ME component of displacement induced by an external unidirectional perturbation and also by corrections of the deviations induced by the perturbation (Mattos et al. 2011, 2013). Our study is one of the first to demonstrate large ME deviations of a multi-finger system under a transient perturbation (see also Mattos et al. 2014). As in the case of indices of the structure of variance, a change in the number of explicitly involved fingers had no effect on the proportion of ME motion in the total motion within the four-finger force (mode) space.

A system stabilized in a task-specific way is expected to display all three aforementioned characteristics: a synergic structure of inter-trial variance, greater variance in directions that do not affect task performance in response to transient perturbations, and relatively large drift in directions that do not affect performance. The one, two, three, and four-finger systems we studied all exhibited these characteristics with no major differences related to the number of explicitly involved fingers. This result allows two interpretations. The first is that all the mentioned characteristics show qualitative changes between redundant and non-redundant systems (for the latter, $V_{UCM} = 0$; ΔV is negative; and ME motion = 0), while the number of extra elements has no effects on the quantitative indices of those characteristics.

This interpretation, however, seems to be at odds with earlier results, which showed that, during accurate finger force production tasks, humans preferentially stabilize the total *moment of force* computed with respect to the longitudinal axis of the hand/forearm (Latash et al. 2001; Scholz et al. 2002). In particular, during two-finger tasks, the structure of variance showed strong stabilization of the total moment of force (positive co-variation of finger forces and modes across trials), which was incompatible with stabilization of total force requiring negative co-variation of finger forces. In three-finger tasks, episodes of force stabilization emerged, and they became more pronounced in four-finger tasks, while stabilization of total moment of force (not instructed!) persisted over two-, three-, and four-finger tasks.

There are two important differences between the cited studies and the current one. First, the earlier studies used cyclical force production, which involved phases with relatively fast force changes, which are known to lead to large V_{ORT} computed for total force resulting in lower

indices of force-stabilizing synergies (Goodman et al. 2005; Friedman et al. 2009). The current study used steady force production thus favoring force-stabilizing synergies. Maybe more importantly, in the earlier studies, only the explicitly involved fingers produced force, while the other fingers of the hand did not even touch force sensors. In our study, across conditions, all four fingers rested on force sensors. So, it is possible that, despite the difference in the instructions, all the tasks were effectively four-finger tasks with different involvement of task and non-task fingers. This conclusion is supported by the results of our analysis that was always performed in the four-dimensional space of finger forces (modes).

5.2 Enslaving: Are Finger Modes Synergies in Themselves?

The two spaces of elemental variables used in our analyses, the finger *force* space and the finger *mode* space, are linked via the phenomenon of enslaving. This term reflects unintentional movement of (or force production by) a finger when another finger of the hand moves (or produces force) intentionally (Kilbreath & Gandevia; Li et al. 1998; Zatsiorsky et al. 2000; Kim et al. 2008). Enslaving results from a variety of factors including multi-digit extrinsic hand muscles, connective tissue links between fingers, and overlapping cortical representations (reviewed in Schieber & Santello 2004; Zatsiorsky & Latash 2008). In all the mentioned studies, patterns of enslaving for a given person have been viewed as a stable characteristic of that person's hand. In particular, the assumption of stable enslaving allowed the introduction of the notion of finger modes (Zatsiorsky et al. 1998; Danion et al. 2003), which has been used in many studies of multi-finger synergies within the framework of the UCM hypothesis (starting from Latash et al. 2001; reviewed in Latash et al. 2007; Latash 2008).

Changes in enslaving have been documented over years of specialized practice (Slobounov et al. 2002), with healthy aging (Shinohara et al. 2003, 2004), and with neurological disorder (Park et al. 2012). Several recent studies have provided evidence for changes in enslaving occurring relatively quickly, over a single one-hour session involving finger fatigue or specialized practice (Singh et al. 2010; Wu et al. 2013). The results presented here suggest that enslaving may be an even more volatile phenomenon than the previously cited papers suggest: we observed changes in enslaving within a single trial, over the time course of seconds (*Figure 6*). Given the speed of these changes, they likely reflect modifications in the control of fingers at a neural level. These observations force us to reconsider the notion of finger modes and its role in the analysis of multi-finger synergies.

Any study of a synergy must begin by selecting a level of analysis, a space of elemental variables within which synergies are quantified. This choice is frequently made to ensure that the central nervous system can change elemental variables one at a time such that co-variation in the space of elemental variables may be interpreted as a reflection of a task-specific neural strategy. Our results suggest that finger modes may be viewed as elemental variables during analysis of multi-finger actions but that their composition may reflect synergies in another state space of elemental variables (e.g., forces or muscle activations), which may stabilize aspects of performance that were not explicitly specified by the task. For example, the very first studies of multi-finger synergies within the framework of the UCM hypothesis used an accurate total force production task in pressing (Latash et al. 2001; Scholz et al. 2002). Even though those subjects were only asked to stabilize total force, they showed strong synergies stabilizing the pronation-supination *moment of force*. This occurred despite the fact that neither feedback nor instruction

regarding moment of force was supplied. Similarly, *mode* composition may change within the UCM to stabilize the moment of force - or another variable - reflecting a self-imposed constraint.

One outcome of this conceptualization of finger modes is that *no task can truly be called a single-finger task*. Even if a single finger mode is involved at the onset of a trial, natural variation in finger forces and muscle activations may lead to modifications of the mode vectors and unintentional deviations of other finger modes from zero values. These deviations may reflect low stability of finger modes in directions within the task-specific UCM. Indeed, Table 2 shows that some subjects produced negative values of finger modes for fingers that were not instructed to produce force. Since the enslaving matrices used to compute modes were based on subjects' performance in flexion tasks ("ramp" tasks; see methods), negative modes reflect a subject's apparent interference with the flexion he or she typically exhibited in non-task fingers during flexion tasks with the corresponding task fingers involved. In other words, these subjects unloaded those fingers (relative to typical action) to ensure that the deviations of overall modes and forces were within the UCM. Similar results are seen in tasks in which certain involved subgroups of fingers press while subjects are *explicitly* asked not to press with other fingers (Kang et al 2004).

5.3 Relating the Findings to Control with Referent Body Configurations

We view the neural control of movement as based on a hierarchical scheme where control variables at each level may be associated with the specification of referent values for salient performance variables (Latash 2010). The referent configuration (RC) hypothesis (Feldman 2009) assumes that, at the task level, a few referent coordinates for task-specific variables are specified (RC_{TASK}). A sequence of few-to-many transformations then leads to RCs at lower levels, extending down to individual alpha-motoneuronal pools where the RC is equivalent to the threshold of the tonic stretch reflex as in the lambda-model (Feldman 1986).

Back-coupling loops, similar to those described in earlier models (Latash et al. 2005; Martin et al. 2009) ensure that variance in the RCs at each level is mostly within the UCM for the RC at the higher level. This sort of back-coupling loop operates in a manner similar to the function of Renshaw cells: when the motor units of a given alpha-motoneuronal pool lengthen to the threshold of the tonic stretch reflex, the activation of that pool inhibits the activation of proximal motor pools, resulting in negative co-variation between pools and thereby stabilizing total activation (and force level). In addition to these neural loops, a sensory-based loop on task-related variables further ensures that the movement ends at the RC_{TASK} or, if the movement is blocked, non-zero forces are generated. Variables recorded in typical experiments are only indirect reflections of corresponding RCs. For example, in our study a finger mode may reflect a shift in RC in another state space such as that of finger forces or muscle activations. On the other hand, RC for total force production is based on RCs in the finger mode space, reflected in changes in the mode magnitudes. Interactions between the RC, the body, and the physical world lead to a given actual configuration of the body moving towards the RC, while the back-coupling loops ensure stability of this process.

Another sort of back-coupling has recently been suggested based on observations of unintentional movements in experiments when actual body configuration is kept away from the RC for long time intervals (Ambike et al. 2014; Zhou et al. 2014b). This process, addressed as *RC-back-coupling*, is thought to result in a relatively slow drift of RC *toward* the actual body configuration. In our experiment, during the perturbation that moved the finger away from its

referent coordinate, finger force dropped and, as a result, total force was significantly lower at the end of the trial than early in the trial (*Figure 5; Figure 11*). This force drop was significantly smaller in the absence of finger perturbation (similar to results of Wilhelm et al. 2013). The modest force drop in the control conditions (without perturbations) has been reported earlier after turning visual feedback off (Slifkin et al. 2000; Vaillancourt & Russell 2002).

Since RC control involves a hierarchy of synergies, and RCs are affected by actual body configuration, we may expect that the synergies which an RC actualizes will also change over time. Specifically, when looking at the development of a task over time, elemental variables on one time scale may turn out to be organized in a synergic fashion when analyzed on another time scale. This suggests that RC-back-coupling may occur on multiple time scales; indeed, RC-back-coupling has been observed with characteristic times varying from 1 s to 15 s (Zhou et al. 2014b; Ambike et al. 2014b) depending on - among other things - the magnitude of the perturbation and the dwell-time during which the body is held away from the RC.

5.4 Equifinality and Motor Equivalence

Within the equilibrium-point and RC hypotheses, transient perturbations during a movement are not expected to affect the end state of that movement as long as neural signals are not changed in response to the perturbation (Feldman & Latash 2005). This phenomenon is termed *equifinality*. While equifinality has been observed experimentally (Bizzi et al. 1976; Kelso & Holt 1980; Latash & Gottlieb 1990; Schmidt & McGown 1980), it can also be violated, in particular during movements performed in a centrifuge (DiZio & Lackner 1995; Lackner & DiZio 1994) and in an unusual velocity-dependent force field (with "negative damping," Hinder & Milner 2003). Our experiment provides an example of a violation of equifinality due to the hypothesized RC-back-coupling: the drop in total force, particularly pronounced in trials with perturbations. Note that the drop in total force was stabilized by synergies in both finger force and finger mode state spaces ($V_{UCM} > V_{ORT}$, Figure 8; Figure 12). These results are consistent with the basic idea of different stability characteristics of a multi-element (abundant) system in directions that affect performance (orthogonal to the UCM) as opposed to those which do not (within the UCM), even when changes in both directions are unintentional.

The stability properties of a system may be tested in multiple ways: analysis of variance across repetitive trials (assuming that all trials start from somewhat different internal body states); administration of external perturbations and observing the response of the body; and analysis of internally generated corrections. We used the first two methods in the experiments presented here. The first method showed higher variance (lower stability) in both finger force and mode spaces *within* the UCM than *orthogonal* to it. The second method showed that changes in finger forces and modes produced by transient perturbation also were characterized by the inequality $V_{UCM} > V_{ORT}$ (as in Wilhelm et al. 2013). The third method was used in earlier studies of movement kinematics and muscle activation patterns during reaching when unexpected perturbations were introduced and the subjects were instructed to correct their movements (Mattos et al. 2011, 2013). Those studies projected the corrections onto the UCM and ORT spaces and showed strong motor equivalent (ME) components within the UCM: large components of the corrective action led to no correction at all. In fact, in those studies, ME components were significantly larger than nME ones, even though only nME components of motion actually corrected the action.

In contrast to the mentioned studies by Mattos and colleagues (2011, 2013), in our experiment, the inequality $ME > nME$ was not always seen. While it was observed in the contrast of I- and IM-pressing tasks with perturbations (*Figure 9*), it failed to generalize across perturbations with more fingers involved. While we observed $ME > nME$ in unperturbed trials with more fingers pressing, ME and nME displacement of statistically indistinguishable magnitude (*Figure 15*) when these systems were subject to perturbations. Note that the shape of the data cloud and the direction of motion can change independently of each other. In our scheme, however, both reflect different stability properties of the four-finger system along the UCM (low stability, large variance, and large ME component) as compared to the ORT direction (high stability, low variance, and small nME component).

The large amount of ME motion in the mentioned experiments with voluntary movement corrections (Mattos et al. 2011, 2013) and in the current study suggests that most motion of the system was wasteful, i.e., inefficient in moving the salient variable. These results seem at odds with the ideas of optimal control (including optimal feedback control) of abundant systems (Diedrichsen et al. 2010; Todorov & Jordan 2002). The fact that large “efforts” were spent on moving within the UCM suggests that no simple optimality principle can account for such data. This result is one of the many reasons (reviewed in Latash 2012) that motor control schemes requiring the CNS to solve computational problems posed by natural movement tasks should be replaced by a physical approach that views the observed motor and neural patterns as direct consequences of laws of nature.

SUMMARY AND CONCLUDING REMARKS

This study explored the stability of the four-finger force production system with various levels of imposed redundancy: from “none” in the single-finger task analyzed in the finger mode space to full redundancy when all four fingers were involved. Stability was tested by observing inter-trial variance of the system in each configuration, and also by applying small, smooth, transient perturbations to the system and observing the structure of variance in the deviations which those perturbations caused. Unexpectedly, there was little qualitative difference in the stability of the system at any level of redundancy and in force and mode spaces – even in the theoretically non-redundant space of finger modes in a single-finger task.

Unexpected as they were, these results generally support a picture of motor control in which intentional movement is organized in a synergic way by means of multiple few-to-many mappings which hierarchically involve various levels of elemental variables. A possible insight from this study, in fact, may be the realization that finger modes themselves can be viewed as task variables which are stabilized with finger forces.

The findings presented here should be somewhat tempered, however, by the need for future studies which investigate related aspects of motor control which this study was not able to disambiguate. The relative independence of the index finger as compared to other fingers has been well documented (Li et al. 1998), so the fact that this study primarily applied perturbations only to the index finger may affect some of the observed effects. Additionally, the exact effect of removal of visual feedback which must accompany a “do not react” instruction has not been thoroughly investigated. In this study, feedback was removed at the same time as perturbation was incurred, which does not yield any further insight into how the removal of feedback contributed to the observed effects, although whatever differences were observed between perturbation conditions should be robust to this effect since perturbation and removal of visual feedback always occurred simultaneously.

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