ABSTRACT

Title of Thesis: THE ORGANIZATION OF MOTOR SYNERGIES IN ONE-PERSON AND TWO-PERSON MULTI-FINGER FORCE PRODUCTION TASKS

Kelsey A. Christensen, Master of Arts, 2017

Thesis Directed By: Dr. Jae Kun Shim, Ph.D.
Department of Kinesiology, Bioengineering, Neuro and Cognitive Sciences (NACS)

Humans perform motor tasks every day, both individually and with others. Performing motor tasks involves the organization of motor synergies, task-specific groupings of individual motor effectors that are temporarily constrained to act as a single unit and whose total combined output ensures stability of the overall task performance. Both intra- and inter-personal motor synergies have been found to exist in one-person and two-person motor tasks, respectively. Not as clear, however, is whether separate synergies can exist simultaneously on multiple levels of control within a given task. The purpose of the current study is to investigate the organization of force-stabilizing motor synergies during one-person and two-person finger-force production tasks using the Uncontrolled Manifold Analysis. We expect to find both intra- and inter-personal motor synergies, an increase in synergy strength as tasks require more motor

effectors, but the lack of simultaneously-occurring motor synergies on multiple levels of control within the given tasks.

THE ORGANIZATION OF MOTOR SYNERGIES IN ONE-PERSON AND TWO-PERSON MULTI-FINGER FORCE PRODUCTION TASKS

by

Kelsey A. Christensen

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Advisory Committee:
Dr. Jae Kun Shim, Chair
Dr. Ross H. Miller
Dr. Hyun Joon Kwon

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Table of Contents

Chapter 1: Introduction

Humans successfully perform various motor tasks every day. In every situation, performing motor tasks successful requires careful coordination. The accomplishment of these tasks may require individual motor action or joint motor action, depending on the task. Joint motor action is any action performed by two or more people together. People engage in joint motor action any time they exchange money at the cash register, exchange documents or merchandise, shake hands, play a sport, or move heavy furniture with another person. Because so much of what humans do in daily life revolves around interacting with others, joint motor action research and the study of how individuals coordinate their actions is important. Specifically, it is valuable to understand how an independent central nervous system (CNS) overcomes the Degrees of Freedom Problem and whether or not it can organize inter-personal motor synergies during joint action. Additionally, understanding the organization of motor synergies on varying levels of control within a task (i.e., whether or not intra-personal motor synergies seen during individual motor action are still present at the between-hands level during joint motor action) will allow us to explore the potential limits of the CNS. This is an area that has been largely ignored by the academic literature. The current study aims to address this gap in the research and hopes to shed valuable light on how the central nervous system executes joint motor action.

Degrees of Freedom Problem

One of the biggest questions in human motor control is how the nervous system controls its many effectors to coordinate and carry-out purposeful movement. When faced with a given motor task, the human body has an excessive number of potential motor effectors, or degrees of freedom (DOF; muscles, limbs, fingers, joints, etc.) it can recruit to stabilize task performance. Stabilization of task performance is seen when the trial-to-trial variability of the task performance variable (e.g. the total force produced in a finger-force production task repeated) is kept low. In general, the human body has hundreds of muscles which then act upon the skeleton and cause movement. During any given movement, each active joint, limb, or segment, can act in a variety of positions and move with a variety of velocities (Turvey, 1990). Because of the overwhelmingly abundant DOF available to the CNS as well as the option for varied kinematics, kinetics, and patterns of muscle activation with each attempt, a given motor task can be performed in a theoretically endless number of ways (Latash, Scholz, & Schoner, 2002). Consider the example of picking up a glass from off a table and repeating that same task several times: with each attempt, the shoulder, elbow, and wrist can each be held at varying degrees, each in three different planes. Varying quantities and arrangements of motor neurons can be recruited in each attempt causing infinite variability in which muscles are used and how much force is produced. Thus, the motor task of picking the glass up from off the table can be performed in an infinite number of ways. In this example and with almost all other human movements, the CNS is faced with the problem of selecting one movement from a nearly infinite number of options. In motor control literature, this problem was first identified by Bernstein as the DOF problem, or the problem of motor redundancy (Bernstein, 1967). The DOF problem questions how the CNS organizes and controls excessive DOF to produce purposeful movement and to execute motor tasks.

Within the context of the DOF problem, working with a co-actor to complete a motor task introduces even more DOF into the system, amplifying the DOF problem. As previously mentioned, humans interact with each other on a daily basis to perform joint, or two-person, motor tasks. How does the CNS handle this enhanced abundance to perform motor tasks involving two people?

Theory of Motor Synergies

An early attempt to answer the DOF problem and to explain motor coordination was the formulation of the theory of optimal control. The theory of optimal control is based on the idea that the CNS optimizes movement behavior with respect to the given motor task. It states that the CNS performs a cost function analysis for the task and defines and implements an optimal solution that achieves the goal of the task (Diedrichsen, Shadmehr, & Ivry, 2010). In other words, when faced with a given motor task, the CNS computes a complex calculation to select the single, best solution for the task. This theory sees abundant DOF as a problem, a burden on the CNS as it works to execute movement.

A second theory within the context of the DOF problem is the theory of optimal feedback control. While related to the theory of optimal control, the theory of optimal feedback control does not suggest that the CNS selects a single, optimized solution for a given motor task. Instead, it states that the CNS uses feedback more intelligently, that instead of enforcing an optimized solution across repetitions of a task, it corrects only those deviations that interfere with successful task performance (Todorov & Jordan, 2002b). This results in a varied range of solutions to a given motor task across multiple repetitions. This aspect of the theory of optimal feedback control is more similar to the principles laid out in the theory of motor synergies, a third theory attempting to answer the DOF problem.

The theory of motor synergies was originally proposed by Bernstein in 1967 (Bernstein, 1967). Bernstein suggests that having many DOF allows the CNS to effectively stabilize important performance variables while still allowing sufficient flexibility to handle possible perturbations (Bernstein, 1967; Latash et al., 2007). With more studies looking at the DOF problem from this point of view, the problem of redundancy has been redefined as the principle of abundance (Latash, 2012). Flexibility within this context is seen when the variability of individual DOF outputs are relatively high while the variability of sum of their combined outputs remains low. The theory of motor synergies states that instead of having to select a single, unique solution for a given motor task as is proposed by the theory of optimal control, the CNS uses motor abundance to its advantage by selecting a family of solutions for the task, defined as a motor synergy. A motor synergy, in this sense, is a functional grouping of relatively independent DOF which are then temporarily constrained to act as a single unit and allow for increased flexibility in performing a given motor task (Romero et al., 2015; Turvey, 2007). It is the organization of DOF in a task-specific way such that, if any individual DOF in the system makes a mistake, other DOF change their behavior to compensate for the error without needing the CNS to send additional signals (Latash et al., 2002). The internal degrees of freedom work together by adjusting to their mutual fluctuations or mistakes as well as to the changes in the environment to stabilize task performance (Turvey, 2007). This way, the CNS only has to make a single command while the synergy itself adjusts for any perturbations, compensates for errors, and stabilizes the overall task performance. Thus, the theory of synergies sees abundant DOF, even those that are added with tasks involving two people, as a luxury for the CNS.

The equilibrium-point (EP) hypothesis is another theory in the field of motor control which, like the theory of motor synergies and those theories mentioned previously, attempts to answer the DOF problem and explain coordinated human movement. According to the EP-hypothesis, the CNS activates muscles by changing the "threshold of activation of alpha-motorneurons to afferent signals related to muscle length (threshold of the tonic stretch reflex) by subthreshold depolarization of the alpha-motorneurons" (Latash, 2010). The hypothesis states that all movements are initiated and carried out by a gradual transition of equilibrium points, or states where the body segments and muscle torques involved in the action are in a state of balance with each other, which is accomplished by the CNS's shifting of thresholds for muscle activation (Feldman, 2009; Latash, 2010). The CNS produces movement and performs motor tasks depending on the pattern of threshold shifts that come from transition from one EP to another (Feldman, 2009). This can be illustrated by a simple example: consider the situation in which an individual holds a heavy book on the palm of a hand with the arm outstretched. There exists an initial EP at this point where body segments, torques, and forces are in a state of equilibrium. However, if the book is suddenly removed or falls off the hand, the arm involuntarily moves to reach a new EP. While this example illustrated the EP-Hypothesis during involuntary movement, the human CNS has the ability to influence the EP, change muscle activation thresholds, and elicit deliberate motor action on its own (Feldman, 2009). When faced with a motor task, the EP-hypothesis suggests that the CNS sets a desired EP and the resulting discrepancies between the current EP and the desired EP lead to muscle activations that cause movement towards the desired EP, a process during which the motor task is accomplished (Latash, 2010).

The EP-hypothesis is linked to the theory of motor synergies and the uncontrolled manifold (UCM) hypothesis (see *The Uncontrolled Manifold Hypothesis* below), the theories upon which the current study and expected results are based. Latash (2010) suggests that the mechanism of the tonic stretch reflex, central to the EP-hypothesis, can be seen as a method of organizing a motor synergy whose goal is to stabilize the level of muscle activation at the single-muscle level. Error compensation in this example exists just as it does for motor synergies during a finger-force production task. For example, if one motor unit within the muscle turns off unexpectedly causing a drop in the total force produced by that muscle, the muscle will stretch and cause the activation of the stretch reflex. The stretch reflex responds by increasing the frequency of spindle afferent firing which increases the overall level of muscle activation, compensating for the original error (Latash, 2010). This could also be seen between repetitions of a motor task as muscles tire, mistakes are made, or as environmental conditions change. Thus, error compensation between the elements or DOF involved in a particular movement is an important part of each of these theories.

Organization and Characteristics of Motor Synergies Found in Research

Intra-Personal Motor Synergies

Intra-personal motor synergies have been widely researched and have been found at the highest level of hierarchical control during motor tasks involving one person (e.g., between the forces of the right and left hands during a two-handed force production task using two fingers per hand). Intra-personal motor synergies are synergies that exist within an individual while the individual performs a given motor task over repeated trials. Intra-personal synergies have been studied and quantified in a variety of contexts, including but not limited to, finger force production (Kang et al., 2004; Olafsdottir et al., 2007; Shapkova et al., 2008; Shim, Latash, & Zatsiorsky, 2003b), prehension (Shim, Latash, &

Zatsiorsky, 2003a; Shim & Park, 2007), reaching and pointing tasks (Domkin et al., 2002; Romero et al., 2015), and postural control (Scholz & Schoner, 1999). The synergies are task-specific but can be seen between digits in unimanual tasks, between hands in bimanual tasks, and among other groups of effectors depending on the type of motor task being performed.

Intra-personal motor synergies have been investigated in healthy populations as well as in populations of participants with movement disorders (Park et al., 2014), atypical development (Scholz et al., 2003), and the elderly (Verrel, Lovden, & Lindenberger, 2012). While some differences in synergy characteristics can be seen in atypical populations, overall results from these population types act as additional evidence that intra-personal motor synergies exist during individual, or one-person, motor task performance.

Much of the research on motor synergies has been done within the framework of finger force production tasks. This is due to the fact that the human hand is made up of so many potential effectors. These excessive DOF make it a good tool to use for investigating motor abundance and the characteristics of synergies. Because of this, the current study will utilize a multi-finger force production task and focus more heavily on the research investigating synergies in similar tasks. The bulk of these studies have found intra-personal motor synergies between individual fingers during tasks involving one hand and between hands in tasks involving both hands.

The characteristics of a force-stabilizing motor synergy, a synergy that acts to ensure low variability of the overall total force produced, seen in motor tasks can vary depending on a variety of factors. One factor that affects the organization and strength of a synergy is the pattern of total force production required in the task. In a study performed by Shim et al. (2005), participants used fingers to produce forces matching a given force profile with ramp-up, steady-state, and ramp-down phases. They found that the force-stabilizing synergies fluctuated with the changes in total force. Specifically, the results showed that strong synergies were formed during the steady-state phase but weakened or completely disappeared during the ramp phases. Another study by Shim et al. (2003b) found that the organization of synergies takes a certain amount of time which varies depending on the specific task. Together, these results indicate that synergies are task-dependent and its characteristics can change as the task's goal or required pattern of force changes.

Another factor affecting the strength of force-stabilizing motor synergies is the number of degrees of freedom involved. A study performed by Karol et al. (2011) found that while receiving visual feedback of the total force during multi-finger force production tasks, the indices of force stabilizing synergies significantly increased as the tasks went from two-finger to four-finger combinations. In this study, participants performed force production tasks with the fingers on their right hand in two-finger, three-finger, and four-finger conditions. They found strong multi-finger force-stabilizing synergies across all conditions and that the magnitude of the synergies significantly increased from two-finger to four-finger combinations.

Type of feedback is another factor that affects the presence and strength of motor synergies. The previously mentioned study by Karol et al. (2011) also found that force-stabilizing synergies were stronger during all tasks with visual feedback compared to tasks in which participants were given no visual feedback. A study by Koh et al. (2015), found that multi-finger synergies within a trial are weaker in trials without tactile feedback as compared to the synergies found in those trials with tactile feedback, suggesting that tactile feedback also influences the strength of synergies.

Inter-Personal Motor Synergies

Though not as well-researched as intra-personal motor synergies, a handful of studies have also found that the CNS is able to organize inter-personal motor synergies, synergies between co-actors during two-person motor tasks, similarly to how intra-personal motor synergies are organized between the digits or hands within a single actor during motor tasks involving only one person. In a recent study on joint motor action by Slomka et al. (2015), participants were separated into pairs and required to stand on adjacent force plates. Ground reaction force data was collected from each force plate while the participants prepared to long-jump from the force plate to a marked target. In each condition, participants were connected to each other with varying degrees of coupling: visual coupling only, haptic coupling (partners gripping the same rod), and strong mechanical coupling (partners placing hands on the other's shoulder). They found that the vertical ground reaction forces of the participants in each pair were negatively correlated in the condition with strong mechanical coupling, suggesting the presence of an inter-personal motor synergy between the pair’s forces. These findings indicate that inter-personal motor synergies can exist between two independent co-actors performing a two-person motor task.

Solnik et al. (2015) also found inter-personal motor synergies between participants during finger-force production tasks. Participants performed a finger-force tracking task both individually and then with a partner. In parallel to previous research, they found that intra-personal motor synergies were present during the one-person task. Additionally, they also found that inter-personal motor synergies also exist between co-actors during the two-person task. Masumoto & Inui (2015) found similar results in a finger-force production task involving two actors. Although they used an oscillating force profile and did not quantify synergies in the same way, they found negative correlation (a common feature of motor synergies) between the total forces produced by each participant in the pair. They concluded that the relationship between each participants’ forces was synergistic, which supports findings from previous joint motor action research.

One drawback of the study by Solnik et al. (2015), however, is that participants did not perform identical tasks between one-person and two-person conditions. The study had participants perform the task using four fingers during the one-person task and only two fingers in the two-person task in an effort to keep the total number of fingers used per task identical across conditions. While this helps identify whether two CNSs can perform a motor task in the same way a single CNS can perform the task, it fails to address how a single CNS responds when a second CNS is added to the motor task. Our study aims to address this weakness by having participants perform an identical task across conditions. Thus, individual CNS behaviors can be compared across conditions.

Organization of Motor Synergies within a Single Task

While the findings of many studies support the theory that motor synergies can be organized on at least one level of control in a given task, findings are varied as to whether synergies can exist simultaneously on two or more levels of hierarchical control during the same task. These levels of hierarchical or within-task control, in this context, refer to the ability of the movement system to be broken down into sets of motor subsystems, or task-specific groups of DOF, that can be analyzed individually within a single task (Turvey, 2007). This notion of hierarchical control has been invoked and investigated in a variety of human movement studies (Airbib, Iberall, & Lyons, 1985; Baud-Bovey & Soechting, 2001; Bernstein, 1967; Gorniak, Zatsiorsky, & Latash, 2007a; Koh et al, 2015; Shim et al., 2003a; Shim & Park, 2007). The hierarchical control hypothesis suggests that human movement is produced by a control hierarchy where task demands are distributed across varying levels of control within the hierarchy (Gorniak, Zatsiorsky, & Latash, 2007b). As an example, consider a two-hand multi-finger force production task where the participant uses two fingers per hand. The highest level of control is the between-hands level where the total task force is shared between the right and left hands. The lower level of control is the between-fingers level where the total force produced by each hand is shared across the two fingers. A representation of this can be see in Figure 1.

Using the example illustrated in Figure 1 and drawing on previous research, it is unclear whether the CNS can organize a force-stabilizing synergy between the total forces produced by each of the two hands (the between-hands level of control) as well as a force-stabilizing synergy between the forces of the individual fingers within each hand (the between-fingers level of control) at the same time. If the two synergies could exist simultaneously, the synergy at the between-hands level would act to stabilize the overall total force produced in the task, while the synergy at the between-fingers level would act to stabilize the total force produced by each hand. Can the CNS organize synergies on multiple levels of control at the same time? Findings in the research are varied.

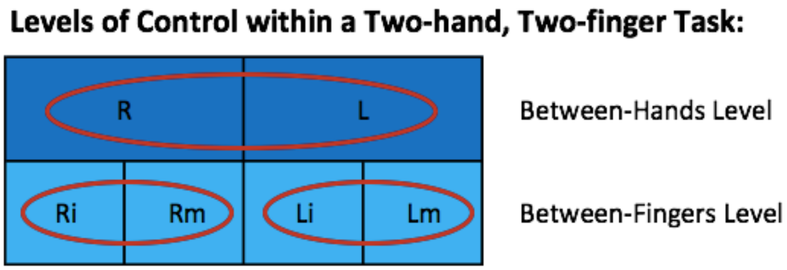


Figure 1: Diagram of the levels of control within a finger-force production task where the participant uses two hands, two fingers per hand.

A handful of studies have looked at intra-personal synergies at two different levels of control. In studies involving two-arm pointing tasks, two separate motor synergies have been found in various studies to stabilize the task performance at the same time (Domkin et al., 2002; Romero et al., 2015). In one study, Domkin et al. (2002) had participants hold a pointer in one hand and a target in the other. The task was to bring the two arms together and touch the pointer to the target. They found intra-personal synergies acting between arms to stabilize the final distance between the pointer and target (between-arms level), as well as synergies within each arm acting to stabilize the trajectory of the endpoint of that arm (within-arm level). These results suggest that intra-personal synergies can exist simultaneously on two levels of control during a two-arm pointing task performed by a single actor. A similar study by Romero et al. (2015) utilized the same task but had two actors perform the task together instead of performing the task individually. Participants sat shoulder-to-shoulder, with one participant using their right arm and one using their left. They found inter-personal motor synergies at the higher, between-arms level of task control as well as intra-personal motor synergies at the lower, within-arm level of control for each individual participant. In addition to finding synergies on two separate levels of control, both studies also found that the synergies present in the higher, between-arm level of control were significantly stronger than the synergies present in the lower, within-arm level of control (Domkin et al., 2002; Romero et al., 2015).

Studies involving multi-finger force production tasks, however, have found results in contrast to the results listed above. In the first study, Gorniak et al. (2007b) investigated the hierarchical organization of intra-personal motor synergies during multi-finger force production tasks performed individually. The study had participants perform two categories of multi-finger force production tasks: a one-handed task using two fingers of a single hand, and a two-handed task using two fingers per hand. Consistent with the body of research investigating intra-personal motor synergy, they found strong force-stabilizing synergies between the two fingers in the one-handed tasks. However, in the two-handed task where two levels of control were present, they found force-stabilizing synergies at the higher, between-hands level of control but either weaker or entirely absent force-stabilizing synergies at the lower, between-fingers level of control. A very similar study in which force-stabilizing motor synergies were analyzed during a finger force production task, led again by Gorniak et al. (2007a), found identical results: when multiple levels of within-task control were present for a task, force-stabilizing synergies were only found at the highest level. These findings bring to light a potential limitation of the CNS to simultaneously organize motor synergies on multiple levels of control within a finger-force production task.

A third study, also investigating the organization of motor synergies during multi-finger force production tasks, found results similar to the those found by Gorniak et al. (2007a, 2007b). The investigation, led by Masumoto & Inui (2015), examined both inter- and intra-personal motor synergies during a two-person, two-hand finger force production task. The investigators had participants perform the force production task individually using the index fingers of both the right and left hands. They then had participants perform the same task but with a co-actor, each participant again using their right and left index fingers to perform the task. The correlation between the two main force signals at one level of the one-person task (right index and left index finger forces) and at two levels of the two-person task (the total force produced by each of the two participants at the higher level of control; and the right index and left index finger forces for each individual separately at the lower level of control) were analyzed. During the two-person task, Masumoto et al. (2015) found negative correlation between the total summed forces produced by each participant (higher, between-subjects level) but positive correlation between the forces produced by the right and left hand within individual participants (lower, between-hands level), indicating the presence of an inter-personal motor synergy at the higher level of control and no synergy at the lower level of control. These findings corroborate the results found in the studies by Gorniak et al. (2007a, 2007b) which indicate that the CNS might be unable to organize synergies on two levels of control at the same time.

One exception to these findings can be seen in a study by Kang et al. (2004) in which a finger force production task was again employed to analyze force-stabilizing motor synergies at two levels of within-task control. Participants performed the same finger force production task every day over a three-day period. During the initial task performance and in parallel to previously mentioned findings for finger force production tasks, force-stabilizing motor synergies were only found at the highest level of within-task control. However, when performing the task again after two days of practice, Kang et al. (2004) found force-stabilizing synergies at both levels of within-task control: between the right and left hands as well as between the fingers within each hand. While these findings support previous research highlighting the potential limitation of the CNS to organize multiple synergies during a single finger force production task, they also suggest that it might be possible for the CNS can learn to overcome this limitation with practice.

The Uncontrolled Manifold Hypothesis

The potential limitation or inability of the CNS to organize synergies on multiple levels of within-task control simultaneously may be explained within the context of the UCM hypothesis. The UCM approach is often used to numerically quantify motor synergies and decomposes motor variability into task-relevant and task-irrelevant dimensions (Riley et al., 2011; Scholz & Schoner, 1999). It quantifies the variance of a set of elemental variables compared to the variance of the performance variable of the whole system across multiple trials of the task. Using a finger-force production task as an example, the UCM approach would quantify the variance of individual finger forces (elemental variables) with respect to the variance of the sum of the individual finger forces, or the variance of total force produced (performance variable). Variance of the elemental variables is assigned to two separate sub-spaces: the UCM subspace that corresponds to a constant value of the total force and wherein changes do not affect overall task performance, and a subspace orthogonal to the UCM that corresponds to changes in the total force. Once the UCM subspace has been selected, the CNS selectively restricts variability of elements outside that space. The CNS allows high variability of the elements within the UCM subspace as long as it does not affect variability of the desired performance variable, or task goal (Latash et al., 2002). The UCM hypothesis allows for an operational definition of motor synergy: if the variance within the UCM subspace (V_{UCM}) is larger than the variance within the space orthogonal to the UCM (V_{ORT}) then it can be concluded that a synergy exists (Latash et al., 2008; Shapkova et al., 2008). This can be tested by calculating an index of synergy (ΔV). It is computed by taking the difference between V_{UCM} and V_{ORT} and normalizing it by the total variance in the system (V_{TOT}) using the following equation:

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

If the above calculation results in an index of synergy significantly greater than 0, it can be concluded that a synergy exists and that the system functions according to the UCM hypothesis. Higher indices of synergy indicate stronger synergies (Latash et al., 2002).

To illustrate how the UCM hypothesis might explain the inability of the CNS to organize motor synergies on multiple levels of within-task control, consider the finger-force production task example previously diagramed in Figure 1: the goal of the task is to produce a constant force by pressing on force sensors with the index and middle fingers of both the right and left hands. When performing the UCM analysis at the between-hands level of control, previous research findings would lead us to expect the presence of a force-stabilizing synergy between the total forces produced by each hand. This would indicate $\Delta V > 0$, or $V_{UCM} > V_{ORT}$, at this level of control within the task. A large V_{UCM} value at the between-hands level, the highest level of control within this task example, can be attributed to the high variance in the total forces produced by the right and left hands. This by definition means V_{ORT} of each individual hand would be rather large as well. At the between-fingers level, the lower level of control within this task example and where the synergy between fingers within individual hands is analyzed, V_{ORT} is large as a function of the large between-hands synergy in the higher level of control. Latash et al. (2008) points out that a high V_{UCM} of a synergy stabilizing the total output at the higher level of control may therefore decrease the likelihood of also seeing a synergy stabilizing the total force of the lower level. The inability of the CNS to organize synergies on multiple levels of control within the same task may be due to this inherent trade-off (Latash et al., 2008; Gorniak et al., 2007a)

To date, no study has attempted to analyze motor synergies on three levels of control within a single finger-force production task. The small handful of studies that have investigated the organization of multiple synergies within a single task only analyzed two levels of within-task control (Domkin et al., 2002; Gorniak et al., 2007a, 2007b; Kang et al., 2004; Masumoto & Inui, 2015; Romero et al., 2015). The current study aims to fill this gap in the literature. We aim to investigate the ability of the CNS to organize force-stabilizing motor synergies on multiple levels of control within a given motor task. The current study will include both one-hand and two-hand tasks performed individually as well as a two-hand, two-person task in which each participant will use the index and middle fingers of each hand to perform the finger-force production task. Including this two-person task will allow us to analyze force-stabilizing motor synergies at three levels of within-task control. Analyzing three levels of control will allow us to investigate whether the trade-off theory still holds at additional lower levels of within-task control. It is possible that as the levels become farther removed from the highest level of within-task control where we expect to see a strong force-stabilizing synergy, the inherent V_{ORT} will become smaller. Thus, it is possible that a force-stabilizing synergy could emerge in these lower levels as it becomes potentially less difficult for V_{UCM} to overcome V_{ORT} and more likely that the inequality $\Delta V > 0$ could be satisfied.

The current study's first hypotheses are based on this synergy trade-off theory presented by both Latash et al. (2008) and Gorniak et al. (2007a), and aim to test it experimentally within the UCM framework. Based on the theory, however, we still expect to only see synergies at the between-subjects level of the IP task and at the between-hands level of the IH task, the highest level of control within each task. While we expect that adding a third level of within-task control to the analysis will provide more information on the CNS's strategy and ability to organize multiple motor synergies within a single task, we also expect that V_{UCM} in both lower levels of control will not be large enough to overcome

V_{ORT} in order to satisfy the inequality $V_{UCM} > V_{ORT}$, ultimately not satisfying the inequality $\Delta V > 0$ which is necessary for the presence of a force-stabilizing synergy to exist.

Magnitude of Force-Stabilizing Motor Synergies

The theory of motor synergies and the principle of abundance suggest that the magnitude of motor synergies is expected to increase as DOF are added to the motor task. This is due to the idea that as more DOF are added to the task more possible solutions become available for the completion of that task. It is expected that the motor synergy would use these added DOF to its advantage and the variability of solutions across repetitions of the task would increase. Within the UCM framework, this would be seen as higher V_{UCM} (task-irrelevant variability) across repetitions of the task. If the task is performed successfully with each repetition as expected, V_{ORT} would remain the same. Thus, this increase in V_{UCM} would cause an increase in the overall magnitude of the force-stabilizing synergy present in the task.

An increase in synergy magnitudes, quantified as higher task-irrelevant variability across repetitions of the task, as tasks involve more DOF is expected according to the principle of minimum intervention as well. The principle of minimal intervention is a theory in the field of motor control which states that the CNS only corrects deviations from the average solution to the task when those deviations are expected to negatively affect the overall task performance. In other words, the CNS allows for variability within the solutions for the task across trials as long as the task is still being performed successfully (Todorov & Jordan, 2002a). When DOF are added to the task, more possible deviations from the average solution become available. Thus according to the principle of minimal intervention, the CNS will allow for this increase in possible solutions to the task as long as the task is still being successfully performed. In the current study, we expect to see this in an increase in synergy magnitudes, or a higher ratio of V_{UCM} to V_{ORT}, as tasks require more DOF.

These theories have been supported by the findings of a study by Karol et al. (2011). In the study, participants performed finger force production tasks with the fingers on their right hand in two-finger, three-finger, and four-finger tasks. Investigators found that while receiving visual feedback of the total force, the magnitude of the force stabilizing synergies significantly increased as the tasks required more fingers, or DOF. A study of this type has not been performed for a two-person task and presents the gap in research our second hypothesis aims to address. The current study aims to investigate whether the principles within the theory of motor synergies and the principle of abundance as well as the findings by Karol et al. (2011) hold when DOF are increased with the addition of a two-person task. We expect that our findings will support the theory of motor synergies, the principle of abundance, and the principle of minimum intervention in that the magnitude of the force-stabilizing synergies will increase as more DOF are required for the task, or as tasks move from one-hand to two-hand for the one-person tasks and then from the one-person tasks to the two-person task.

Purpose of Current Study

The purpose of the current study is to investigate the ability of the CNS to organize multiple force-stabilizing motor synergies within a single task as well as to investigate the change in motor synergy magnitude, or strength, as DOF are added to the task. Specifically, we aim to address the gaps in research where study has failed to investigate the organization of force-stabilizing synergies within a single task on three levels of within-task control as well as the effect that increasing DOF with a two-person task has on the magnitude of force-stabilizing synergies. Participants will perform three finger-force production tasks: a one-person task using only one hand (IE, inter-effector task), a one-person task using both the right and left hands together (IH, inter-hemispheric task), and a two-person task with each participant using both their right and left hands (IP, inter-personal task). Synergies between force signals will be quantified as a comparison of V_{UCM} and V_{ORT} using the UCM analysis and then compared across tasks as well as across levels of control within each task. Based on the synergy trade-off theory (Latash et al., 2008; Gorniak et al., 2007a), the Theory of Motor Synergies, the Principle of Abundance, and previous study findings, we hypothesize and expect to find that 1) force-stabilizing synergies will be present during the IP task only at the highest, between-subjects, level of control, 2) force-stabilizing synergies will be present during the IH task only at the highest, between-hands, level of control, and 3) the magnitude of synergies at the highest level of control within each task will increase as tasks involve more DOF.

<u>Specific Aim #1:</u> To investigate the ability of the CNS to organize synergies on multiple levels of within-task control during both one-person and two-person multi-finger force production tasks.

<u>Hypothesis #1a:</u> Within the IP task, the inequality $\Delta V > 0$ will be true only at the between-subjects level, which will indicate the presence of a force-stabilizing synergy between the total forces produced by each participant stabilizing their total combined force.

<u>Hypothesis #1b:</u> Within the IH task, the inequality $\Delta V > 0$ will be true only at the between-hands level, which will indicate the presence of a force-stabilizing synergy between the forces produced by the right and the left hands stabilizing the total force produced by the individual.

<u>Specific Aim #2:</u> To compare the characteristics of force-stabilizing synergies across one-person and two-person multi-finger force production tasks.

<u>Hypothesis #2:</u> The magnitude of ΔV_Z in the highest level of the main tasks will increase significantly as tasks move from requiring less DOF to more DOF, or as the tasks move from IE, to IH, to IP.

Chapter 2: Methods

Participants

Young adults aged 18-30, both male and female, were recruited through undergraduate courses at the University of Maryland, College Park. We collected data from 42 participants in total. In the literature, there is a wide range in participant numbers. In general, similar studies recruited anywhere from 5 to 20 participants. Because our study involved one task in which participants perform the task in pairs, we wanted the number of pairs, not the number of individual participants, to fall within this range. Participants were given a list of available testing times and were able to sign up for the time slot of their choosing. Participants were tested in pairs, two participants per time slot. All participants gave written informed consent before participating in the study based on the procedures approved by the University of Maryland's Internal Review Board (IRB). The participants also completed a general questionnaire which collected information on participant name, gender, age, race, height, weight, handedness, history of upper limb trauma, and history of neurocognitive impairments or disease. The data of any participants reporting history of neurocognitive impairments or disease was excluded from data analysis. We analyzed data from 17 pairs of participants, or 34 individual participants (23 females, 11 males), in total. Participants included in the analysis ranged in age from 19 to 29 years (21.5 ± 2.27), in height from 152 cm to 196 cm (170.59 ± 10.51), and in weight from 47.63 kg to 131.54 kg (70.96 ± 19.56). Of the 34 participants, 29 were self-reported right-hand dominant.

Procedure

The experimental apparatus consisted of two computer monitors atop one table separated by a curtain. Each participant was seated in a chair at the testing table facing their respective computer monitor on which they received visual feedback of the experimental task and real-time force data. Both arms rested on the table with the upper arm at approximately 45° abduction in the frontal plane and 45° flexion in the sagittal plane and the elbow at approximately 45° flexion. The index and middle fingers of each hand rested on piezoelectric force sensors [Models 208 M182 and 484B, Piezotronics, Inc.] positioned on the table in front of the participant. The sensors were attached to the table with double-sided tape to allow the positions to be adjusted according to individual hand anatomy. Plastic supports for the forearm and palm were attached to the table with Velcro and could also be adjusted according to individual anatomy. The forearm and hand were secured to the plastic supports by Velcro straps. These supports allowed for enhanced comfort at the wrist when performing the finger-force production task. Signals from the force sensors were amplified and digitized at 100 Hz with a 16-bit A/D board [PCI 6034E, National Instruments Corp.] using a customized software program created with LabVIEW [LabVIEW 7.1, National Instruments Corp.]. The experimental setup can be seen in Figure 2.

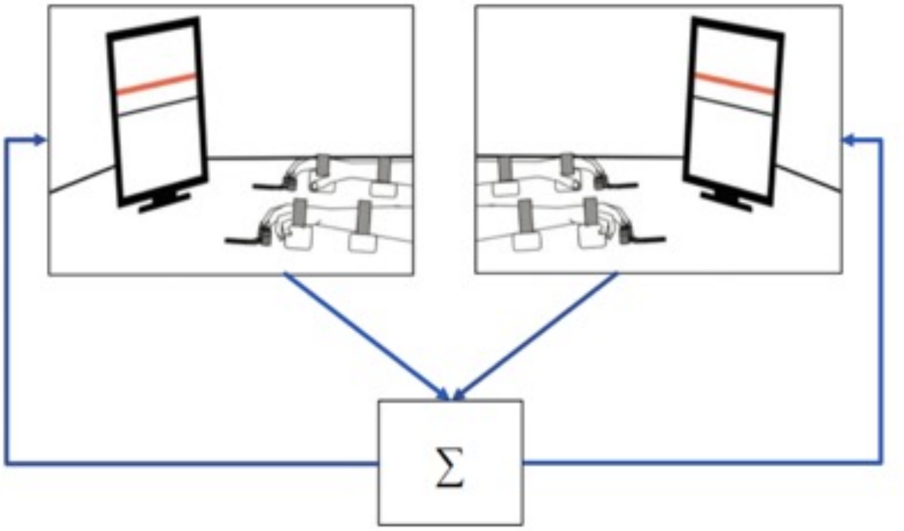


Figure 2: The experimental setup. Participants pressed force sensors with the index and middle fingers of each hand. The feedback screen displayed the task-specific target force (red line) and real-time total force produced by subjects (black line).

Each participant performed four separate tasks: interpersonal (IP), intrapersonal inter-hemispheric (IH), intrapersonal inter-effector of the right hand (IE_R), and intrapersonal inter-effector of the left hand (IE_L), in that order. The IP task was a two-person task which required the two participants in each pair to work together to complete the finger-force production task each using the index and middle fingers of both the right and left hands (P1: Ri, Rm, Li, Lm; P2: Ri, Rm, Li, Lm). The IH task was a one-person task which required that each participant complete the task individually using the index and middle fingers of both the right and left hands (Ri, Rm, Li, Lm). Both IE tasks, IE_R and

IE_L, were one-person tasks completed by each participant individually, the first with the right hand only (Ri, Rm) and the second with left hand only (Li, Lm). Each task consisted of 20 trials. In the finger-force production literature, it is quite common to have participants perform 12-15 trials of each task. Because we plan to analyze the data across trials, we decided to increase the number of trials so we could have more data to analyze in an effort to get a clearer view of participant behavior from trial to trial. Each trial was 10 seconds long in duration with a 10-second rest period between trials to avoid effects due to fatigue.

In the IP task, both participant and co-participant were instructed to work as a pair to produce and maintain a 32N target force for the duration of each 10-second trial. A large portion of finger-force production studies either used 20% of MVC (maximal voluntary contraction; Gorniak et al., 2007b; Karol et al., 2011) or 20N (Koh et al., 2015; Shim et al., 2005; Solnik et al., 2015) as the individual target force during steady-state task phases. In studies specifically involving college student participants, 20% MVC generally fell within the range of 11N-20N (Kang et al., 2004; Shim et al., 2004). Based on the previously mentioned literature, we determined that 16N of force for an individual participant would be a suitable target. Because the IP task is performed by two participants together, we ultimately selected a total target force of 32N. In the current study, a pre-selected target force was only required for the IP task because all target forces in subsequent tasks were computed based on the forces produced by individual participants in the IP task. During the IP task, participants were asked not to speak or make noise and were obstructed from view of their co-actor by a curtain hanging across the table. Participant pairs received identical visual feedback of the experimental task and real-time force data on their monitor screens. Each monitor displayed a horizontal red line that sat motionless midway up the screen. This line represented the experimental task, the target force of 32N. The monitor also displayed a horizontal black line. This line represented the participants' real-time total combined force and traveled vertically up and down the screen according to the sum of the combined forces across all 8 force sensors (P1: Ri, Rm, Li, Lm; P2: Ri, Rm, Li, Lm). An audio signal sounded at both the beginning and end of each 10-second trial. Participants were told to start pressing on all 4 of their force-sensors as soon as possible after the first audio signal sounded with the goal of keeping the black line (real-time total force) as close as possible to the red target line for the duration of the trial. The audio signal at the end of the 10-second trial indicated to the participants that the trial had ended and that they should stop pressing the force sensors.

The remaining three tasks required participants to perform tasks individually and utilized a varying number of force sensors, but each task remained nearly identical to the IP task. There was always a given target force and real-time total force data displayed as a stationary red line and moving black line on the feedback screen, respectively. Again, each task contained 20 trials, 10 seconds per trial, and 10 seconds of rest between trials. Testing for these tasks alternated between the two participants in each pair. The participant not being tested waited in a separate room.

In the IH task, the participant performed the finger-force production task by pressing on four force sensors with the Ri, Rm, Li, and Lm fingers. The target force in this task was the participant's mean total force produced over the 20 trials of the IP task. The purpose of this was to ensure that each subject was performing as similar a task as possible across all tasks. The real-time total force displayed on the monitor in this task was the sum of the participant's forces across all 4 force sensors.

In the IE_R task, the participant performed the finger-force production task by pressing on two force sensors with the Ri and Rm fingers. The target force in this task was the participant's mean total force produced by the right hand (Ri, Rm) over the 20 trials of the IP task. The real-time total force displayed on the monitor in this task was the sum of the participant's forces across both force sensors. The IE_L task was identical except participants used the Li and Lm fingers and the target force was the calculated mean total force of the left hand (Li, Lm) produced by the participant over the 20 trials of the IP task.

Data Processing

For each task, we defined various levels of hierarchical or within-task levels of control. In the IP task, we defined three levels of within-task control. The highest level is the between-subjects level and is where the overall IP task force is shared between participants in the pair. The middle level is the between-hands level and is where each participant's total force is shared between their right (R) and left (L) hands. The lowest level is the between-fingers level and is where each hand's force is shared between its index and middle fingers. Although this level includes both the R and L hand, analyses were done for each hand separately and each analysis was considered a separate grouping within that level of control. In the IH task, we defined two levels of within-task control. The highest level is the between-hands level and is where the overall IH task force is shared between the R and L hands. The lower level is the between-fingers level and is where each hand's force is shared between its index and middle fingers. Again, this level includes both the R and L hand but analyses were done for each hand separately and each analysis was considered a separate grouping within that level of control. In each of the IE tasks, only one level of within-task control was present. This level was the between-fingers level and is where the IE task force is shared between the index and middle fingers.

The finger force data was processed so that we had two force signals at each level of control within each task. With the UCM analysis, we are interested in quantifying the synergies between the two main forces of each level that act to stabilize the total force produced at that level. The UCM analysis compares the variance of elemental variables, which in the case of this study is finger forces. The two force signals at each level of control act as the elemental variables, A and B, in our UCM analyses. The between-subjects level of the IP task includes data from a pair of participants since this level is where the task force is shared between participants. In every other task and in all lower levels of within-task control, the data is organized for each participant individually. A description of how individual finger forces will be grouped into signals A and B at each level of control across tasks can be seen in Table 1.

Grouping of Finger Forces for UCM Analysis

Task	Control Level	Label	Force Signal A	Force Signal B
IP	Between-Subjects	IP	total force of P1 (Ri+Rm+Li+Lm)	total force of P2 (Ri+Rm+Li+Lm)
	Between-Hands	ip - RL	total force of R hand (Ri+Rm)	total force of L hand (Li+Lm)
	Between-Fingers$_R$	ip - RiRm	force of R index finger (Ri)	force of R middle finger (Rm)
	Between-Fingers$_L$	ip - LiLm	force of L index finger (Li)	force of L index finger (Li)
IH	Between-Hands	IH	total force of R hand (Ri+Rm)	total force of L hand (Li+Lm)
	Between-Fingers$_R$	ih - RiRm	force of R index finger (Ri)	force of R middle finger (Rm)
	Between-Fingers$_L$	ih - LiLm	force of L index finger (Li)	force of L index finger (Li)
IE$_R$	Between-Fingers$_R$	IE - R	force of R index finger (Ri)	force of R middle finger (Rm)
IE$_L$	Between-Fingers$_L$	IE - L	force of L index finger (Li)	force of L index finger (Li)

Table 1: Table showing how the individual finger forces within each task were grouped to create force signal A and force signal B for each level of within-task control. The UCM analysis will be performed at each of these control levels using force signals A and B as the elemental variables.

From each 10-second trial, the 6-second window from 3 seconds to 9 seconds where the total force produced was relatively constant was extracted for analysis (Koh et al., 2015) in order to avoid the initial force stabilization in the beginning of each trial and premature cessation of force production at the end (Masumoto & Inui, 2015; Shim et al., 2003b, 2005).

In this study, we decided against using the analysis based on finger modes. Because of the anatomy of the hand, actions of individual fingers are often influenced by the actions of other fingers during motor tasks. This phenomenon is known as enslaving. In experimental tasks where multiple fingers sit on force sensors but only one finger is instructed to apply force, small forces have been found to be unintentionally produced by the other fingers as well (Zatsiorsky et al., 2000). Latash et al. (2007) proposes organizing finger forces into finger modes, hypothetical commands to the fingers, for analyses involving forces of multiple fingers in an effort to correct for the effects of finger enslaving. The current study, after the pattern of similar studies (Gorniak et al., 2007b; Koh et al., 2015; Shim et al., 2005; Solnik et al., 2015), will perform analyses within the state of finger forces only. Additionally, the finger mode analysis assumes that finger enslaving is constant, which may not be true during finger force production (Martin et al., 2009). The potential for changes in the degrees of finger enslaving presents an analytical challenge with the finger mode method.

Task Performance Error

Task performance error for each participant across the four main tasks (IP, IH, IE_R, and IE_L) was assessed using root-mean-square error (RMSE):

$$\mathrm{RMSE} = \sqrt{\frac{\sum_{i=1}^{n} \Delta F_i^2}{n}} \tag{2}$$

where ΔF is the difference between the task-specific target force and the actual total force produced, and *n* is the sample number. Again, the target force for the IP task was 32N while the target forces in each of the remaining tasks differed across participants as those target forces were based on individual participants' performance during the IP task. The sample number used in the current study was 600 due to the fact that data was collected at a frequency of 100 Hz and we analyzed data from a 6-second window of the 10-second trial. RMSE for each task was averaged across the task's 20 trials performed by each participant and then averaged across participants.

We also calculated the biased task performance error using the following constant error (CE) formula:

$$\mathrm{CE} = \frac{\sum_{i=1}^{n} \Delta F}{n} \tag{3}$$

again, where ΔF is the difference between the task-specific target force and the actual total force produced, and *n* is the sample number. While performance error assessed by RMSE above measures the magnitude of error without respect to direction, constant error measures the biased error and indicates the direction of error. In other words, it measures the participant's deviation from the target force and indicates whether that deviation was higher or lower the target force. CE for each task was averaged across the task's 20 trials performed by each participant and then averaged across participants.

UCM Analysis

The UCM Analysis (see *The Uncontrolled Manifold Hypothesis* above; Scholz & Schoner, 1999) was chosen as the method of data analysis in this study because part of our aim was to investigate whether V_{UCM} at the lower levels of within-task control would be able to overcome the inherently large V_{ORT} at those levels that comes from strong motor synergies in the highest level of within-task control. We investigated this by calculating V_{TOT}, V_{ORT}, V_{UCM}, and ΔV at each level of control for each participant.

The first step of the UCM analysis was to select the elemental variables. As previously stated, the elemental variables for each level of control in this study are the force signals A and B, which are the individual finger forces grouped according to the scheme displayed in Figure 4. The next step was to partition trial-to-trial variance into task-relevant and task-irrelevant dimensions, or V_{ORT} and V_{UCM}, respectively. The following calculations were performed for each task and associated within-task levels of control for every participant.

We first calculated the total variance within the system, which is the sum of the variances of force signals A and B. This was done by calculating the mean force of signal A and the mean force of signal B in each trial then calculating the variance of those mean values across the 20 trials in each task. This gave us the trial-to-trial variance for signals A and B, Var(A) and Var(B), which were then used to calculate V_{TOT} in the formula below.

$$V_{TOT} = \mathrm{Var}(A) + \mathrm{Var}(B) \tag{4}$$

We then calculated V_{ORT}, the variance of the total force produced. Again, we calculated the mean force of signal A and the mean force of signal B within each trial. We added those mean forces together within each trial then calculated the variance of the combined mean force across the 20 trials. The final value was divided by two to normalize the variance by the number of effectors involved, the two force signals.

$$V_{ORT} = V(A+B)/2 \tag{5}$$

Given V_{TOT} and V_{ORT}, we then calculated V_{UMC}.

$$V_{UCM} = (V_{TOT} – V_{ORT}) \tag{6}$$

If V_{UCM} is higher than V_{ORT}, it can be concluded that the UCM hypothesis is supported and a synergy stabilizing the total task force exists in the system. This can be verified by calculating an index of synergy (ΔV). If the index of synergy is statistically significantly greater than zero, it can be concluded that a force-stabilizing synergy exists and that the system functions according to the UCM hypothesis. Higher indices of synergy indicate stronger synergies (Latash et al., 2002). Calculating ΔV will also allow us to compare the magnitude of synergies across tasks. There are several methods for calculating ΔV. We chose the following equation because we want to normalize the index by V_{TOT} as we expect the force levels in each level of control to be of differing magnitudes.

$$\Delta V = (V_{UCM}– V_{ORT}) / V_{TOT} \tag{7}$$

Because this method of calculating ΔV naturally creates values within a bounded distribution between –1 (all variance is V_{ORT}) and +1 (all variance is V_{UCM}), it was expected that ΔV distributions would deviate from the normal distribution and violate the ANOVA test's assumption of normality. Thus, all ΔV values used in the ANOVA tests were transformed using Fisher's z-transformation, resulting in the index ΔV_Z.

Statistical Analysis

One-Sample T-Test

A one-sample t-test was applied to ΔV for each task and their associated levels of within-task control separately. These tests were performed with the purpose of investigating our first hypotheses. The tests identified which group means were significantly different from zero, or where the inequality $\Delta V > 0$ was satisfied, identifying in which tasks and on which levels of within-task control force-stabilizing synergies were present. In those tasks where statistical significance was found, only a positive mean difference indicated the presence of a force-stabilizing synergy ($V > 0$). A negative ($\Delta V < 0$) or non-existent ($\Delta V = 0$) mean difference indicated that no force-stabilizing synergy was present.

Paired Samples T-Test

A paired samples t-test was applied to the dependent variables V_{UCM} and V_{ORT} for each task and their associated levels of within-task control separately. These tests determined whether the mean difference between V_{UCM} and V_{ORT} was significantly different from zero and was used to verify the results of the one-sample t-test, again with the purpose of investigating our first hypotheses. A significant positive mean difference indicated that V_{UCM} was significantly higher than V_{ORT} and that a force-stabilizing synergy was present. A negative ($V_{ORT} > V_{UCM}$) or non-existent ($V_{ORT} = V_{UCM}$) mean difference indicated that no force-stabilizing synergy was present.

One-Way Repeated Measures ANOVA

A one-way repeated measures ANOVA was applied to each of the following dependent variables separately: V_{UCM}, V_{ORT}, and the index ΔV_Z, each across all tasks and their associated levels of within-task control. The distributions for both V_{UCM} and V_{ORT} were strongly, positively skewed and deviated from the normal distribution which violated the ANOVA's assumption of normality. Thus, a logarithmic transformation was applied to both V_{UCM} and V_{ORT} variables before performing the ANOVAs. Post hoc pairwise comparisons were performed with Bonferroni adjustments. The results of the ANOVA performed on the ΔV_Z index were used to investigate our second hypothesis, as it allowed us to compare the magnitude of synergies across tasks. The results of the ANOVAs performed on the V_{UCM} and V_{ORT} variables illuminated differences in the components of force-stabilizing synergies across tasks as well as helped clarify why synergies were present in some levels of control within a task but not others.

Chapter 3: Results

Task Performance Error

For each task, participants were able to generally match the given target force without much difficulty as assessed by using RMSE and CE in a task performance error analysis. Figure 3 shows a typical performance from a sample participant over a single trial in each of the four main tasks with the task-specific target force included as a horizontal dashed line for reference.

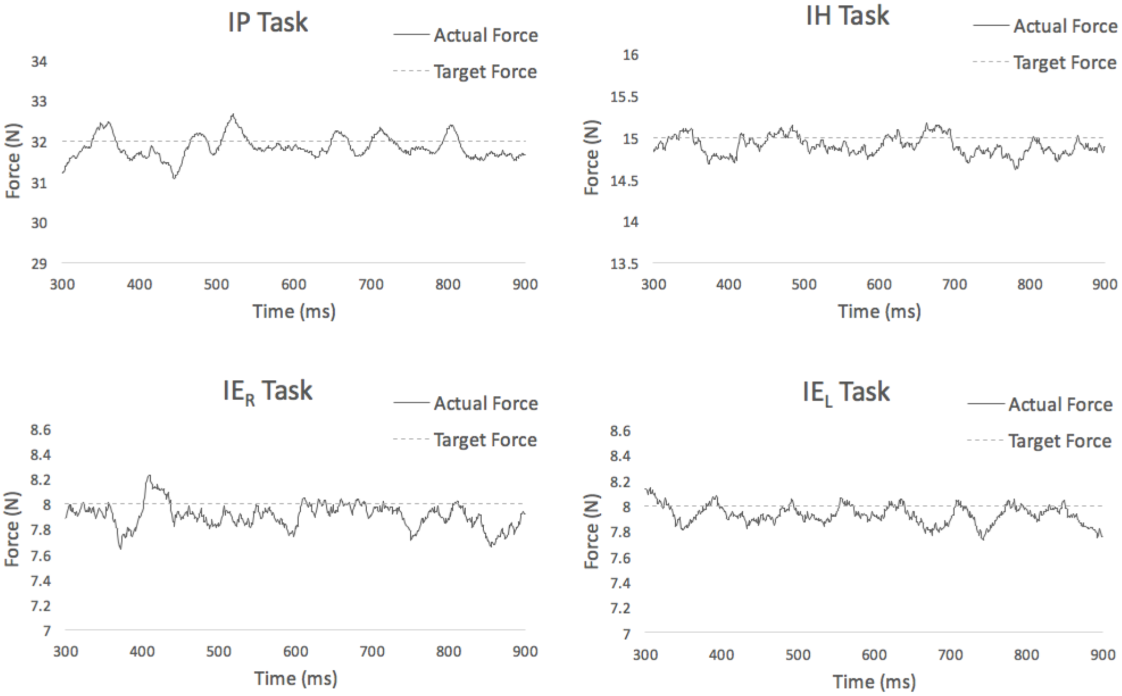


Figure 3: Task-specific target force and profile of total force produced by a sample participant in one trial from each main task: IP, IH, IE$_R$, and IE$_L$.

Results of the RMSE analysis indicated that participants deviated from the target force in the IP task by a mean force (measured in N) of 1.074 ± 0.625, in the IH task by a mean force of 1.363 ± 4.913, in the IE_R task by a mean force of 1.104 ± 2.737, and in the IE_L task by a mean force of 2.011 ± 3.299. These results, however, involved data from two extreme outliers, or two participants who were not able to perform the one-person tasks without difficulty. We were aware of these outliers and, while they made no difference in subsequent analyses, the did make a difference in the overall picture presented by the RMSE analysis for the IH, IE_R, and IE_L tasks. This difference was especially noticeable in the standard deviation values. With the two extreme outliers removed, deviation from the target force was 0.478 ± 0.517 in the IH task, 0.452 ± 0.692 in the IE_R task, and 1.259 ± 1.182 in the IE_L task. In the IP task, the co-actors of these two outlying participants must have compensated for their partner's unstable task performance as we did not see any extreme outliers in the RMSE performance data for the IP task.

Results of the CE analysis indicated that participant's generally undershot the target force. Participants deviated from the target force in the IP task by a mean force (measured in N) of -0.275 ± 0.511, in the IH task by a mean force of -1.003 ± 4.982, in the IE_R task by a mean force of -0.951 ± 2.783, and in the IE_L task by a mean force of -1.245 ± 3.657. Again, the overall picture of task performance in the one-person tasks was more accurate when the performance data from the two extreme outliers were removed. With the outliers removed, participants deviated from the target force by -0.213 ± 0.538 in the IH task, -0.288 ± 0.724 in the IE_R task, and -0.444 ± 1.654 in the IE_L task.

As demonstrated by these results, most participants were able to match the given target force without much difficulty. On average, participants undershot the target force in each of the four tasks by a small margin.

UCM Analysis

The Uncontrolled Manifold Analysis (UCM) was used to numerically quantify synergies. UCM analysis results confirmed findings from previous studies and found force-stabilizing synergies between forces in one-person and two-person finger-force production tasks. A plot of demeaned forces can be seen in Figure 4.

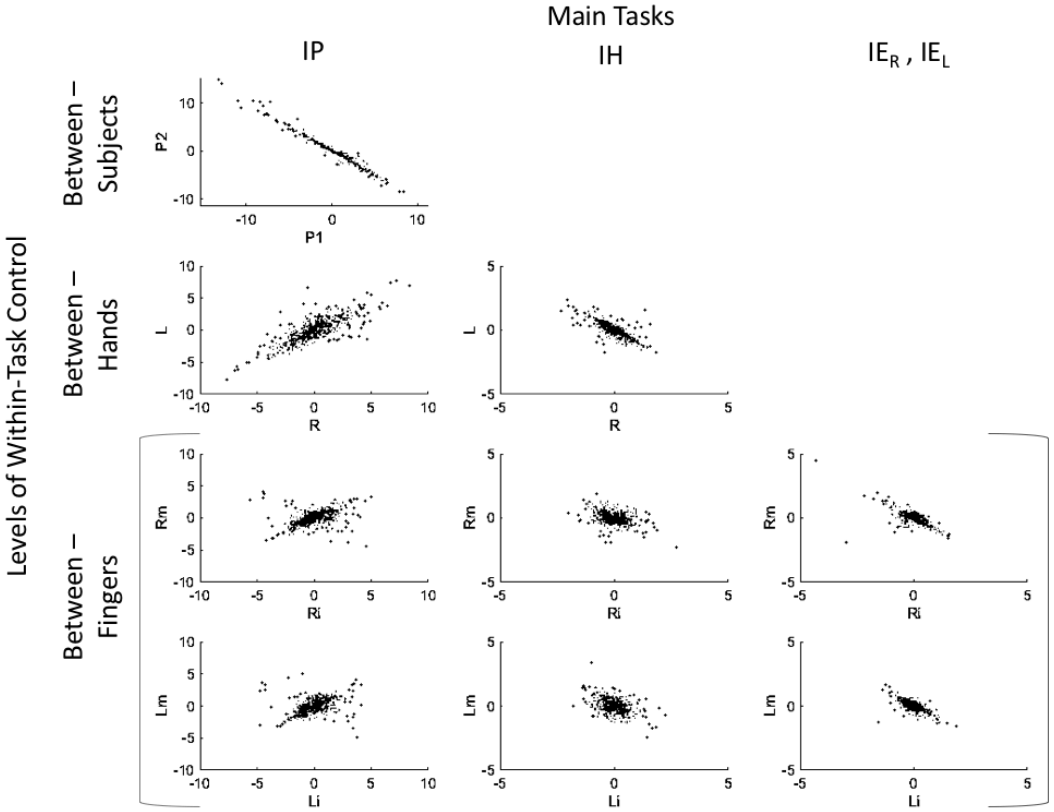


Figure 4: Plot of demeaned forces (measured in N) produced in each trial by all participants across each task and the associated levels of within-task control.

The data illustrated in Figure 4 includes the demeaned force produced in each trial by all participants for each task as well as their associated levels of within-task control. The data clouds provide a general idea of where force-stabilizing synergies might be present. An oblong data cloud with a negative slope indicates $V_{UCM} > V_{ORT}$ and suggests a synergy is present. An oblong data cloud with a positive slope indicates $V_{ORT} > V_{UCM}$ and suggests that no synergy is present. A circular data cloud suggests that V_{UCM} and V_{ORT} are roughly equal and that no synergy is present.

For each task and its associated levels of within-task control, ΔV, ΔV_Z, V_{UCM}, V_{ORT}, and V_{TOT} indices were calculated. These indices represent the calculated index of synergy and its components for each participant. The changes in ΔV, ΔV_Z, V_{UCM}, and V_{ORT} across tasks and levels of within-task control can be seen in Figure 5.

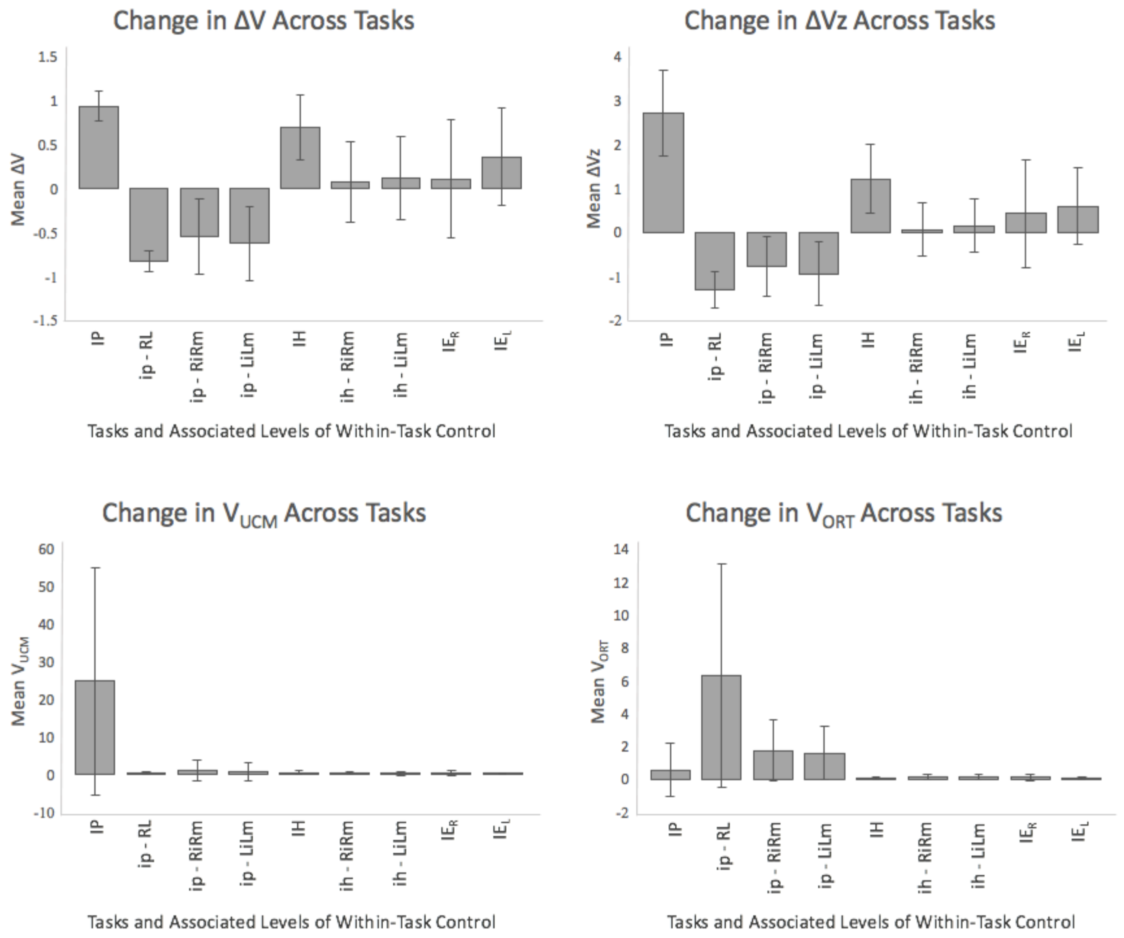


Figure 5: Changes in participant mean ΔV, ΔV_Z, V_{UCM}, and V_{ORT} across each task and its associated levels of within-task control. Error bars: ± 1 standard deviation.

Statistical Analysis

Results from the one-sample t-tests and paired-samples t-tests supported both parts of our first hypothesis, that force-stabilizing synergies would be present only at the highest level of control within both the IP and IH tasks. The results from the one-sample t-tests confirmed that force-stabilizing synergies were present in three of the four main tasks: IP, IH, and IE_L. The test was run to determine whether ΔV was significantly higher than zero in each of the tasks and levels of within-task control, which indicated the presence of a force-stabilizing synergy. Again, only a statistically significant mean difference higher than zero indicated the stabilization of task force, or the presence of a force-stabilizing synergy, as it represents $V_{UCM} > V_{ORT}$. A negative mean difference represents $V_{ORT} > V_{UCM}$ and indicates a destabilization of task force, or that no force-stabilizing synergy was present. ΔV was not normally distributed for every task and level of within-task control, as assessed by Shapiro-Wilk's test ($p >$ .05) and there were a total of four extreme outliers, as assessed by inspection of a boxplot. Although this violates two of the assumptions of the one-sample t-test, we choose to run the test on this data regardless as the interpretation is more straightforward and test comparisons run on data with extreme outliers removed and data transformed to be normally distributed produced identical results.

The inequality $\Delta V > 0$, indicating the presence of a force-stabilizing synergy, was found in only three of the tasks: the highest level of control within the IP task, the highest level of control within the IH task, and the IE_L task. In each of these tasks, ΔV was statistically significantly greater than zero. The ΔV in the IP task (0.938 ± 0.166) was statistically significantly greater than zero by a mean of 0.938, 95% CI [0.853, 1.023], $t(16) = 23.349$, $p < 0.001$, $d = 5.66$. The ΔV in the IH task (0.701 ± 0.369) was statistically significantly greater than zero by a mean of 0.701, 95% CI [0.511, 0.891], *t*(16) = 7.826, $p < 0.001$, *d* = 1.90. The ΔV in the IE_L task (0.362 ± 0.558) was statistically significantly greater than zero by a mean of 0.362, 95% CI [0.075, 0.648], *t*(16) = 2.674, $p = 0.017$, *d* = 0.65.

No force-stabilizing synergies were found in the IE_R task or in any of lower levels of control within the IP and IH tasks. ΔV for the lower levels of control within the IH task were not significantly different from zero, indicating that no force-stabilizing synergies were present. ΔV for the lower levels of control within the IP task were significantly different from zero but with negative mean differences. Descriptive statistics and detailed results of the analysis are displayed in Appendix A.

In addition to the one-sample t-tests, paired-samples t-tests were also run on V_{UCM} and V_{ORT} for each task and associated levels of within-task control separately to determine where force-stabilizing synergies were present by finding where V_{UCM} was significantly larger than V_{ORT}. The majority of V_{UCM} and V_{ORT} distributions deviated from the normal distribution, as assessed by Shapiro-Wilk's test ($p > .05$), and contained several extreme outliers, as assessed by inspection of a boxplot. However, a test comparison was done on logarithmic-transformed variables with mostly normal distributions and no extreme outliers and results produced were identical to those found with the original variables. Because the interpretation of results using the original V_{UCM} and V_{ORT} variables is more straightforward and did not change the results, we decided to perform the analyses using these variables. The results of the paired-samples t-tests were in parallel to our findings from the one-sample t-test: force-stabilizing synergies were found in the highest level of control within the IP, IH, and IE_L tasks as indicated by a significantly higher mean V_{UCM} than V_{ORT}. V_{UCM} was statistically significantly higher than V_{ORT} in the highest level of control within the IP task by a mean increase of 2.365, 95% CI [1.931, 2.799], $t(16) = 11.554$, $p < 0.001$, $d = 2.80$, in the highest level of control within the IH task by a mean increase of 1.055, 95% CI [0.706, 1.404], $t(16) = 6.408$, $p < 0.001$, $d = 1.55$, and in the IE_L task by a mean increase of 0.514, 95% CI [0.126, 0.902], $t(16) = 2.808$, $p < 0.001$, $d = 0.68$. Descriptive statistics and detailed results can be seen in Appendix B. The combined findings from the one-sample and paired-samples t-tests support both parts of our first hypothesis that the inequality $\Delta V > 0$ would be true, or that force-stabilizing synergies would be found, only in the highest level of within-task control in both the IP and IH tasks.

As previously mentioned and as indicated by the results of the one-sample t-tests, ΔV for the lower levels of control within the IP task were statistically significantly different from zero but with highly negative mean differences. The ΔV index at the between-hands level of control within the IP task (-0.829 ± 0.115) was statistically significantly less than zero by a mean of -0.829, 95% CI [-0.888, -0.770], $t(16) = -29.745$, $p < 0.001$, $d = 7.21$. The ΔV index at the between-fingers level of control for both the right (-0.546 ± 0.435) and left (-0.627 ± 0.420) hands within the IP task were statistically significantly less than zero by a mean of -0.546, 95% CI [-0.770, -0.323], $t(16) = -5.183$, $p < 0.001$, $d = 1.26$, and -0.627, 95% CI [-0.843, -0.411], $t(16) = -6.150$, $p < 0.001$, *d* = 1.49, respectively. This overall finding was surprising as we expected a total lack of synergy, or a ΔV statistically similar to zero, at these lower levels of control within the IP task like was found for the lower levels of control within the IH task. Instead, we found ΔV at the lower levels of control within the IP task to be statistically significantly lower than zero. Likewise, results from the paired=samples t-tests indicated that for each of the lower levels of control within the IP task, V_{UCM} was statistically significantly larger than V_{ORT}. This also differed from what we expected and from what we found in the lower levels of control within the IH task. Within the IH task, V_{UCM} and V_{ORT} were statistically similar in the lower levels of within-task control as is expected with a lack of force-stabilizing synergies. Within the IP task, V_{UCM} was statistically significantly smaller than V_{ORT} by -1.132, 95% CI [-1.319, -0.946], *t*(16) = -12.879, *p* < 0.001, *d* = 3.13 at the between-hands level, by -0.683, 95% CI [-0.986, -0.380], *t*(16) = -4.781, *p* < 0.001, *d* = 1.16 at the between-fingers level for the right hand, and by -0.829, 95% CI [-1.153, -0.505], *t*(16) = -5.428, *p* < 0.001, *d* = 1.32 at the between-fingers levels for the left hand.

Our second hypothesis was partially supported by our findings from the one-way repeated measures ANOVA applied to the ΔV_Z index. Our second hypothesis stated that the magnitude of force-stabilizing synergies at the highest level of control within each of the main tasks would increase as DOF were added to the task, or as tasks moved from IE, to IH, to IP tasks. We expected to find significant differences between each of the main tasks where force-stabilizing synergies were found but found significant differences only for the IP task. We performed a test comparison on the original ΔV variable and confirmed that the distributions largely deviated from normal and included several extreme outliers, both of which are in violation of two ANOVA assumptions. Additionally, and likely as a result of the assumption violations, the results of that test comparison largely differed from the results of the test performed on the ΔV_Z index. Thus, we ultimately decided to perform the ANOVA on the ΔV_Z index. There were no extreme outliers in the data, as determined by inspection of a boxplot. The distributions of ΔV_Z were normally distributed in three of the four tasks, as assessed by Shapiro-Wilk's test ($p > 0.05$). Because the one-way repeated measures ANOVA is fairly robust to deviations from normality, we determined this data to be acceptable despite the non-normal distribution in one of the tasks. Mauchly's test of sphericity indicated that the assumption of sphericity had not been violated, $\chi^2(5) = 8.992$, $p = 0.110$. The results of the ANOVA indicated that the magnitude of ΔV_Z was significantly different across the four main tasks, $F(3, 48) = 24.61$, $p < 0.001$, $\eta^2_{partial} = 0.606$.

Post hoc analysis with Bonferroni adjustments revealed that the magnitude of ΔV_Z in the IP task (2.723 ± 0.972) was statistically significantly higher than the magnitude of ΔV_Z in the IH task (1.215 ± 0.782) by 1.508, 95% CI [0.520, 2.497], $p = 0.002$, the IE_R task (0.426 ± 1.238) by 2.297, 95% CI [1.122, 3.471], $p < 0.001$, and the IE_L task (0.594 ± 0.869) by 2.129, 95% CI [1.152, 3.107], $p < 0.001$. The magnitude of ΔV_Z in the IH task was statistically significantly higher than the IE_R task by 0.788, 95% CI [0.161, 1.416], $p < 0.010$. The higher ΔV_Z in the IP and IH tasks compared to the IE_R task is not surprising as it was previously confirmed in the current study's findings that no force-stabilizing synergy was present in the IE_R task so ΔV_Z was expected to be small. There was no significant difference in ΔV_Z between the IH and IE_L tasks or between the IE_R and IE_L tasks. Although not significant at the level of $p < 0.05$, the mean ΔV_Z for the IH task was higher than the mean ΔV_Z for the IE_L task by 0.621, 95% CI [-0.036, 1.278], $p < 0.070$. While we expected to see a significant difference in ΔV_Z between the IH and IE_L task, these results still mostly support our second hypothesis that the magnitude of force-stabilizing synergies increases as DOF are added to the task. Descriptive statistics and detailed results from the post hoc pairwise comparisons with Bonferroni adjustments can be seen in Appendix C. A graphical representation of the changes in ΔV_Z across these four main tasks can be seen in Figure 5.

Results from the one-way repeated measures ANOVAs done on the components of the ΔV index, V_{UCM} and V_{ORT}, help shed further light on some of our previous findings. Again, a logarithmic transformation was applied to both V_{UCM} and V_{ORT} variables before performing the ANOVAs, due to the distributions for both V_{UCM} and V_{ORT} being strongly, positively skewed and deviating from the normal distribution as assessed by Shapiro-Wilk's test ($p > 0.05$). We performed a test comparison on the original V_{UCM} and V_{ORT} variables and confirmed their non-normal distributions as well as the presence of several extreme outliers, both of which are in violation of ANOVA assumptions. As a result, the results of the test comparisons largely differed from the results of the tests performed on the log-transformed variables. Because of this, we decided to perform the ANOVAs on the log-transformed V_{UCM} and V_{ORT} variables. Significant results will be listed below, but descriptive statistics and more detailed results from the post hoc pairwise comparisons with Bonferroni adjustments applied to both the log-transformed V_{UCM} and V_{ORT} variables can be seen in Appendices D and E, respectively.

In the ANOVA applied to the log-transformed V_{UCM} variable across tasks and associated levels of within-task control, the majority of distributions were normal as assessed by Shapiro-Wilk's test ($p > 0.05$), and there were no extreme outliers. Mauchly's test of sphericity indicated that the assumption of sphericity had been violated, χ^2 (35) = 125.18, $p < 0.001$. Epsilon (e) was 0.296, as calculated according to Greenhouse & Geisser (1959), and was used to correct the one-way repeated measures ANOVA. The results of the ANOVA indicated that V_{UCM} was significantly different across tasks and levels of within-task control, F(2.37, 37.91) = 29.476, $p < 0.001$, $\eta^2_{partial} = 0.648$. In the ANOVA applied to the log-transformed V_{ORT} variable, distributions were normal as assessed by Shapiro-Wilk's test ($p > 0.05$), but there was one extreme outlier. We decided to include this data point as it did not make a difference in test results compared to when it was excluded. Sphericity was again violated according to Mauchly's test of sphericity, $\chi^2(35) = 166.375$, $p < 0.001$. Epsilon (e) was 0.357 and was used to correct the one-way repeated measures ANOVA. The ANOVA results indicated that V_{ORT} was significantly different across tasks and levels of within-task control, F(2.855, 45.687) = 32.127, $p < 0.001$, $\eta^2_{partial} = 0.668$.

Subsequent pairwise comparisons with Bonferroni corrections revealed that, across the three tasks in which force-stabilizing synergies were found (IP, IH, IE_L), V_{UCM} increased significantly as tasks involved more fingers, or DOF. All results listed indicate means and standard deviations. V_{UCM} in the IP task (1.110 ± 0.556) was statistically significantly higher than in the IH task (-0.588 ± 0.675) by 1.698, 95% CI [.976 , 2.420], $p < 0.001$, and in the IE_L task (-1.315 ± 1.113) by 2.424, 95% CI [1.261, 3.587], $p < 0.001$. Likewise, V_{UCM} was statistically significantly higher in the IH task than in the IE_L task by 0.727, 95% CI [.146, 1.307], $p = 0.007$. All three tasks had statistically similar V_{ORT} values: IP (-1.255 ± 0.964), IH (-1.643 ± 0.619), and IE_L (-1.829 ± 0.822).

In the IP task, results indicated that force-stabilizing synergies were not present in the lower levels of control due to significantly lower V_{UCM} and significantly higher V_{ORT} in those levels as compared to the highest level of control within the IP task where a force-stabilizing synergy was found. V_{UCM} at the lower, between-hands level (-0.599 ± 0.498) was statistically significantly lower than V_{UCM} at the highest, between-subjects level (1.11 ± 0.556) of the IP task by -1.709, 95% CI [-2.083, -1.334], $p < 0.001$. V_{UCM} at the lowest, between-fingers levels for both the right (-0.726 ± 0.823) and left hands (-0.866 ± 0.784) was statistically significantly lower than V_{UCM} of the highest, between-subjects level by -1.836, 95% CI [-2.451, -1.220], $p < 0.001$ and -1.976, 95% CI [-2.596,

-1.356], $p < 0.001$, respectively. Additionally, V_{ORT} at the between-hands level (0.534 ± 0.556) was statistically significantly higher than V_{ORT} at the between-subjects level (-1.255 ± 0.964) by 1.789, 95% CI [1.060, 2.518], $p < 0.001$. V_{ORT} at the between-fingers levels for both the right (-0.043 ± 0.597) and left hands (-0.037 ± 0.526) was statistically significantly higher than V_{ORT} at the between-subjects level (-1.255 ± 0.964) by 1.212, 95% CI [0.455, 1.969], $p < 0.001$ and 1.218, 95% CI 0.509, 1.927], $p < 0.001$, respectively.

In the IH task, the lack of force-stabilizing synergies in the lower levels can be attributed to a combination of lower V_{UCM} levels and higher V_{ORT} levels. While the difference was only significant for the right hand, the between-fingers levels of both the right (-1.053 ± 0.932) and left hands (-1.030 ± 0.934) had lower mean V_{UCM} than the higher, between-hands level (-0.588 ± 0.675) of the IH task. V_{UCM} at the lower, between-fingers level of the right hand was statistically significantly lower than V_{UCM} at the higher, between-hands level by -0.465, 95% CI [-0.867, -0.064], $p = 0.014$. V_{ORT} for the lower levels of the IH task were slightly larger than the V_{ORT} in the highest IH level, but results were not statistically significant. These results suggest that synergies were not present in the lower levels likely due to the drop in V_{UCM} but could also have been due in part to the slightly larger V_{ORT}.

A similar comparison of V_{UCM} and V_{ORT} was made between the three lower levels of the IP task and the highest level of the IH task and the IE_L task. Results revealed no statistically significant differences in the mean V_{UCM} values between each of the three lower levels of the IP task (Between-Hands: -0.599 ± 0.498, Between-Fingers$_R$: -0.726 ± 0.823, Between-Fingers$_L$: -0.866 ± 0.784). Additionally, no statistically significant differences were found between the mean V_{UCM} values in any of the lower levels of control within the IP task and the mean V_{UCM} in the highest level of control within the IH task (-0.588 ± 0.675) or between the mean V_{UCM} in the lower levels of control within the IP task and the mean V_{UCM} of the IE$_L$ task (-1.315 ± 1.113). However, there were statistically significant differences found in the V_{ORT} analysis across these same comparisons. V_{ORT} was significantly higher in each of the lower IP levels of control compared to V_{ORT} in both the main IH (-1.643 ± 0.619) and IE$_L$ (-1.829 ± 0.822) tasks. V_{ORT} at the between-hands level of the IP task was statistically significantly higher than V_{ORT} at the highest level of the IH task by 2.177, 95% CI [1.406, 2.947], $p < 0.001$, and higher than V_{ORT} at the IE$_L$ task by 2.362, 95% CI [1.381, 3.344], $p < 0.001$. V_{ORT} at the between-fingers level the IP task for the right hand was statistically significantly higher than V_{ORT} in the highest level of the IH task by 1.600, 95% CI [0.817, 2.383], $p < 0.001$, and higher than V_{ORT} in the IE$_L$ task by 1.786, 95% CI [0.788, 2.783], $p < 0.001$. V_{ORT} at the between-fingers level of the IP task for the left hand was statistically significantly higher than V_{ORT} in the highest level of the IH task by 1.606, 95% CI [0.847, 2.365], $p < 0.001$, and higher than V_{ORT} in the IE$_L$ task by 1.792, 95% CI [0.832, 2.752], $p < 0.001$. Even though the V_{UCM} distributions are statistically similar across these tasks, these findings suggest that the lack of force-stabilizing synergies at the lower levels of control within the IP tasks can be explained by the significantly higher V_{ORT}. It seems that for the IP task, the V_{UCM} in the three lower levels of control is not large enough to overcome the inherently large V_{ORT} in order to satisfy the inequality $V_{UCM} > V_{ORT}$.

Chapter 4: Discussion

Our findings confirm those of previous studies where force-stabilizing synergies were found in both one-person and two-person motor tasks. The inequality $\Delta V > 0$ was satisfied in the IP, IH, and IE_L tasks, indicating the presence of force-stabilizing synergies. Supporting both parts of our first hypothesis, force-stabilizing synergies in the IP and IH tasks were only found at the highest level of within-task control. Unexpectedly, we did not find a force-stabilizing synergy in the IE_R task. A similarly unexpected finding and especially surprising when compared to the non-significant differences found in the lower levels of within-task control for the IH task, we found highly negative ΔV values in each of the lower levels of within-task control for the IP task. The ΔV indices were statistically significantly lower than zero at each of these levels of control. These findings may suggest that, when performing a task with another individual with unpredictable behavior, the CNS simplifies control at all lower levels of within-task control as a means to performing the two-person task as successfully as possible.

In support of our second hypothesis and consistent with the theory of motor synergies, the principle of abundance, the principle of minimum intervention, and findings from the study by Karol et al. (2011), we found that as more DOF were added to the task, the strength of the force-stabilizing synergies increased as determined by the magnitude of each task's ΔV_Z index. The magnitude of ΔV_Z was significantly larger in the IP task compared to the magnitudes of ΔV_Z in both the IH and IE_L tasks. Likewise, the magnitude of ΔV_Z in the IH task was larger than the magnitude of ΔV_Z in the IE_L task, though this comparison was not statistically significant. Although we expected each comparison of synergy magnitudes to produce significant results, these findings still mostly support our second hypothesis in which we expected to find stronger synergies as the tasks moved from IE, to IH, to IP tasks.

Degrees of Freedom Problem and the Principle of Abundance

One aim of this study was to investigate how the CNS handles the DOF problem as the number of DOF increase across tasks. Specifically, we aimed to investigate how the CNS reacts to working with a co-actor to perform a two-person motor task. The problem of redundancy in the context of the DOF problem has been recently redefined as the principle of abundance. Instead of eliminating excessive DOF, the the principle of abundance posits that the CNS takes advantage of the many DOF to allow for more flexibility while still maintaining task performance (Bernstein, 1967; Latash et al., 2007, Latash, 2012). The results of this study provide evidence suggesting that as more DOF are added to the system of the motor task the CNS employs the principle of abundance. Across the three tasks in which force-stabilizing synergies were found, V_{UCM} increased as the number of fingers, or DOF, required to perform the task increased, or as tasks moved from IE to IH to IP tasks. This increase in variability within the UCM suggests that, as more DOF are required for the task, the CNS employs the principle of abundance by taking advantage of the excessive DOF and allowing for more task-irrelevant flexibility while still stabilizing overall task performance.

Organization of Motor Synergies

Intra-Personal Motor Synergies

Intra-personal motor synergies have been found to exist within an individual while the individual performs a given one-person motor task over repeated trials. The current study found intra-personal motor synergies in both the IH and IE_L tasks where participants met a target force by pressing on force sensors with four fingers and two fingers, respectively. The current study’s findings are consistent with findings from several previous studies in which intra-personal force-stabilizing motor synergies in finger-force production tasks were found to exist between the finger forces produced by a single participant at the highest level of control within a one-person task (Kang et al., 2004; Olafsdottir et al., 2007; Shim et al., 2003b; Solnik et al., 2015).

Inter-Personal Motor Synergies

Inter-personal motor synergies have also been found to exist but are not as well-researched as intra-personal motor synergies. Inter-personal motor synergies are found between two or more individuals while those individuals perform a two-person motor task. The current study found inter-personal motor synergies in the IP task where participants worked in pairs to meet a combined target force, each participant pressing on force sensors with four fingers. These findings parallel a small handful of finger-force production studies where intra-personal motor synergies were found between individual participant's forces in pairs of participants (Masumoto & Inui, 2015; Solnik et al., 2015). Our findings in the IP task, paired with the findings from the IH and IE_L tasks, further support the theory of motor synergies (Bernstein, 1967).

An unexpected finding, however, was the lack of a force-stabilizing synergy in the IE_R task. Results revealed a force-stabilizing synergy in the IE_L task, but we expected to see a synergy in the IE_R task as well. Out of the 34 participants, 29 identified as being right-hand dominant. This could suggest that perhaps the motor effectors of the dominant hand are more independent and less likely to depend on the function of a synergy. However, this remains unclear as several previous studies have reported finding force-stabilizing synergies in right-handed tasks performed by right-handed participants. To examine this phenomenon in more depth, further study is required.

Lack of Multiple Synergies within a Single Task

Across the three tasks in which force-stabilizing synergies were found, synergies were only present at the highest level of control within each tasks. Results indicated an absence of force-stabilizing synergies in all of the lower levels of control within both the IP and IH tasks. Finding force-stabilizing synergies only at the highest level of control in both the IP and IH tasks suggests that the CNS is not able to organize synergies on multiple levels of control simultaneously during a single task. These findings are consistent with findings from previous studies performed using similar finger-force production tasks. Gorniak et al. (2007b) and Masumoto & Inui (2015) both found force-stabilizing synergies only at the highest levels of control in each of their employed tasks, tasks similar to the current study's IH and IP tasks.

Additionally, our findings support the theory presented by Latash et al. (2008) and Gorniak et al. (2007a) that states simultaneously-occurring force-stabilizing synergies on multiple levels of within-task control may be impossible during natural behaviors. The theory suggests that having a strong synergy (or high V_{UCM}) in the highest level of control within a task inherently causes V_{ORT} in the lower levels to be too high for the V_{UCM} to overcome in order to satisfy the inequality $V_{UCM} > V_{ORT}$. In the IP task, V_{UCM} is extremely high which means the total variance of each individual participant is also very high. This can be seen in the top, left box of Figure 4. When we consider one level lower in the hierarchy where an individual participant's force is shared between their R and L hands, the participant's large task-irrelevant variance from the higher level now becomes task-relevant variance, or V_{ORT}, at this level. In order for a synergy to also exist at this level of within-task control, V_{UCM} has to be very large for the inequality $V_{UCM} > V_{ORT}$ to be satisfied.

In the current study, participants were not able to satisfy the inequality $V_{UCM} > V_{ORT}$ on any of the lower levels of control within either of the IP or IH tasks. An interesting finding from our study that may explain this is the extremely large V_{ORT} found in the lower levels of the IP task. While V_{UCM} for each of the three lower IP levels were statistically similar to V_{UCM} in all other tasks excepting those in the highest level of control within the IP task, V_{ORT} in the three lower levels of the IP tasks were each significantly higher than V_{ORT} in any other task or associated level of within-task control. The IH task exhibited a similar pattern in regards to V_{ORT}, although not with statistically significant differences. The two lower levels of control within the IH task had slightly higher V_{ORT} than the highest IH level of control and higher V_{ORT} than both the IE_R and IE_L tasks. These findings support the synergy trade-off theory previously mentioned (Latash et al., 2008; Gorniak et al., 2007a). The findings suggest that this trade-off is too big an obstacle for the CNS to overcome and that perhaps the CNS is only able to organize synergies on one level of control within a given finger-force production task, whether the task is performed individually or with a co-actor.

Unexpectedly and not found in previous motor synergy research, our results indicated strong, negative ΔV values in each lower level of control within the IP task. We expected to find a complete lack of synergy, or ΔV values not statistically different from zero, at these levels, similar to the lack of synergy found at the lower levels of control within the IH task. These findings are significant because they have not been found in motor synergy research before now and indicate not a lack of synergy, but perhaps a synergy with a different purpose than the force-stabilizing synergy at the highest level of within-task control. A complete lack of synergy would have suggested that the DOF, or fingers in the case of the current study, were acting independently. What we found, however, was that the DOF in each of the lower levels of control within the IP are paired so that their action outputs were nearly identical, acting in parallel. This can be seen by the extremely large V_{ORT} values at these lower levels. This suggests that, in order to perform a two-person task with another individual whose behavior is unpredictable, the CNS may simplify action at the lower levels of control within the task. In other words, it appears that the CNS pairs DOF so that they act in parallel with the other DOF at that level of within-task control. This could mean that, instead of sending individual signals to each hand at the between-hands level of control or to each finger at the between-fingers level of control so that each DOF acts individually, the CNS sends only one signal so that individual DOF activity is paired. Because this behavior was not seen in the lower levels of within-task control for the IH task, this can potentially be seen as an effort by the CNS to simplify control and compensate for the uncertainty that comes with working with a co-actor. Further research would likely be able to shed more light on these unexpected findings.

Magnitude of Motor Synergies Across Tasks

In support of our second hypothesis, the current study found that the magnitude of force-stabilizing synergies significantly increased from the IE_L to IP task and from the IH to the IP task. Although not significant, we also saw an increase in synergy magnitude from the IE_L to IH task. These findings indicate that the magnitude of force-stabilizing synergies increases as more DOF are required for the task. These findings are similar to the findings of a previous study by Karol et al. (2011). Karol et al. found force-stabilizing synergies in two-finger, three-finger, and four-finger force production tasks performed by each participant individually. As tasks required more fingers, they found significant increases in the magnitude of the synergies present. While not every relationship was significant, we did find a similar increase in the magnitude of synergies as tasks moved from IE_L, to IH, to IP tasks. Of note, however, is that while the number of fingers required for the overall task increased from the IH to IP task, the total number of required fingers for each individual participant remained the same. In both tasks, individual participants were only required to press on force sensors with four fingers: Ri, Rm, Li, and Lm. So, while the IH task required a total of four fingers, the IP task required the participants to combine their forces to complete the task and so required a total of eight fingers. This suggests that during two-person finger-force production tasks the magnitude of force-stabilizing synergies may depend solely on the total number of DOF involved across the task, not just the DOF required by the individual participant. These findings add support to the theory of motor synergies, the principle of abundance, and the principle of minimum intervention.

Future Directions for this Study

While our findings shed valuable light on the organization of force-stabilizing motor synergies and the limitations of the CNS during finger-force production tasks, the only type of feedback participants received was visual feedback. In real-life scenarios and as determined by the type of task, actors may have additional types of feedback available to them as they complete both one-person and two-person motor tasks. While there have been several studies exploring the effects of feedback type on the organization of motor synergies during various one-person motor tasks, there have been very few studies to do this for two-person motor tasks. In a two-person jumping study, participants were required to jump off force plates with a co-actor with varying degrees of haptic feedback across conditions (Slomka et al., 2015). They found stronger inter-personal motor synergies in the condition where co-actors were coupled by placing hands on each others' shoulders as they jumped compared to the condition in which they experienced no physical coupling at all and had to rely solely on visual feedback. This indicates that feedback type plays a role in the organization of inter-personal motor synergies during two-person motor tasks. This, however, has not yet been examined in two-person finger-force production tasks. All studies specifically investigating force-stabilizing motor synergies between co-actors in two-person motor tasks have used visual feedback only. It would be beneficial to do a study similar to the current study in which participants performing a two-person finger-force production task are provided with haptic or audio feedback, as the results may differ.

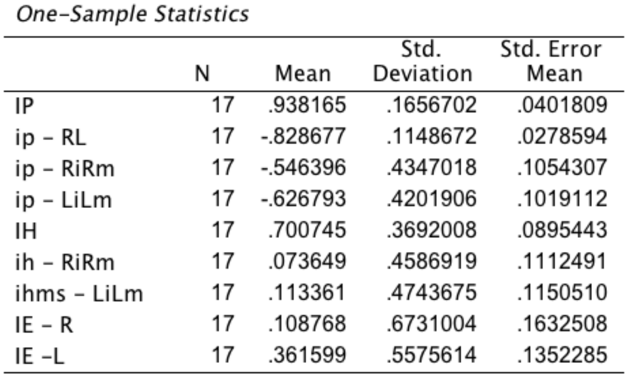
As previously mentioned, it would likewise be beneficial for future studies to investigate the differences in force-stabilizing synergies between dominant and non-dominant hands during finger-force production tasks. The current study found a force-stabilizing synergy in the IE task for the left hand but no synergy in the IE task for the right hand. An overwhelming majority of participants in our study were self-reported right-hand dominant, the fact of which may have influenced our findings. While intuitive that handedness influences the performance of various motor tasks, interesting results from a study by Bagesteiro and Sainburg (2003) suggest that the non-dominant arm performed more effective load compensation during rapid elbow joint movements than the dominant hand. It has been suggested that the non-dominant arm may be more effective in performing steady-state tasks than the dominant arm while the dominant arm is more effective in performing tasks requiring quick, accurate actions (Zhang et al., 2006). However, a search of the literature produced very few studies in which the effects of handedness were explicitly investigated in context of force-stabilizing motor synergies during finger-force production tasks. One study by Zhang et al. (2006) examined the differences in motor synergies between dominant and non-dominant hands in a variety of finger force production tasks. They did find that the non-dominant hand experienced a larger drop in ΔV in anticipation of a change in task force, but no differences were found in the steady-state tasks which were most similar to the tasks of the current study. It would be interesting and beneficial to perform a study similar to the current study but with a group of left-hand dominant participants and a group of right-hand dominant participants from which results are compared. With an experimental design of that nature, it may be possible to better explain whether our findings were coincidence, an actual factor of handedness, or if further study is required.

Lastly, future study on motor synergy behavior during two-person tasks could help explain the unexpected findings of strong, negative ΔV values at the lower levels of control within the IP task of the current study. It would be beneficial to investigate this phenomenon in more depth to further investigate the strategy being employed by the CNS during the performance of two-person finger-force production tasks.

Conclusion

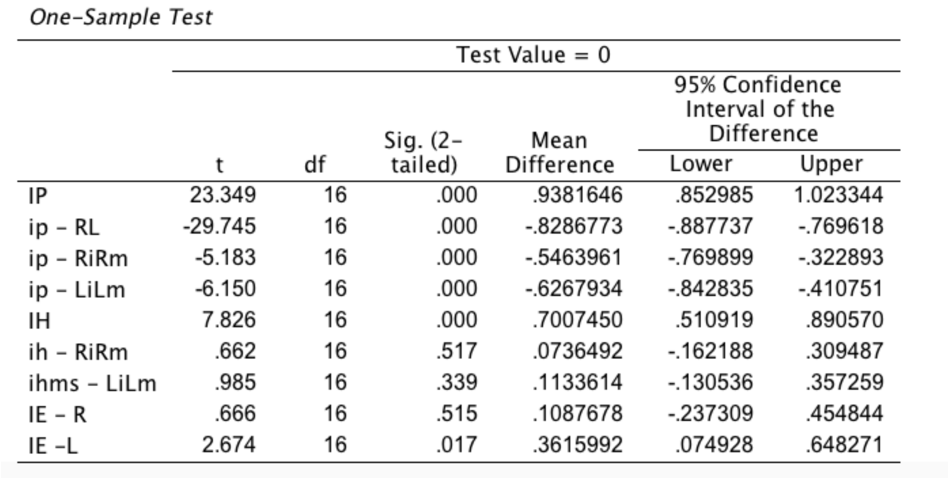
Overall, the results of the study support the hypotheses. We found force-stabilizing synergies in the highest level of control only for both the IP and IH tasks as well as in the IE_L task. Additionally, we found that the magnitude of the synergy in the IP task was significantly greater than the magnitude of the synergies in the IH and IE_L tasks. It was unexpected to find such highly negative ΔV values, statistically significantly lower than zero, in the lower levels of control within the IP task. This phenomenon has not been found in motor synergy research up until the current study and would suggest that the CNS may simplify control at the lower levels of within-task control when performing a two-person task. Similarly, we did not expect to see the significantly larger V_{ORT} in the lower levels of the IP task compared to the V_{ORT} in every other task and their associated levels of within-task control and view this as a direct result of the extremely high V_{UCM} in the main IP task. We conclude that, because V_{UCM} in the lower levels cannot overcome the inherently large V_{ORT} that is a direct result of the synergy present in a higher level, force-stabilizing synergies cannot be organized on multiple levels of control within a single finger-force production task.

Appendix A
Results of One-Sample T-Test on ∆V Index for Each Task and Associated Levels of Within-Task Control



One-Sample Statistics

	N	Mean	Std. Deviation	Std. Error Mean
IP	17	.938165	.1656702	.0401809
ip – RL	17	-.828677	.1148672	.0278594
ip – RiRm	17	-.546396	.4347018	.1054307
ip – LiLm	17	-.626793	.4201906	.1019112
IH	17	.700745	.3692008	.0895443
ih – RiRm	17	.073649	.4586919	.1112491
ihms – LiLm	17	.113361	.4743675	.1150510
IE – R	17	.108768	.6731004	.1632508
IE –L	17	.361599	.5575614	.1352285

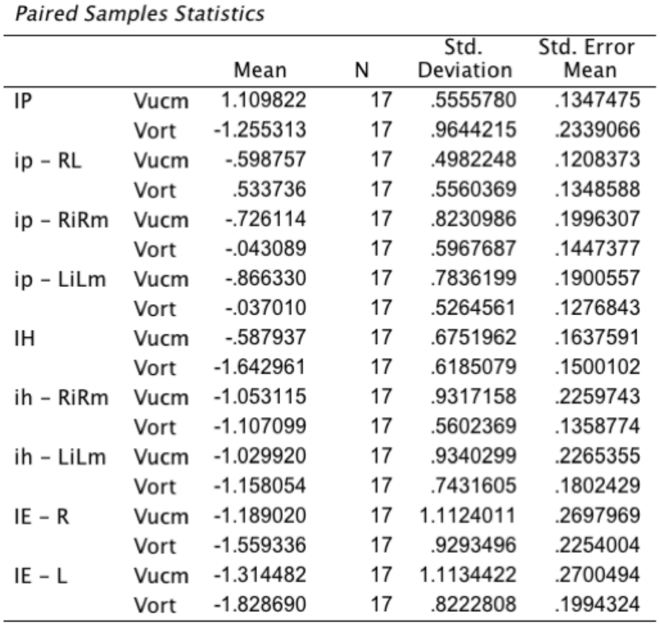


One-Sample Test

	Test Value = 0					
					95% Confidence Interval of the Difference	
	t	df	Sig. (2-tailed)	Mean Difference	Lower	Upper
IP	23.349	16	.000	.9381646	.852985	1.023344
ip – RL	-29.745	16	.000	-.8286773	-.887737	-.769618
ip – RiRm	-5.183	16	.000	-.5463961	-.769899	-.322893
ip – LiLm	-6.150	16	.000	-.6267934	-.842835	-.410751
IH	7.826	16	.000	.7007450	.510919	.890570
ih – RiRm	.662	16	.517	.0736492	-.162188	.309487
ihms – LiLm	.985	16	.339	.1133614	-.130536	.357259
IE – R	.666	16	.515	.1087678	-.237309	.454844
IE –L	2.674	16	.017	.3615992	.074928	.648271

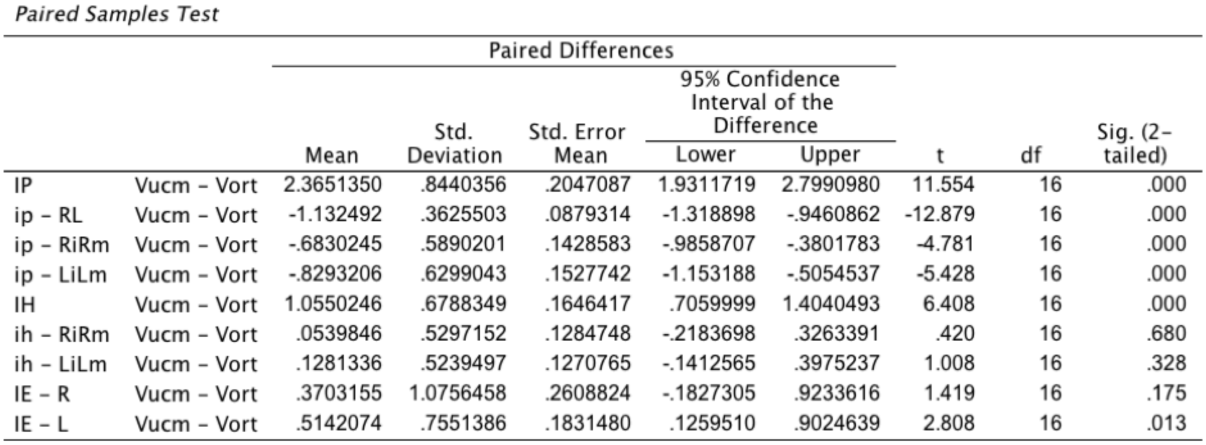
Appendix B

Results of Paired Samples T-Tests on Paired V_{UCM} and V_{ORT} Variables for Each Task and Associated Levels of Within-Task Control Separately



Paired Samples Statistics

		Mean	N	Std. Deviation	Std. Error Mean
IP	Vucm	1.109822	17	.5555780	.1347475
	Vort	-1.255313	17	.9644215	.2339066
ip – RL	Vucm	-.598757	17	.4982248	.1208373
	Vort	.533736	17	.5560369	.1348588
ip – RiRm	Vucm	-.726114	17	.8230986	.1996307
	Vort	-.043089	17	.5967687	.1447377
ip – LiLm	Vucm	-.866330	17	.7836199	.1900557
	Vort	-.037010	17	.5264561	.1276843
IH	Vucm	-.587937	17	.6751962	.1637591
	Vort	-1.642961	17	.6185079	.1500102
ih – RiRm	Vucm	-1.053115	17	.9317158	.2259743
	Vort	-1.107099	17	.5602369	.1358774
ih – LiLm	Vucm	-1.029920	17	.9340299	.2265355
	Vort	-1.158054	17	.7431605	.1802429
IE – R	Vucm	-1.189020	17	1.1124011	.2697969
	Vort	-1.559336	17	.9293496	.2254004
IE – L	Vucm	-1.314482	17	1.1134422	.2700494
	Vort	-1.828690	17	.8222808	.1994324

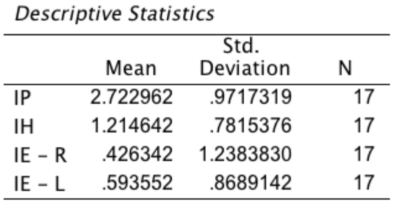


Paired Samples Test

		Paired Differences							
					95% Confidence Interval of the Difference				
		Mean	Std. Deviation	Std. Error Mean	Lower	Upper	t	df	Sig. (2-tailed)
IP	Vucm – Vort	2.3651350	.8440356	.2047087	1.9311719	2.7990980	11.554	16	.000
ip – RL	Vucm – Vort	-1.132492	.3625503	.0879314	-1.318898	-.9460862	-12.879	16	.000
ip – RiRm	Vucm – Vort	-.6830245	.5890201	.1428583	-.9858707	-.3801783	-4.781	16	.000
ip – LiLm	Vucm – Vort	-.8293206	.6299043	.1527742	-1.153188	-.5054537	-5.428	16	.000
IH	Vucm – Vort	1.0550246	.6788349	.1646417	.7059999	1.4040493	6.408	16	.000
ih – RiRm	Vucm – Vort	.0539846	.5297152	.1284748	-.2183698	.3263391	.420	16	.680
ih – LiLm	Vucm – Vort	.1281336	.5239497	.1270765	-.1412565	.3975237	1.008	16	.328
IE – R	Vucm – Vort	.3703155	1.0756458	.2608824	-.1827305	.9233616	1.419	16	.175
IE – L	Vucm – Vort	.5142074	.7551386	.1831480	.1259510	.9024639	2.808	16	.013

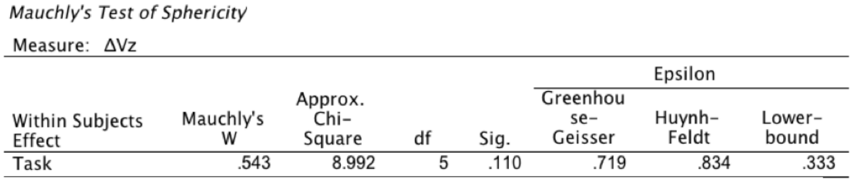
Appendix C

Results of One-Way Repeated Measures ANOVA and Pairwise Comparisons Applied to ΔV_Z with Bonferroni Adjustments Across the Four Main Tasks: IP, IH, IE_R, And IE_L



Descriptive Statistics

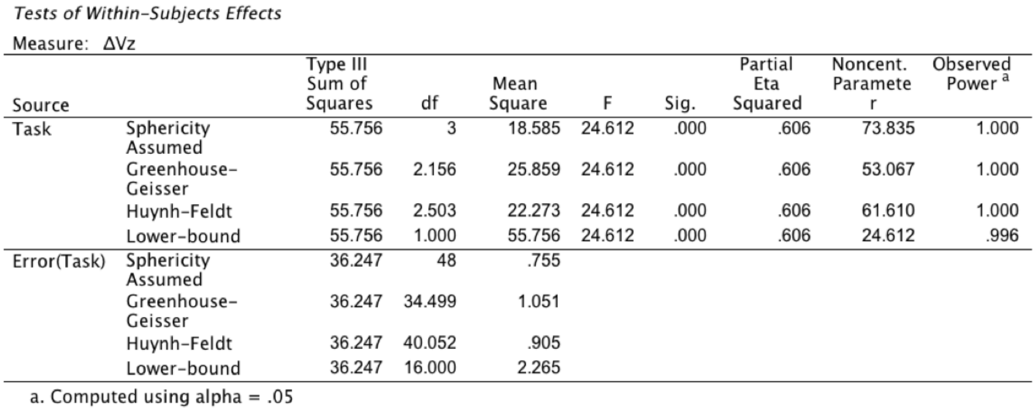
	Mean	Std. Deviation	N
IP	2.722962	.9717319	17
IH	1.214642	.7815376	17
IE – R	.426342	1.2383830	17
IE – L	.593552	.8689142	17



Mauchly's Test of Sphericity

Measure: ΔVz

Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Epsilon		
					Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Task	.543	8.992	5	.110	.719	.834	.333

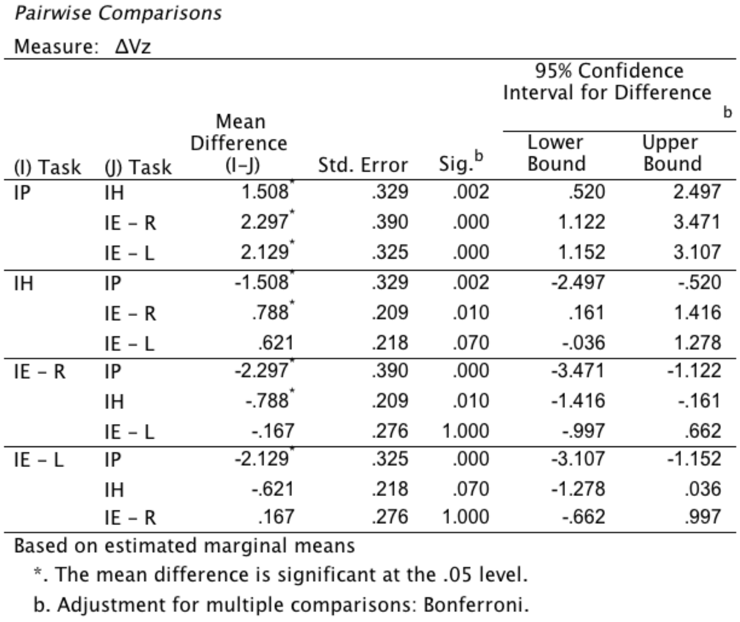


Tests of Within-Subjects Effects

Measure: ΔVz

Source		Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared	Noncent. Parameter	Observed Power [a]
Task	Sphericity Assumed	55.756	3	18.585	24.612	.000	.606	73.835	1.000
	Greenhouse-Geisser	55.756	2.156	25.859	24.612	.000	.606	53.067	1.000
	Huynh-Feldt	55.756	2.503	22.273	24.612	.000	.606	61.610	1.000
	Lower-bound	55.756	1.000	55.756	24.612	.000	.606	24.612	.996
Error(Task)	Sphericity Assumed	36.247	48	.755					
	Greenhouse-Geisser	36.247	34.499	1.051					
	Huynh-Feldt	36.247	40.052	.905					
	Lower-bound	36.247	16.000	2.265					

a. Computed using alpha = .05



Pairwise Comparisons

Measure: ΔVz

(I) Task	(J) Task	Mean Difference (I-J)	Std. Error	Sig. [b]	95% Confidence Interval for Difference [b]	
					Lower Bound	Upper Bound
IP	IH	1.508*	.329	.002	.520	2.497
	IE – R	2.297*	.390	.000	1.122	3.471
	IE – L	2.129*	.325	.000	1.152	3.107
IH	IP	-1.508*	.329	.002	-2.497	-.520
	IE – R	.788*	.209	.010	.161	1.416
	IE – L	.621	.218	.070	-.036	1.278
IE – R	IP	-2.297*	.390	.000	-3.471	-1.122
	IH	-.788*	.209	.010	-1.416	-.161
	IE – L	-.167	.276	1.000	-.997	.662
IE – L	IP	-2.129*	.325	.000	-3.107	-1.152
	IH	-.621	.218	.070	-1.278	.036
	IE – R	.167	.276	1.000	-.662	.997

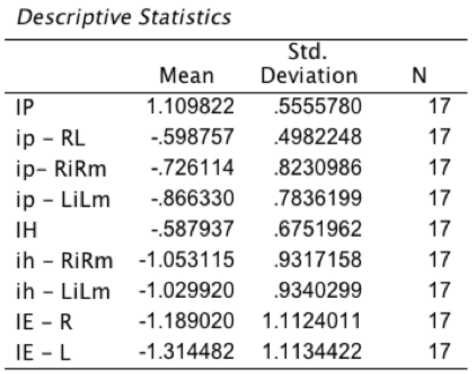
Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

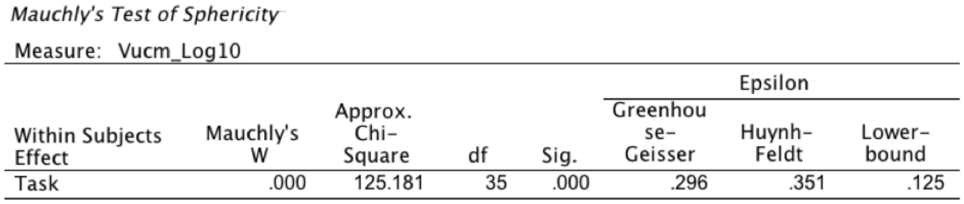
Appendix D

Results of One-Way Repeated Measures ANOVA and Pairwise Comparisons Applied to Log-Transformed V_{UCM} with Bonferroni Adjustments Across All Tasks and Associated Levels of Within-Task Control



Descriptive Statistics

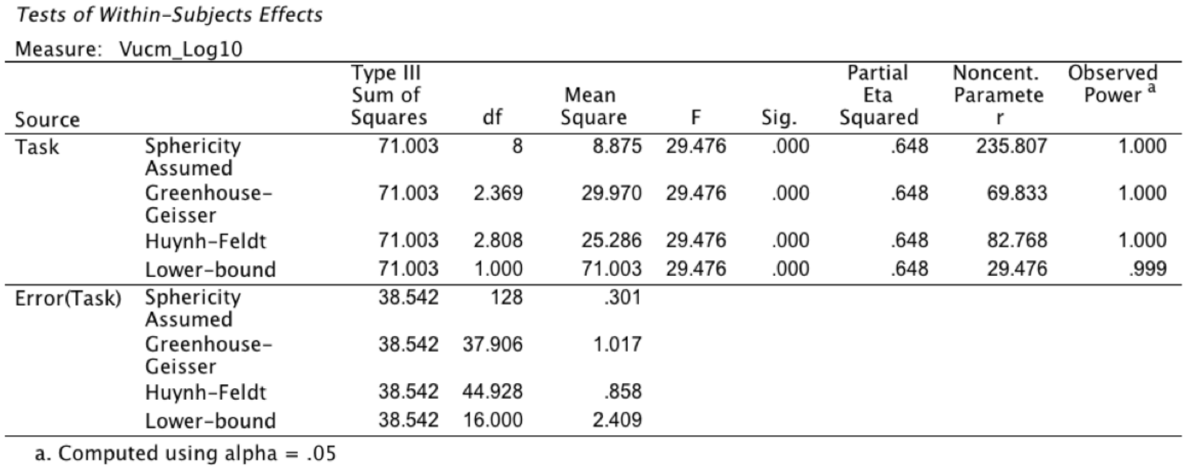
	Mean	Std. Deviation	N
IP	1.109822	.5555780	17
ip – RL	-.598757	.4982248	17
ip– RiRm	-.726114	.8230986	17
ip – LiLm	-.866330	.7836199	17
IH	-.587937	.6751962	17
ih – RiRm	-1.053115	.9317158	17
ih – LiLm	-1.029920	.9340299	17
IE – R	-1.189020	1.1124011	17
IE – L	-1.314482	1.1134422	17



Mauchly's Test of Sphericity

Measure: Vucm_Log10

					Epsilon		
Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Task	.000	125.181	35	.000	.296	.351	.125

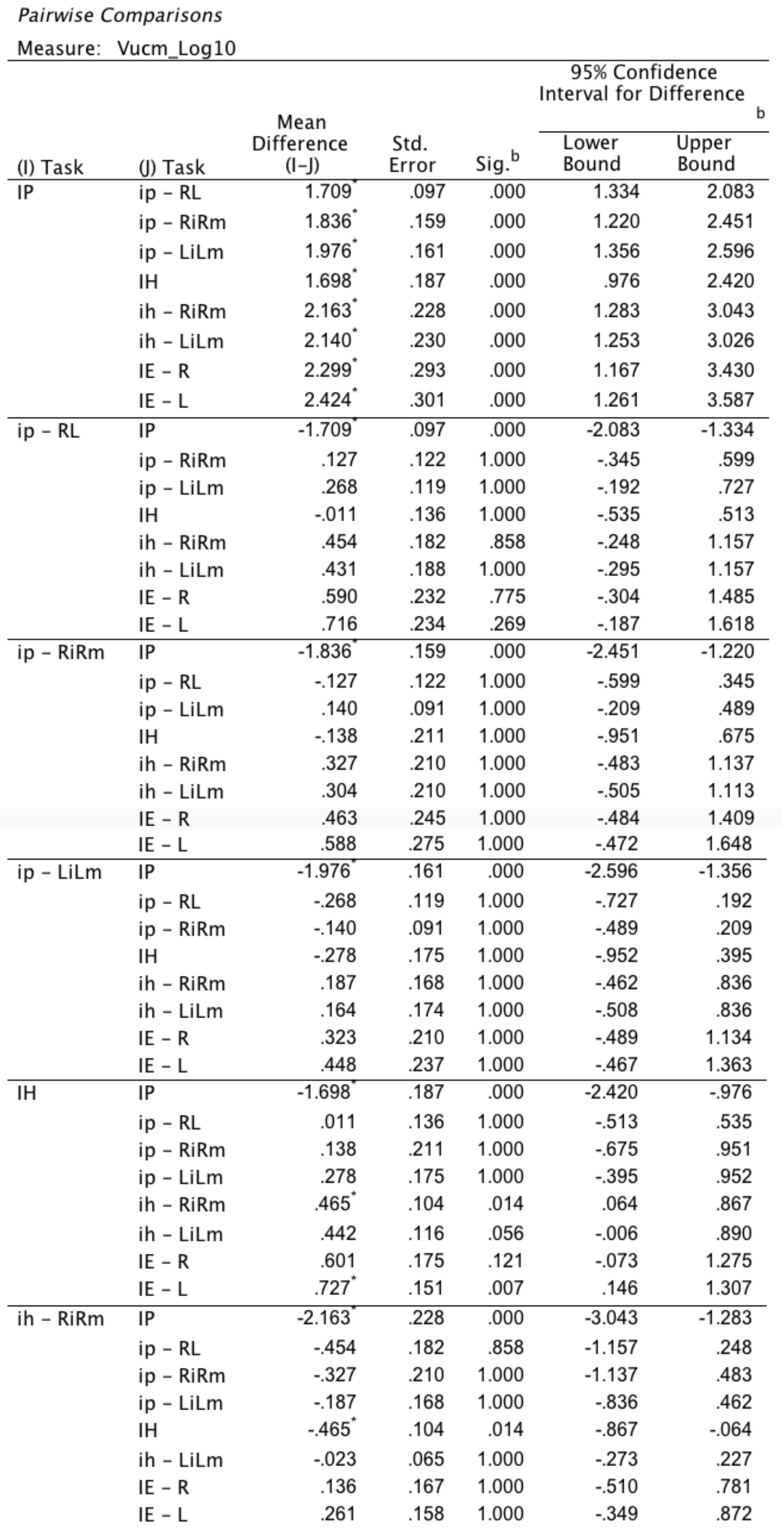


Tests of Within-Subjects Effects

Measure: Vucm_Log10

Source		Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared	Noncent. Parameter	Observed Power [a]
Task	Sphericity Assumed	71.003	8	8.875	29.476	.000	.648	235.807	1.000
	Greenhouse-Geisser	71.003	2.369	29.970	29.476	.000	.648	69.833	1.000
	Huynh-Feldt	71.003	2.808	25.286	29.476	.000	.648	82.768	1.000
	Lower-bound	71.003	1.000	71.003	29.476	.000	.648	29.476	.999
Error(Task)	Sphericity Assumed	38.542	128	.301					
	Greenhouse-Geisser	38.542	37.906	1.017					
	Huynh-Feldt	38.542	44.928	.858					
	Lower-bound	38.542	16.000	2.409					

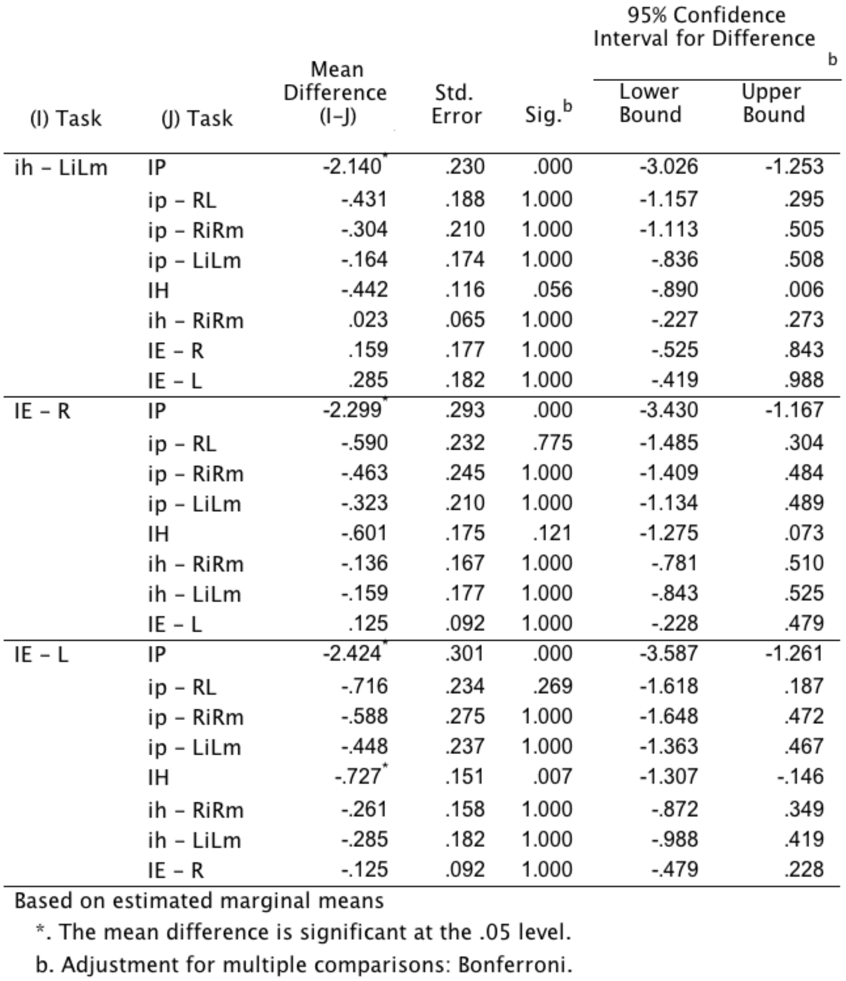
a. Computed using alpha = .05



Pairwise Comparisons

Measure: Vucm_Log10

(I) Task	(J) Task	Mean Difference (I–J)	Std. Error	Sig.b	95% Confidence Interval for Differenceb	
					Lower Bound	Upper Bound
IP	ip – RL	1.709*	.097	.000	1.334	2.083
	ip – RiRm	1.836*	.159	.000	1.220	2.451
	ip – LiLm	1.976*	.161	.000	1.356	2.596
	IH	1.698*	.187	.000	.976	2.420
	ih – RiRm	2.163*	.228	.000	1.283	3.043
	ih – LiLm	2.140*	.230	.000	1.253	3.026
	IE – R	2.299*	.293	.000	1.167	3.430
	IE – L	2.424*	.301	.000	1.261	3.587
ip – RL	IP	-1.709*	.097	.000	-2.083	-1.334
	ip – RiRm	.127	.122	1.000	-.345	.599
	ip – LiLm	.268	.119	1.000	-.192	.727
	IH	-.011	.136	1.000	-.535	.513
	ih – RiRm	.454	.182	.858	-.248	1.157
	ih – LiLm	.431	.188	1.000	-.295	1.157
	IE – R	.590	.232	.775	-.304	1.485
	IE – L	.716	.234	.269	-.187	1.618
ip – RiRm	IP	-1.836*	.159	.000	-2.451	-1.220
	ip – RL	-.127	.122	1.000	-.599	.345
	ip – LiLm	.140	.091	1.000	-.209	.489
	IH	-.138	.211	1.000	-.951	.675
	ih – RiRm	.327	.210	1.000	-.483	1.137
	ih – LiLm	.304	.210	1.000	-.505	1.113
	IE – R	.463	.245	1.000	-.484	1.409
	IE – L	.588	.275	1.000	-.472	1.648
ip – LiLm	IP	-1.976*	.161	.000	-2.596	-1.356
	ip – RL	-.268	.119	1.000	-.727	.192
	ip – RiRm	-.140	.091	1.000	-.489	.209
	IH	-.278	.175	1.000	-.952	.395
	ih – RiRm	.187	.168	1.000	-.462	.836
	ih – LiLm	.164	.174	1.000	-.508	.836
	IE – R	.323	.210	1.000	-.489	1.134
	IE – L	.448	.237	1.000	-.467	1.363
IH	IP	-1.698*	.187	.000	-2.420	-.976
	ip – RL	.011	.136	1.000	-.513	.535
	ip – RiRm	.138	.211	1.000	-.675	.951
	ip – LiLm	.278	.175	1.000	-.395	.952
	ih – RiRm	.465*	.104	.014	.064	.867
	ih – LiLm	.442	.116	.056	-.006	.890
	IE – R	.601	.175	.121	-.073	1.275
	IE – L	.727*	.151	.007	.146	1.307
ih – RiRm	IP	-2.163*	.228	.000	-3.043	-1.283
	ip – RL	-.454	.182	.858	-1.157	.248
	ip – RiRm	-.327	.210	1.000	-1.137	.483
	ip – LiLm	-.187	.168	1.000	-.836	.462
	IH	-.465*	.104	.014	-.867	-.064
	ih – LiLm	-.023	.065	1.000	-.273	.227
	IE – R	.136	.167	1.000	-.510	.781
	IE – L	.261	.158	1.000	-.349	.872



(I) Task	(J) Task	Mean Difference (I–J)	Std. Error	Sig.[b]	95% Confidence Interval for Difference[b]	
					Lower Bound	Upper Bound
ih – LiLm	IP	-2.140*	.230	.000	-3.026	-1.253
	ip – RL	-.431	.188	1.000	-1.157	.295
	ip – RiRm	-.304	.210	1.000	-1.113	.505
	ip – LiLm	-.164	.174	1.000	-.836	.508
	IH	-.442	.116	.056	-.890	.006
	ih – RiRm	.023	.065	1.000	-.227	.273
	IE – R	.159	.177	1.000	-.525	.843
	IE – L	.285	.182	1.000	-.419	.988
IE – R	IP	-2.299*	.293	.000	-3.430	-1.167
	ip – RL	-.590	.232	.775	-1.485	.304
	ip – RiRm	-.463	.245	1.000	-1.409	.484
	ip – LiLm	-.323	.210	1.000	-1.134	.489
	IH	-.601	.175	.121	-1.275	.073
	ih – RiRm	-.136	.167	1.000	-.781	.510
	ih – LiLm	-.159	.177	1.000	-.843	.525
	IE – L	.125	.092	1.000	-.228	.479
IE – L	IP	-2.424*	.301	.000	-3.587	-1.261
	ip – RL	-.716	.234	.269	-1.618	.187
	ip – RiRm	-.588	.275	1.000	-1.648	.472
	ip – LiLm	-.448	.237	1.000	-1.363	.467
	IH	-.727*	.151	.007	-1.307	-.146
	ih – RiRm	-.261	.158	1.000	-.872	.349
	ih – LiLm	-.285	.182	1.000	-.988	.419
	IE – R	-.125	.092	1.000	-.479	.228

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

Appendix E

Results of One-Way Repeated Measures ANOVA and Pairwise Comparisons Applied to Log-Transformed V_{ORT} with Bonferroni Adjustments Across All Tasks and Associated Levels of Within-Task Control

Descriptive Statistics

	Mean	Std. Deviation	N
IP	-1.255313	.9644215	17
ip – RL	.533736	.5560369	17
ip – RiRm	-.043089	.5967687	17
ip – LiLm	-.037010	.5264561	17
IH	-1.642961	.6185079	17
ih – RiRm	-1.107099	.5602369	17
ih – LiLm	-1.158054	.7431605	17
IE – R	-1.559336	.9293496	17
IE – L	-1.828690	.8222808	17

Mauchly's Test of Sphericity

Measure: Vort_Log10

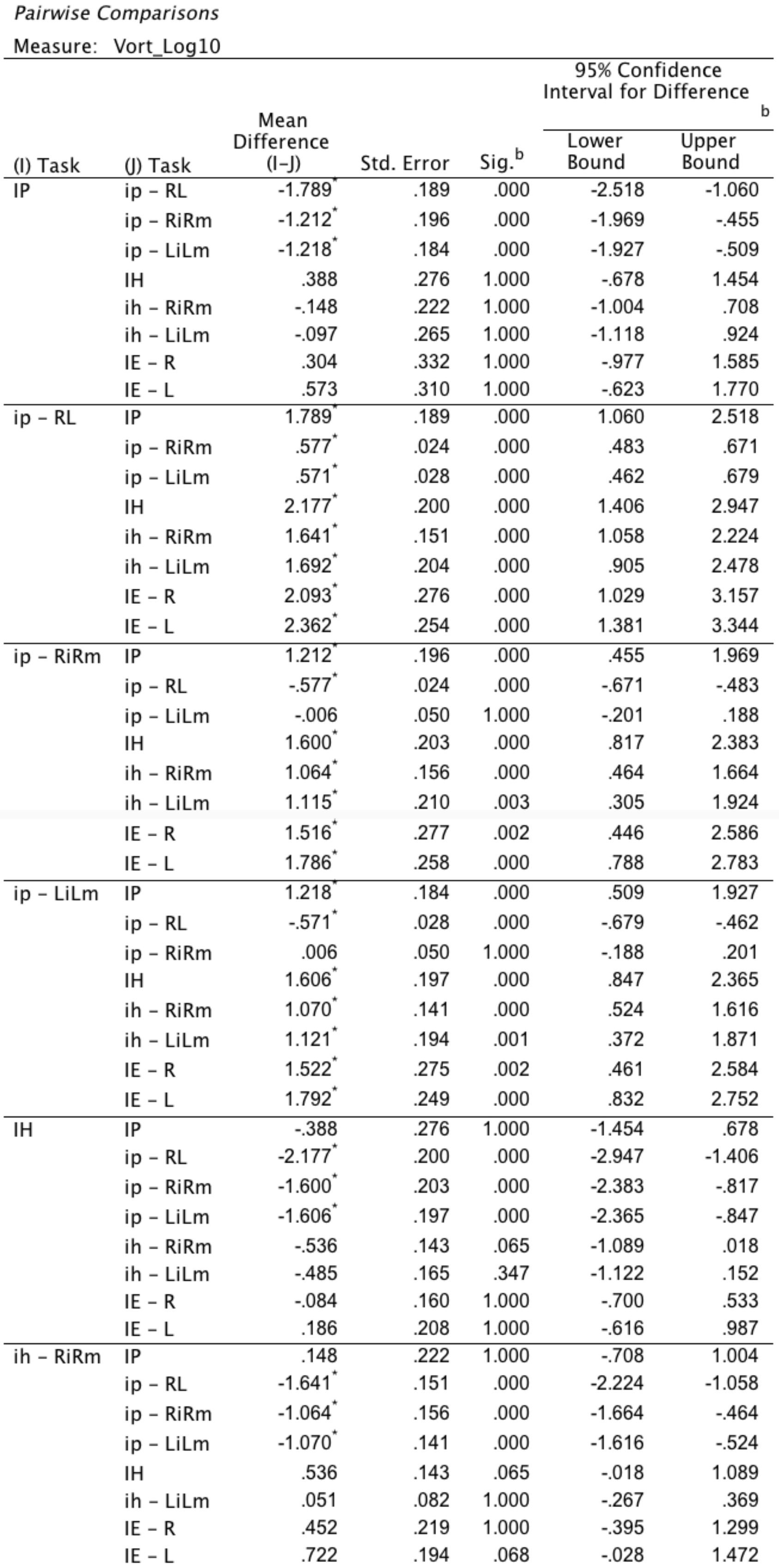
					Epsilon		
Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Task	.000	166.375	35	.000	.357	.443	.125

Tests of Within-Subjects Effects

Measure: Vort_Log10

Source		Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared	Noncent. Parameter	Observed Power^a
Task	Sphericity Assumed	95.532	8	11.942	32.127	.000	.668	257.019	1.000
	Greenhouse-Geisser	95.532	2.855	33.456	32.127	.000	.668	91.738	1.000
	Huynh-Feldt	95.532	3.541	26.980	32.127	.000	.668	113.758	1.000
	Lower-bound	95.532	1.000	95.532	32.127	.000	.668	32.127	1.000
Error(Task)	Sphericity Assumed	47.577	128	.372					
	Greenhouse-Geisser	47.577	45.687	1.041					
	Huynh-Feldt	47.577	56.654	.840					
	Lower-bound	47.577	16.000	2.974					

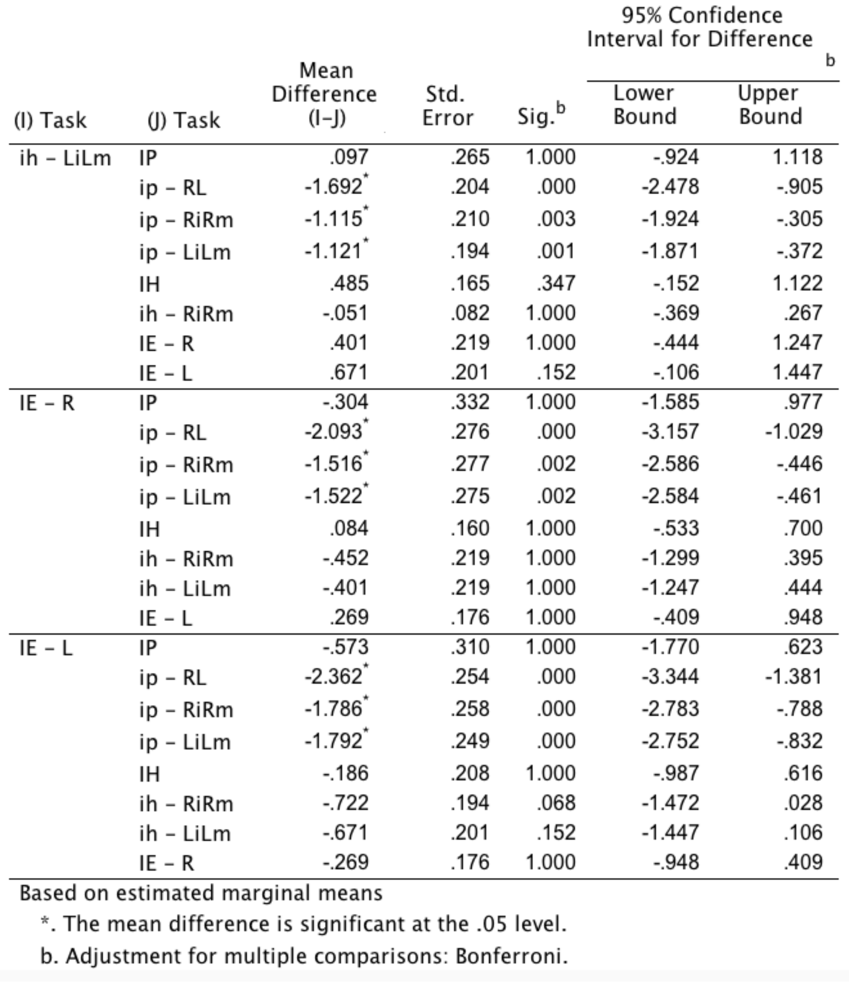
a. Computed using alpha = .05



Pairwise Comparisons

Measure: Vort_Log10

(I) Task	(J) Task	Mean Difference (I-J)	Std. Error	Sig.b	95% Confidence Interval for Differenceb Lower Bound	Upper Bound
IP	ip – RL	-1.789*	.189	.000	-2.518	-1.060
	ip – RiRm	-1.212*	.196	.000	-1.969	-.455
	ip – LiLm	-1.218*	.184	.000	-1.927	-.509
	IH	.388	.276	1.000	-.678	1.454
	ih – RiRm	-.148	.222	1.000	-1.004	.708
	ih – LiLm	-.097	.265	1.000	-1.118	.924
	IE – R	.304	.332	1.000	-.977	1.585
	IE – L	.573	.310	1.000	-.623	1.770
ip – RL	IP	1.789*	.189	.000	1.060	2.518
	ip – RiRm	.577*	.024	.000	.483	.671
	ip – LiLm	.571*	.028	.000	.462	.679
	IH	2.177*	.200	.000	1.406	2.947
	ih – RiRm	1.641*	.151	.000	1.058	2.224
	ih – LiLm	1.692*	.204	.000	.905	2.478
	IE – R	2.093*	.276	.000	1.029	3.157
	IE – L	2.362*	.254	.000	1.381	3.344
ip – RiRm	IP	1.212*	.196	.000	.455	1.969
	ip – RL	-.577*	.024	.000	-.671	-.483
	ip – LiLm	-.006	.050	1.000	-.201	.188
	IH	1.600*	.203	.000	.817	2.383
	ih – RiRm	1.064*	.156	.000	.464	1.664
	ih – LiLm	1.115*	.210	.003	.305	1.924
	IE – R	1.516*	.277	.002	.446	2.586
	IE – L	1.786*	.258	.000	.788	2.783
ip – LiLm	IP	1.218*	.184	.000	.509	1.927
	ip – RL	-.571*	.028	.000	-.679	-.462
	ip – RiRm	.006	.050	1.000	-.188	.201
	IH	1.606*	.197	.000	.847	2.365
	ih – RiRm	1.070*	.141	.000	.524	1.616
	ih – LiLm	1.121*	.194	.001	.372	1.871
	IE – R	1.522*	.275	.002	.461	2.584
	IE – L	1.792*	.249	.000	.832	2.752
IH	IP	-.388	.276	1.000	-1.454	.678
	ip – RL	-2.177*	.200	.000	-2.947	-1.406
	ip – RiRm	-1.600*	.203	.000	-2.383	-.817
	ip – LiLm	-1.606*	.197	.000	-2.365	-.847
	ih – RiRm	-.536	.143	.065	-1.089	.018
	ih – LiLm	-.485	.165	.347	-1.122	.152
	IE – R	-.084	.160	1.000	-.700	.533
	IE – L	.186	.208	1.000	-.616	.987
ih – RiRm	IP	.148	.222	1.000	-.708	1.004
	ip – RL	-1.641*	.151	.000	-2.224	-1.058
	ip – RiRm	-1.064*	.156	.000	-1.664	-.464
	ip – LiLm	-1.070*	.141	.000	-1.616	-.524
	IH	.536	.143	.065	-.018	1.089
	ih – LiLm	.051	.082	1.000	-.267	.369
	IE – R	.452	.219	1.000	-.395	1.299
	IE – L	.722	.194	.068	-.028	1.472



(I) Task	(J) Task	Mean Difference (I–J)	Std. Error	Sig.[b]	95% Confidence Interval for Difference[b]	
					Lower Bound	Upper Bound
ih – LiLm	IP	.097	.265	1.000	-.924	1.118
	ip – RL	-1.692*	.204	.000	-2.478	-.905
	ip – RiRm	-1.115*	.210	.003	-1.924	-.305
	ip – LiLm	-1.121*	.194	.001	-1.871	-.372
	IH	.485	.165	.347	-.152	1.122
	ih – RiRm	-.051	.082	1.000	-.369	.267
	IE – R	.401	.219	1.000	-.444	1.247
	IE – L	.671	.201	.152	-.106	1.447
IE – R	IP	-.304	.332	1.000	-1.585	.977
	ip – RL	-2.093*	.276	.000	-3.157	-1.029
	ip – RiRm	-1.516*	.277	.002	-2.586	-.446
	ip – LiLm	-1.522*	.275	.002	-2.584	-.461
	IH	.084	.160	1.000	-.533	.700
	ih – RiRm	-.452	.219	1.000	-1.299	.395
	ih – LiLm	-.401	.219	1.000	-1.247	.444
	IE – L	.269	.176	1.000	-.409	.948
IE – L	IP	-.573	.310	1.000	-1.770	.623
	ip – RL	-2.362*	.254	.000	-3.344	-1.381
	ip – RiRm	-1.786*	.258	.000	-2.783	-.788
	ip – LiLm	-1.792*	.249	.000	-2.752	-.832
	IH	-.186	.208	1.000	-.987	.616
	ih – RiRm	-.722	.194	.068	-1.472	.028
	ih – LiLm	-.671	.201	.152	-1.447	.106
	IE – R	-.269	.176	1.000	-.948	.409

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

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