

**ADAPTATIONS TO POSTURAL AND MANUAL CONTROL DURING
TOOL USE**

by

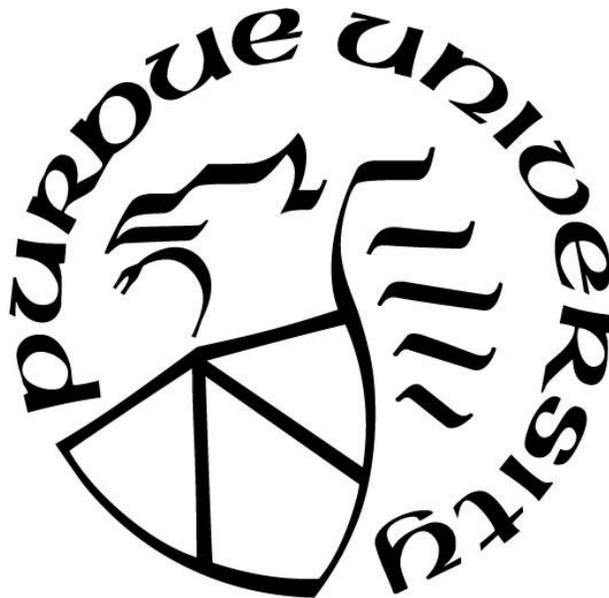
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To my parents, John and Jennifer Liddy, for all the support over the years

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DEFINITIONS AND ABBREVIATIONS

Center of mass (CoM) – the point location where the weighted sum of distributed body segment masses sums to zero.

Center of pressure (CoP) – the point location of the weighted sum of the force applied under the feet

Time-to-boundary (TtB) - a temporal margin that represents how long it would take the CoP or CoM to reach the base of support based on its instantaneous position, velocity, and acceleration.

Anteroposterior (AP) – reference to the forwards and backwards motion of the body with respect to the sagittal plane.

Mediolateral (ML) – reference to left and right lateral motion of the body with respect to the front plane.

ABSTRACT

Tool use is an important area of research in psychology, neurophysiology, and motor behavior because it provides insights into the organization of perception, cognition, and action. Tool use research has traditionally focused on the neural structures or cognitive processes that contribute to body-tool integration, while there has been comparatively little interest in motor control. When tool use actions are studied, adaptations have mainly been examined at the level of manual control, while postural control and multi-segment coordination have received less attention. Examining these components of behavior in the context of tool use is vital for developing a better understanding of how humans integrate tools into goal-directed actions.

The goals of this dissertation were to 1) characterize adaptations to postural control over time when performing a manual task with a tool under different levels of postural constraint and determine their relation to manual task performance, 2) examine postural-manual coupling under different levels of postural constraint during tool use, and 3) determine how multi-segment coordination supports postural stability and suprapostural task performance under different levels of postural constraint during tool use. To address these questions, we adopted a sensorimotor adaptation paradigm to examine postural-manual control and multi-segment coordination before, during, and after an extended bout of tool use.

Tool-use adaptations were found to extend beyond the end-effector. Postural control played a crucial role in facilitating improvements in the manual control of tools. Placing constraints on posture interfered with these adaptations, disrupting the coordination of postural-manual behaviors during tool use. However, multi-segment coordination was modified to overcome this challenge and facilitate postural stability and manual performance. These results demonstrate that healthy young adults are capable of flexibly recruiting and exploiting available degrees of freedom in a task-dependent manner the potential challenges associated with integrating tools into movements. This dissertation provides preliminary support for the importance of considering postural control in tool use actions and highlights the utility of examining interactions across multiple levels of motor behavior—postural control, manual control, postural-manual coupling, and multi-segment coordination—to elucidate how tools are integrated into complex, goal-directed behaviors.

CHAPTER 1 – DEVELOPMENT OF THE PROBLEM

1.1. Background

Tools are often used by humans to mediate interactions with their environment. Tool use, as defined here, refers to the intentional manipulation of objects that augment perception-action capabilities to achieve goal-directed actions (Reed, 1988; Smitsman, 1997). This definition emphasizes the way that tools supplement our natural abilities, allowing us to overcome bodily limitations to produce an intended effect on, or detect information in the environment (Baber, 2006; Gibson, 1979).

Tool use is a defining feature of humanity and an important area of research in psychology, neurophysiology, and motor behavior because it provides insights into the organization of perception (Farnè & Ládavas, 2000), cognition (Povinelli, 2000), as well as motor learning and control (Biryukova & Bril, 2012). The difficulty of integrating tools into goal-directed actions is exemplified by the protracted development of tool use behaviors from infancy to adolescence (Lockman, 2000) and the lack of technological accumulation in other animals (Vaesen, 2012). A fundamental question in human motor behavior is how tools are integrated into goal-directed actions.

Research on tool use has primarily focused on the neural structures or cognitive processes that contribute to body-tool integration (Holmes & Spence, 2004; Johnson-Frey, 2004; Maravita & Iriki, 2004), while there has been comparatively little interest in tool use actions. When tool use actions were studied, adaptations have mainly been examined at the level of manual control (Cardinali, Frassinetti, et al., 2009; Heuer & Sülzenbrück, 2009; Kahrs, Jung, & Lockman, 2013), while postural control (Bongers, Michaels, & Smitsman, 2004; Bongers, Smitsman, & Michaels, 2003) and multi-segment coordination (Valk, Mouton, & Bongers, 2016; van der Steen & Bongers, 2011) have received less attention.

While there are substantial, independent bodies of research on the integration of postural and manual behaviors and manual adaptations to tool use, the importance of postural-manual integration in tool use has received less attention. The thesis pursued in this dissertation is that tool use is a whole-body activity that requires the ongoing adaptation of postural and suprapostural behaviors and the coordination of multiple bodily degrees of freedom. Examining

these components of behavior in the context of tool use is vital for developing a better understanding of how humans integrate tools into goal-directed actions. This dissertation broadly addresses the question, how is postural control, postural-manual coupling, and multi-segment coordination adapted to support tool use?

In the following sections, I provide background on the integration of postural and manual control. Next, I describe current research on manual adaptations to tool use. Then, I review the research on postural adaptations to tool use, which focuses more on foot placement and body configuration than postural control, postural-manual coupling, or multi-segment coordination. From this background information, the research questions and hypotheses are identified. Finally, the significance of the dissertation—in terms of its broader theoretical and translational impact—is discussed.

1.2. Postural-manual control

Postural control refers to the capability to control and orient the body to itself or environmental surfaces and objects to facilitate perception and action (Ricchio, 1993; Ricchio & Stoffregen, 1988; Stoffregen & Ricchio, 1988). Research on postural control has traditionally focused on mechanisms that stabilize upright stance with the assumption that the goal of postural control is minimize movements of the center of mass (CoM), leading to the assumption that increased postural variability is indicative of reduced postural stability (Massion, 1994; Nashner & Mccollum, 1985).

Standing upright is useful to the extent that it allows people to engage in suprapostural behaviors (Bernstein, 1967; Ricchio, 1993; Ricchio & Stoffregen, 1988). From this perspective, “good” postural control refers to the ability to adaptively modulate standing posture to meet the demands of concurrent behavioral goals, rather than indiscriminately reduce body movements (Haddad, Rietdyk, Claxton, & Huber, 2013).

1.2.1. Postural control for suprapostural tasks

Task-dependent postural control provides a means to continuously modify postural responses to changing task demands (Haddad et al., 2013). Postural variability is reduced during precision manual tasks, suggesting that task-dependent adaptations to postural control are

undertaken to support manual performance (Balasubramaniam, Riley, & Turvey, 2000; Haddad, Ryu, Seaman, & Ponto, 2010; Riley, Stoffregen, Grocki, & Turvey, 1999). Decreased postural variability also facilitates visual fixation on near, but not far, objects (Stoffregen, Pagulayan, Bardy, & Hettinger, 2000). Counterintuitively, reducing postural stability can also improve task performance. For example, decreases in postural stability during unipedal, but not bipedal, stance is associated with improved visual tracking performance (Deprá, Amado, & van Emmerik, 2019). Thus, the capability to increase *and* decrease postural variability is necessary to adapt to changing suprapostural task constraints.

Changes to postural and manual control also occur over repeated performances of the same task. For example, learning to perform a serial reaching task while standing led to concurrent increases in postural stability and improvements in manual performance early in learning, while postural responses continued to be modified throughout late learning (Galgon, Shewokis, & Tucker, 2010). These findings collectively indicate that 1) the degree of postural stabilization is adaptively related to the concurrent task constraints and 2) postural adaptations support improvements manual performance, especially early in learning (Galgon et al., 2010).

Task-dependent changes to postural control may also occur during tool use. Grasping and manipulating objects alters the limb geometry and dynamics, which impacts the ability to control the end-effector. Adaptive modifications to postural control may therefore contribute to improvements in manual control during tool use. Moreover, increasing the difficulty of maintaining standing balance—for example, by reducing the base of support—may diminish tool-use-related postural adaptations and interfere with manual task performance.

1.2.2. Postural-manual coupling

Postural and manual actions exhibit varying degrees of coordination depending on the task demands (Amado, Palmer, Hamill, & van Emmerik, 2016; Balasubramaniam, 2013; Cluff, Boulet, & Balasubramaniam, 2011; Haddad et al., 2010; Huys, Daffertshofer, & Beek, 2003). Postural-manual coupling varies within task performance (Cluff et al., 2011), with extended practice (Huys et al., 2003), or when increasing postural or task-related constraints (Amado et al., 2016). These studies suggest that 1) postural-manual coupling varies with practice, 2) improvements in performance are associated with weaker postural-manual coupling, and 3) postural and manual control become systematically decoupled as postural and manual task

constraints increase. Weaker postural-manual coupling is thought to decrease the risk of postural variability interfering with manual task performance.

Tools that extend arm length are more challenging to control because of the disproportionate influence of proximal joint rotations on the end-effector position, particularly when the arm is extended. Weaker postural-manual coupling may be expected when manipulating tools, at least when the precision demands are high. Decreases in postural-manual coupling may occur as people become better at using a tool. Increasing the postural constraints may impair postural-manual coupling since focus will be shifted to maintaining balance. Postural challenges may therefore impair the postural corrections needed to compensate for reductions in manual control when integrating tools into motor behaviors while standing.

1.2.3. Multi-segment coordination and postural-manual control

Skilled, coordinated movements are characterized by the coordination of multiple body segments. During upright standing, the joints of both the upper and lower limbs contribute to CoM stabilization (Hsu, Scholz, Schoner, Jeka, & Kiemel, 2007). When postural constraints are increased by reducing the base of support width, increases in CoM motion are accompanied by concurrent increases in joint angle variability that leave the stability of the CoM position unchanged (Hsu, Lin, Yang, & Cheng, 2014). When performing a manual task while standing, increases in joint angle variability do not adversely affect CoM position, indicating that the nervous system exploits motor redundancy to stabilize multiple performance variables (Hsu & Scholz, 2012).

Reaching while standing is characterized by two distinct synergies of the lower and upper extremities that ensure postural stability and transport the hand to the target (Kaminski, 2007; Kaminski & Simpkins, 2001). When reaching within arm length, lower and upper limb movements occur relatively independently. By contrast, when reaching beyond arm length, lower limb and upper limb movements become more coupled to transport the body *and* hand towards the target, which is inconsistent with the idea that the goal of postural control is to minimize CoM movement (Pozzo, Stapley, & Papaxanthis, 2002). Together, these findings demonstrate that 1) postural stability is achieved by interactions among multiple body segments, 2) the nervous system readily recruits and exploits available degrees of freedom in a context-dependent

manner during postural-manual tasks, and 3) multi-segment coordination facilitates the simultaneous maintenance of postural stability and suprapostural performance.

Standing and reaching with tools that extend arm length presents an additional challenge because postural variability exacerbates the difficulty of controlling the end-effector. Increasing joint angle variability while preserving joint angle covariation across the lower and upper limbs may reduce the influence of extraneous postural variability on manual control, as well as mitigate threats to balance associated with arm movements. Moreover, simultaneously increasing postural and manual task constraints—by reducing the base of support during tool use—may lead to further increases in joint angle variability to maintain postural stability and manual performance.

1.2.4. Summary

Tool use poses several challenges for the integration of postural and manual control. The current literature indicates that multiple dimensions of postural-manual control are adapted to concurrently maintain postural stability and manual task performance. Despite this extensive body of research, postural-manual integration has been overlooked in the domain of tool use. To date, studies of tool use actions have independently focused on manual control (described below) or postural control (also described below). There is reason to suspect that tool use adaptations are not limited to the end-effector. Changes to postural control, postural-manual coupling, and multi-segment coordination are likely to occur when people engage in tool use. Moreover, it is possible that extended practice with a tool elicits further postural-manual adaptations to improve task performance.

1.3. Manual adaptations to tool use

Recent research has focused on manual control and coordination during reaching with and without tools to develop a better understanding of how tool use is integrated into goal-directed actions. Two approaches have been adopted: 1) comparing movements performed with and without tools or 2) examining changes to movements before and after extended tool use training.

1.3.1. Comparing manual actions without and without tools

Several studies have investigated changes to endpoint trajectories during seated reaching with and without tools. Reaching movements made with pointers that extend arm length are characterized by longer durations that increase proportionally with tool length (Baird, Hoffmann, & Drury, 2002; Valk et al., 2016). Reaching with longer tools produces higher peak velocities and longer deceleration times, as well as more curved reach trajectories (Valk et al., 2016). Greater endpoint variability is observed for longer rods (Valk et al., 2016), which can have deleterious effects on performance depending on the target size (Baird et al., 2002). These modifications are thought to result from changes to the inertial properties of the arm and the disproportionate influence of proximal joint rotations on the end-effector position, which reduces the controllability of the tool.

Tools alter the forces required to manipulate the limb, which requires modifying the coordination among degrees of freedom. The coordination among arm degrees of freedom during seated reaching with and without tools of different lengths was examined using the uncontrolled manifold (UCM) analysis to determine whether the tool tip was stabilized to the same degree as the hand (Valk et al., 2016; van der Steen & Bongers, 2011). The stability of the tool tip trajectory was similar across tool lengths and did not differ from the fingertip during free hand reaching. Concurrent increases joint covariation despite increases in end-effector variability led to no differences in the stability of the end-effector across changes in rod length. Thus, changes in tool length do not affect the stability of the end-effector and have been interpreted as evidence that similar control strategies are employed when reaching with or without tools.

One limitation of these studies is that only seated reaching was examined. Reaching while standing is common in daily life. Changes to the end-effector trajectory described above may not be obligatory because of interactions between postural and manual control. Postural adaptations could also play an important role in supporting manual control when people switch between reaching with and without a tool. Examining reaching with and without tools while standing will provide information about how multi-segment coordination contributes to maintaining postural stability *and* manual performance.

1.3.2. Comparing manual actions before and after tool use

Several studies have used adaptation paradigms to examine changes to manual control during tool use. These experiments consist of three stages: 1) a baseline bout of seated reaching without a tool, 2) an extended bout of seated reaching with a tool that extends arm length, and 3) a second bout of seated reaching without a tool. Tool-use-dependent adaptations to manual control occur rapidly—requiring only a few trials, even when participants are not familiar with the tool—and do not emerge when reaching with a wrist-worn load of similar weight (Cardinali, Frassinetti, et al., 2009; Lacquaniti, Soechting, & Terzuolo, 1982). Longer reach durations, lower peak velocities and accelerations, and longer peak velocity and acceleration latencies were observed during tool use. Subsequent free hand reaching initially exhibited longer durations, lower peak velocities and accelerations, and longer peak velocity and acceleration latencies compared to pre-tool-use. These modifications are referred to as tool-use-dependent aftereffects (Cardinali, Frassinetti, et al., 2009). The nature of the tool use actions, specifically, whether the tool causally interacts with a target object or surface, influences the strength of the aftereffects (Cardinali et al., 2012). Tool use adaptations *and* aftereffects are restricted to the transport parameters when reaching with a tool that extends arm length, whereas prehensile parameters are influenced when using tools that modify finger length (Cardinali, Brozzoli, Finos, Roy, & Farne, 2016; Cardinali, Frassinetti, et al., 2009; Cardinali et al., 2012).

Tool-use-dependent aftereffects were attributed to changes to the Body Schema—the multisensory neural representation of the body dimensions and configuration (Holmes & Spence, 2004). Support for this hypothesis came from 1) overestimations of arm length following tool use and 2) comparable pre-tool-use results after stratifying participants into groups with short and long arms. An alternative interpretation is that temporary changes to the geometric and inertial properties of the arm that delayed re-adaptation to free hand reaching. Overall, these findings provide evidence that 1) manual control adapts rapidly when reaching with tools, 2) reaches made following prolonged tool use are initially similar to those observed during tool use, and 3) tools that extend arm length only influence reach transport. Although these studies only examined tool use during seated reaching, postural adaptations to tool use could exhibit similar tendencies—i.e. adaptations to postural control would carry over to actions performed following an extended bout of tool use.

1.4. Postural adaptations to tool use

Less attention has been given to postural adaptations that support tool use. Successful tool use requires bringing the effective part of the tool into specific relations with environmental objects or surfaces. Postural control provides a means of maintaining stable actor-environment relations over time (Reed, 1989). When perception-action capabilities are changed—such as during tool use—then different postural configurations or patterns of sway help to maintain the relation between the end-effector and the target object or surface.

Previous studies have primarily focused on how changes to tool characteristics and task constraints influence the standing position (i.e., distance from the feet to the target object) and postural configuration (i.e., joint angles) when displacing an object (Bongers et al., 2004; Bongers et al., 2003). Stance location and postural configuration depended on the geometric and dynamic properties of the body + tool system (Bongers et al., 2003). For example, when the precision demands of the task were increased, closer standing positions were adopted and the arm was held closer to the body. These findings are consistent with the idea that body and arm postures are adapted to mitigate threats to balance and improve the controllability of the tool (Bongers et al., 2004).

These studies provided important insights into the role of posture during tool use but are of limited utility for understanding postural control, postural-manual coupling, and multi-segment coordination. There are also several notable limitations. First, task performance was not measured, meaning that associations between postural control and manual performance could not be drawn. Second, postural measures were limited to the static configuration of body segments immediately prior to object manipulation. Thus, it was unclear whether postural adjustments were undertaken to improve postural stability, support manual task performance, or both. To address these limitations, this dissertation examined changes in postural control, postural-manual coupling, and multi-segment coordination during tool use movements (i.e., reaching) and postures (i.e., maintaining position) while quantifying task performance.

1.5. Statement of the problem

Studies of motor control and learning strongly suggest that multiple dimensions of postural-manual control are adapted to simultaneously maintain postural stability and manual

task performance. To date, studies of tool use have independently focused on postural and manual control while not examining the integration of postural-manual control. This dissertation was undertaken to develop a better understanding of how postural-manual control supports the integration of tools into goal-directed actions.

Previous studies of tool use have primarily focused on manual aspects of behavior. Comparatively, there has been little consideration for postural control, postural-manual coordination, or multi-segment coordination beyond the upper limb because most studies have examined seated reaching (Cardinali et al., 2016; Cardinali, Frassinetti, et al., 2009; Cardinali et al., 2012; Valk et al., 2016; van der Steen & Bongers, 2011). Functional behaviors, such as reaching, are also embedded in complex behavioral sequences and nested within a postural setting (Reed, 1989). Tool use adaptations may go unnoticed if the analysis is confined to the end-effector because important changes may occur at the support surface or between body segments.

Part of the difficulty of tool use is identifying the appropriate postural configuration(s) and dynamics that create the conditions permitting controlled, skillful actions. Tool-use relies on the capability to integrate external objects into bodily postures and movements (Reed, 1989). But tool use creates its own action problems - potentially requiring new postural configurations, patterns of coordination, and/or control strategies to maintain task performance. Studying tool use enables us to investigate what aspects of behavior need to be adapted to take advantage of the tool and identify commonalities between actions performed with and without tools (Smitsman and Bongers, 2003). This is important because some details of tool use actions may be coopted from previously developed skills (Lockman, 2008).

1.6. General approach

This dissertation examined bodily adaptations during and following goal-directed actions while standing and using a tool that extended arm length. Because there has been little focus on postural and suprapostural aspects of behavior in the context of tool use, only healthy adults were examined. The goals of the research were to 1) characterize adaptations to postural control over time when performing a manual task with a tool under different levels of postural constraint and how these adaptations relate to manual task performance during and following an extended bout of tool use, 2) examine postural-manual coupling under different levels of postural constraint

during and following an extended bout of tool use, and 3) determine how multi-segment coordination supports postural stability and suprapostural task performance under different levels of postural constraint during and following an extended bout of tool use.

To address these aims, a well-studied experimental task consisting of standing and performing a precision manual task (Haddad et al., 2010; Haddad, Van Emmerik, Wheat, & Hamill, 2008; Liddy, Arnold, Cho, Romine, & Haddad, 2019) was modified to accommodate performance with and without a tool that extended arm length. The task consisted of acquiring, transporting, and fitting a block through an opening using the dominant hand while standing. The object was then held in the opening for five seconds. This created two distinct behavioral subphases related to movement (i.e., transport) and posture (i.e., fitting).

Tools alter body dimensions and mass distributions, which require task-specific adaptations to posture and movement. The experimental paradigm was adapted from studies conducted by Cardinali and colleagues, which resemble sensorimotor adaptation paradigms (Krakauer, 2009; Krakauer & Mazzoni, 2011; Shadmehr, Smith, & Krakauer, 2010). This paradigm consisted of two periods performing the precision manual task without the tool separated by an extended period performing the same task with a tool. The tools examined in this dissertation extended arm length, similar to previous studies (Cardinali, Frassinetti, et al., 2009; Cardinali et al., 2012; Valk et al., 2016; van der Steen & Bongers, 2011). Tools extended arm length by 50% and reach distances were scaled to 120% of arm + tool length to ensure that the trunk and lower limbs contributed to reaching.

1.6.1. Specific Aim 1

Previous studies examining manual control during tool use have shown that movement characteristics are modified during and following an extended bout of tool use (Baird et al., 2002; Cardinali, Frassinetti, et al., 2009; Cardinali et al., 2012; Valk et al., 2016). Tool use adaptations may not be confined to the end-effector because reaching is normally a whole-body action involving the lower and upper limbs. To date, few studies have examined postural control during or following tool use. Changes to body and arm postures prior to tool use have been interpreted as adaptive modifications to reduce threats to balance and improve the controllability of the tool (Bongers et al., 2004). But it remains unclear whether modifications of postural control occur during or following tool use and how those changes are related to manual task

performance. Because manipulating tools alters the arm geometry and dynamics, adaptive modifications of postural control may contribute to improvements in manual task performance, while increasing constraints on standing posture may attenuate tool-use-related postural adaptations and interfere with manual task performance.

Therefore, the first aim of this dissertation was to characterize adaptations to postural control during tool use under different levels of postural constraint and how these adaptations support manual task performance. To examine how postural constraints influence postural adaptations during and following tool use, one group of participants performed the experimental tasks while standing with a normal base of support (Normal BoS) while a second group of participants performed the same tasks while standing on a reduced base of support (Reduced BoS). The primary focus was to examine spatiotemporal and boundary relevant measures of the center of pressure (CoP) while learning to use a tool and how these changes influence suprapostural task performance. Time-to-boundary (TtB) measures a temporal margin that represents how long it would take the CoP to reach the base of support based on its instantaneous position, velocity, and acceleration (Haddad, van Emmerik, Whittlesey, & Hamill, 2006).

Note: The CoP was selected instead the CoM on the basis that the CoP is a high-dimensional variable representing the interaction between the body and support surface that is used to control CoM movements. The primary disadvantage of using the CoP is that it does not have the same mechanical consequences for balance as the CoM because it cannot contact the base of support. This limitation aside, the CoP was selected on the basis that nearly identical TtB measures are obtained for both variables during quiet stance (Haddad, van Emmerik, et al., 2006).

H1.1a: *During tool use, postural adaptations characterized by reductions in postural stability will be observed during the transport stage in the Normal BoS group. Postural adaptations will not occur in the Reduced BoS group because of limitations on postural sway. CoP excursion will increase during tool use compared to pre- and post-tool-use, allowing the tool to be held closer to the body while reaching to enhance endpoint control (Bongers et al., 2004). Concurrent changes in maximum CoP velocity will occur to maintain the timing of the postural contributions to reaching. These changes will collectively result in shorter minimum TtB, indicating a closer proximity to the stability limits. No changes in CoP excursion, maximum CoP velocity, or minimum TtB are expected across conditions in the Reduced BoS group due to the limitations on generating postural sway. The expected findings will 1) provide evidence of adaptations during*

dynamic postural control when using a tool, 2) demonstrate that reductions in postural stability occur when reaching beyond arm length during tool use, which may be related to improvements in manual control (see below), and 3) show that placing constraints on standing posture attenuates postural adaptations to tool use, which are expected to interfere with manual control (see below).

Note: CoP excursion and mean velocity were included to quantify spatiotemporal patterns of postural sway during object transport because the body is displaced towards the target when reaching beyond arm length (Kaminski, 2007). Minimum TtB was included to quantify the temporal proximity to the stability boundaries. Together, these measures provide an index of postural stability.

H1.1b: *During tool use, postural adaptations characterized by reduced postural sway during the fitting stage will be observed in both groups. Decreased postural variability and longer minimum TtB is observed during precision manual tasks (Haddad et al., 2010). Decreases in postural variability will occur during tool use compared to pre- and post-tool-use to compensate for reductions to manual control (see below). Sway area and mean CoP velocity will decrease during tool use in both groups. However, shorter minimum TtB will be observed in the Normal BoS group because of greater forward lean during tool use (H1.1a). The Reduced BoS group will exhibit reduced sway area and mean CoP velocity compared to the Normal BoS group because of the combined postural and manual constraints. However, similar minimum TtB will be observed between groups because the Reduced BoS group will not engage in substantial forward lean during tool use (H1.1a). These findings will provide first evidence of adaptations during static postural control when using a tool, which may be undertaken to improve endpoint control (see below).*

H1.1c: *Further increases postural sway and reductions in postural stability will occur throughout the transport stage of tool use in the Normal BoS group. Postural constraints will prevent adaptations throughout tool use in the Reduced BoS group. These results are expected due to the adoption of a conservative ‘posture first’ strategy (Shumway-Cook, Woollacott, Kerns, & Baldwin, 1997) that aims to initially ensure postural stability followed by exploration of postural solutions to allow for greater behavioral flexibility (Riccio, 1993; van Emmerik & van Wegen, 2002). Increased CoP excursion and maximum CoP velocity and shorter minimum*

TtB are expected during late compared to early tool use in the Normal BoS group. No changes in CoP excursion, maximum CoP velocity, and minimum TtB are expected in the Reduced BoS group due to the prevention of postural exploration, leading to a conservative strategy of postural maintenance. These findings will 1) provide evidence of postural adaptations over repeated tool use actions, which may be associated with improvements in manual control (see below), 2) support the role of exploratory activity in the ongoing adaptation of postural control, and 3) show that increasing the postural challenge stifles postural adaptations during tool use, which may be associated with reductions in manual control (see below).

H1.1d: *No changes to postural variability or stability are expected to occur throughout the fitting phase of tool use in either group.* The adaptations described in **H1.1c** are expected due to the adoption of an initially conservative postural control strategy. For this reason, people will be unable to further reduce postural variability, which will account for the lack of adaptations to postural control throughout tool use during the fitting stage. No changes in sway area, mean CoP velocity, or minimum TtB are expected throughout tool use in either group, indicating the limitations on further reducing postural variability. However, changes in other domains, such as postural-manual coupling (Aim 2) or multi-segment coordination (Aim 3), may occur.

H1.2a: *Manual control will decrease when performing the task with the tool but will be worse in the Reduced BoS group due to postural interference.* End-effector variability increases when reaching with a tool (Valk et al., 2016), which results from geometric and dynamic modifications to the arm, as well as the disproportionate influence of proximal joint rotations on the end-effector position. Greater numbers of fitting errors, less smooth reaches, and more variable end-effector movements will be observed compared to pre- and post-tool use. The Reduced BoS group will exhibit worse manual control due to the combined postural and manual task constraints, as evidenced by greater support surface variability during tool use compared to pre- and post-tool use. These findings will 1) provide additional evidence of the difficulty of controlling and coordinating actions with hand-held tools and 2) demonstrate that increasing the demands on standing posture has detrimental consequences for manual control during tool use.

Note: Normalized mean squared jerk was quantified to measure manual control during the transport stage because the end-effector path represents the coordinated output of postural-manual control during reaching. Reach duration, peak velocity, and velocity latency may change for mechanical reasons when using a tool, whereas reach smoothness is considered a signature of skilled, coordinated movement (Hogan & Sternad, 2009). The summed of variances of the end-effector position in the mediolateral (ML) and vertical directions was quantified to measure manual control during the fitting stage because extraneous movements of the endpoint are more likely to result in fitting errors.

H1.2b: *Manual control will improve throughout tool use in both groups, but the relative improvements will be smaller in the Reduced BoS group due to postural interference.* Previous studies examining reaching during tool use did not examine task performance or participants never made errors because the task was too easy (Bongers et al., 2004; Bongers et al., 2003; Cardinali, Brozzoli, & Farne, 2009; Cardinali et al., 2012). Fewer fitting errors, smoother reaches, and less variable end-effector movements are expected during late compared to early tool use particularly in the Normal BoS group. Improvements in the Reduced BoS group are expected to accompany lower support surface variability throughout tool use, indicating reductions in postural interference. These findings will 1) provide evidence of practice-related improvements in manual control during tool use movements (i.e., reaching) and postures (i.e., fitting) and 2) demonstrate that postural constraints attenuate ongoing adaptations to manual control when using a tool.

H1.3a: *Postural and manual control during tool use will be strongly associated in the Normal BoS group but not the Reduced BoS group during the transport stage.* Improvements in manual control (**H1.2b**) and adaptations to postural control (**H1.1c**) are expected to throughout tool use in the Normal BoS group. Postural adaptations are expected to be strongly associated with changes in manual control because postural control provides the foundation for suprapostural performance. Relatively smaller improvements in manual control (**H1.2b**) but no postural adaptations (**H1.1c**) are expected to occur throughout tool use in the Reduced BoS group. For this reason, postural control will not be associated with improvements in manual control. This would indicate that changes in manual control in the Reduced BoS group during the transport stage were achieved by other means, for example postural-manual coupling (Aim 2) or multi-segment coordination (Aim 3). Furthermore, this would provide additional support for the idea

that reduced postural stability is not universally associated with degraded task performance (Deprá et al., 2019).

H1.3b: *Postural and manual control during tool use will not be associated during the fitting stage in the Normal and Reduced BoS groups.* Improvements in manual control (**H1.2b**) are expected to occur throughout tool use in both groups. However, no changes in postural control are expected to occur during the fitting stage because people will be unable to further reduce postural variability (**H1.1d**). Again, this would indicate that changes in manual control in both groups during the fitting stage were achieved by other means, for example postural-manual coupling (Aim 2) or multi-segment coordination (Aim 3).

H1.4: *Postural and manual control will exhibit tool-use dependent aftereffects, during the transport but not fitting stage, in both groups. Weaker manual and no postural aftereffects will be observed in the Reduced BoS group due to limited adaptations to postural and manual control.* After an extended bout of reaching with a tool, free hand reaching exhibits tool-use-dependent aftereffects, which are restricted to reach transport parameters (Cardinali, Frassinetti, et al., 2009). For this reason, no differences pre- and post-tool-use differences are expected for measures of postural or manual control during the fitting stage. Reach smoothness is expected to be lower during early post-tool-use than late pre-tool-use. The differences are expected to be smaller in the Reduced BoS group because of the relatively reduced adaptations to manual control (**H1.2b**). Greater CoP excursion and maximum velocity and shorter minimum TtB will be observed during early post-tool-use compared to late pre-tool-use in the Normal BoS group. Because the Reduced BoS group is not expected to demonstrate postural adaptations across conditions (**H1.1c**), no postural aftereffects are predicted. These findings would demonstrate that 1) tool-use-dependent aftereffects are not limited to the end-effector, which provide further evidence of the integration between postural and manual control during and following tool use, and 2) postural and manual adaptations to tool use extend beyond the tool use window.

1.6.2. Specific Aim 2

Postural and manual actions exhibit varying degrees of coordination depending on the task demands (Amado et al., 2016; Balasubramaniam, 2013; Cluff et al., 2011; Haddad et al.,

2010; Huys et al., 2003). Postural and manual control become systematically decoupled as postural and manual task difficulty increase (Amado et al., 2016) and weaker postural-manual coupling is associated with improvements manual task performance (Huys et al., 2003). Learning-related changes to postural-manual coupling are thought to decrease the risk of postural variability interfering with manual task performance.

Tools that extend arm length are challenging to control because of changes to the arm geometry and dynamics as well as the disproportionate influence of proximal joint rotations on the end-effector position when the arm is extended, such as during reaching. Weaker postural-manual coupling may occur when using a tool because endpoint variability may be more susceptible to postural variations, especially during static postural control. Weaker coupling may also emerge with tool use practice because postural and manual control tend to become decoupled as people become more proficient at manual tasks (Cluff et al., 2011; Huys et al., 2003). Increasing the difficulty of maintaining standing balance may further weaken postural-manual coupling because of the immediate threat to balance and manual performance (Amado et al., 2016). Postural challenges—such as reducing the base of support width—may impair the ability to make the postural corrections needed to compensate for reductions in manual control when using tools, requiring the adoption of other strategies, such as multi-joint error corrections (Cluff, Manos, Lee, & Balasubramaniam, 2012).

Therefore, the second aim examined postural-manual coupling under different levels of postural constraint during and following an extend bout of tool use. The primary outcomes measures focused on postural-manual coupling and how it changed over time before, during, and after tool use. The primary focus was on an information-theoretic measure—average mutual information—to examine relative independence/dependence of the CoP and end-effector.

H2.1: *During tool use, AP postural-manual coupling will be stronger during object transport and increase over time in the Normal BoS because of greater postural contributions to reaching.* Postural manual coupling is expected to be stronger during object transport as people shift their CoM forward and transport the object to the opening. Reductions to the support surface extent are expected to limit postural displacements while reaching, which will reduce postural-manual coupling and prevent it from changing over time (**H1.1c**). Postural-manual coupling will increase over time in the Normal BoS group as the postural contributions to reaching increase (**H1.1c**).

The expected results would 1) provide evidence of systematic adaptations to postural-manual coordination over repeated performances with a tool during *dynamic* postural control and 2) demonstrate that postural constraints inhibit modifications of postural-manual coupling.

H2.2: *During tool use, weaker postural-manual coupling will be observed while fitting particularly in the Reduced BoS group because of the combined postural and manual challenges.*

Weaker postural-manual coupling may be expected when using a tool and engaging in static postural control, such as during fitting. This would reduce the influence of postural movements on hand position, which is especially important when the precision demands are high.

Decreasing the support surface extent is expected to further reduce postural-manual coupling because increased postural constraints have been associated with decoupling of postural and manual control (Amado et al., 2016). These expected results would 1) demonstrate that postural-manual coupling decreases when performing a precision manual task with a tool and 2) provide additional evidence that increasing task constraints leads to the de-coupling of postural and manual control.

H2.3: *During tool use, postural-manual coupling will become weaker over time while fitting in the Normal BoS group to improve manual performance.* This expectation is based on previous findings demonstrating that postural-manual coupling decreases as people become more proficient at a postural-manual skill (Cluff et al., 2011; Huys et al., 2003; Huys, Daffertshofer, & Beek, 2004a, 2004b). Coupling is expected to further decrease as people become more proficient with the tool. No changes are expected in the Reduced BoS group because of the already weaker coupling associated with the postural constraints. These expected results would 1) provide evidence of systematic adaptations to postural-manual coordination over repeated performances with a tool during *static* postural control and 2) show that increasing postural constraints produces a floor effect preventing changes to postural-manual coupling during tool use because of the combined postural and manual challenges.

1.6.3. Specific Aim 3

Standing postural stability is achieved by interactions among multiple body segments (Hsu et al., 2007). When standing and reaching, both the lower and upper body ensure postural

stability and transport the hand to the target (Kaminski, 2007; Kaminski & Simpkins, 2001), indicating that available degrees of freedom are recruited and exploited in a task-dependent manner (Riccio, 1993; Riccio & Stoffregen, 1988). Multi-segment coordination may therefore play an important role in the maintenance of postural stability and suprapostural performance during tool use.

Examining how multiple body segments are coordinated to stabilize task-relevant performance variables has been investigated using UCM analysis (Scholz & Schoner, 1999). The UCM framework has been employed to study neuromuscular synergies that stabilize one or more task-relevant variables by examining covariation among body-level variables (e.g., finger forces, joint angles, etc.). UCM analysis has been applied to many different tasks: pointing (Tseng, Scholz, Schoner, & Hotchkiss, 2003), reach-to-grasp movements (Jacquier-Bret, Rezzoug, & Gorce, 2009), pistol-shooting (Scholz, Schoner, Latash, 2000), sit-to-stand movements (Scholz & Schoner, 1999), and standing posture (Hsu et al., 2007).

This work has recently been extended into the domain of tool use (Valk et al., 2016; van der Steen & Bongers, 2011). These studies demonstrate greater endpoint variability (i.e., ORT variability) when reaching with tools. Parallel increases in UCM variability led to similar endpoint stability across changes in rod length, indicating that joint angle covariation tends to stabilize the end-effector position independent of changes to arm geometry. One limitation of these studies is that they focused on seated reaching, meaning that there are no postural requirements. Part of the attraction of the UCM analysis is that it can identify multiple task-relevant variables that may be differentially stabilized throughout performance (Scholz & Schoner, 1999).

Tools introduce a disturbance to the geometry and dynamics of the arm, which has the potential to affect postural stability and manual control. It is unclear how multi-joint coordination facilitates postural stability and suprapostural performance during tool use. Therefore, the third aim of this dissertation is to determine how multi-segment coordination supports postural control and suprapostural task performance under normal and challenging postural conditions with and without tools. To achieve this goal, UCM analysis will be applied to sagittal plane joint angles to examine their influence on the center of mass and end-effector position during fitting.

Note: The CoM was selected the hypothesized postural control variable for the UCM analysis because 1) the CoM can be defined based on a geometric model of the kinematic chain whereas the CoP cannot and 2) the CoM movements have mechanical consequences for balance. As stated above, the CoP is a high-dimensional control variable used by the nervous to generate or limit movements of the CoM. As such, we assumed that the nervous system is concerned with controlling the CoM position, which is accomplished by modulating the CoP or, in this case, through covariation among multiple body segments.

H3.1: *End-effector stability will be lower during tool use.* The AP and vertical end-effector position will be stabilized while fitting. During tool use, both groups will exhibit significantly greater V_{UCM} despite increases in V_{ORT} , which would indicate the contributions of multiple body segments to end-point stability. Leading to similar end-point stability between groups. V_{UCM} and V_{ORT} will be elevated in the Reduced BoS group due to the increased postural-manual constraints.

H3.2: *Postural stability will be elevated during tool use.* The AP and vertical center of mass position will be stabilized while fitting. During tool use, both groups will exhibit significantly greater V_{UCM} and reductions in V_{ORT} . This would indicate the contribution of various body segments to postural stability while reducing postural variability to accommodate the manual constraints during tool use. V_{UCM} and V_{ORT} will be elevated in the Reduced BoS group due to the increased postural-manual constraints.

H 3.3. *Learning based changes during tool use will drive down both V_{UCM} and V_{ORT} but less so in the Reduced BoS group because of the support surface constraints.* Both groups are expected to exhibit reductions in V_{UCM} and V_{ORT} for the center of mass and end-effector positions throughout tool use. This expectation is based on findings that reductions in both variance components occurs during reaching to novel, velocity-dependent force fields (Yang, Scholz, & Latash, 2007). The reductions are expected to be larger in the normal base of support group because increases in total joint angular variance—specifically V_{UCM} —support postural stability while standing on a reduced base of support (Hsu et al., 2014) and manual task performance while standing (Hsu & Scholz, 2012).

1.7. Significance of the dissertation

Understanding how postural and manual components of behavior are integrated and adapted to accommodate tool use will provide several key contributions. First, it will provide a foundation for studying postural control in the context of tool use behaviors. From a tool-use perspective, there has been limited interest in studying postural control or postural-manual integration because tool use has been attributed to higher-order cognitive abilities (Johnson-Frey, 2003, 2004), neurophysiological structures (Iriki, Tanaka, & Iwamura, 1996; Maravita & Iriki, 2004), and the plasticity of neural representations of the body and external space (Cardinali, Brozzoli, et al., 2009; Farnè & Làdavas, 2000; Holmes, Calvert, & Spence, 2004). Studying how tools are integrated into whole-body, goal-directed actions is of both theoretical and practical value for researchers in motor behavior. Under most conditions, tool use relies on the ability to embed manual actions within whole-body postures and movements. Even though tool use relies on cognitive abilities and neurophysiological adaptations, perception-action problems related to control and coordination still need to be solved. From this perspective, not only does tool use serve an important inroad for studying action, but action is an equally important inroad for studying tool use (Bongers et al., 2003).

Second, tool use can be understood as a form of sensorimotor adaptation. Sensorimotor adaptation, which refers to the error-based modification of movements (Martin, Keating, Goodkin, Bastian, & Thach, 1996). Many of the experimental paradigms used to study sensorimotor learning and adaptation—such as force fields, prism, or visuomotor rotation—are limited in their applicability to daily life (Ingram & Wolpert, 2011). Tool use is a useful paradigm for studying sensorimotor adaptation because grasping and manipulating objects alters the limb geometry and dynamics (Bock, 1990; Lacquaniti et al., 1982). Maintaining task performance while manipulating tools may therefore rely on modifications to postural and manual behaviors.

Third, tool use paradigms can provide information that informs the design of prostheses. devices. Prosthetic devices are tools because they mediate between the body and environment. Despite significant technological advances, upper limb amputees rarely use their prostheses or only wear them during specific activities (Biddiss & Chau, 2007; J. Davidson, 2002). For some people, having no limb (or a partially intact limb) is preferable to using a prosthetic due to technological limitations (e.g., poor ergonomic design, short battery life, or excessive weight). In

rehabilitative settings, a long-term goal is to restore autonomy by focusing on functional integration—a person’s ability to use the prosthetic to carry out goal-directed actions, such as reaching, grasping, and manipulating objects (Horgan & MacLachlan, 2004). Recent research has shown that upper limb amputees exhibit perceptuomotor deficits related to their ability to reach to objects with their prosthetic arm (Gouzien et al., 2017). This occurs even though the intact and prosthetic arms are the same length. Movements made with prostheses are slower, less smooth, and show more asymmetric speed profiles (Bouwsema, van der Sluis, & Bongers, 2010). Reach and grasp components of the movement are also decoupled relative to able-bodied participants, possibly due to a lack of proprioception and mechanical properties of the devices (Bouwsema et al., 2010). Developing an understanding of how tools become integrated into whole-body, goal-directed actions may enhance prosthetic design, improve training paradigms, and provide alternative measures of functional integration.

CHAPTER 2 – LITERATURE REVIEW

2.1. Background

Humans frequently use tools to exploit or alter the environment. The regularity with which humans use, construct, and combine tools has provided significant evolutionary advantages (Shumaker, Walkup, & Beck, 2011). Tool use is defined as the intentional manipulation of external objects that augment perception-action capabilities to facilitate goal-directed actions (Reed, 1988; Smitsman, 1997). This definition emphasizes how tools supplement our behavioral repertoires, allowing us to overcome bodily limitations to produce effective action on or detect perceptual information in the environment (Baber, 2006; Gibson, 1979).

Tool use occurs in response to an inability, inefficiency, or heightened risk associated with solving action problems. Hand-held tools—eating utensils, writing instruments, and power tools—are among the most common objects encountered in daily life. Tools are initially experienced as awkward and unfamiliar, but with experience, become transparently integrated into our actions (Dreyfus, 1991; Heidegger, 1962; Merleau-Ponty, 1962). The development of skillful, coordinated tool use requires the ability to integrate external objects into bodily movements.

While there has been extensive focus on higher-order cognition (Johnson-Frey, 2003, 2004), sociocultural factors (Nagell, Olguin, & Tomasello, 1993; Vygotsky, 1978), neurophysiological structures (Iriki et al., 1996; Maravita & Iriki, 2004), and the plasticity of neural representations of the body and external space (Cardinali, Brozzoli, et al., 2009; Cardinali, Frassinetti, et al., 2009; Farnè & Làdavas, 2000; Holmes et al., 2004), the motor adaptations underlying human tool use are understudied.

Part of this discrepancy stems from theoretical assumptions derived from the computer metaphor of the brain and information-processing approaches (Cisek, 1999; Searle, 1990), which treat perception, cognition, and action as discrete, serial units of behavior. Perception and action are considered the inputs and outputs while cognition represents the intermediate processes involved in decision-making and planning. Action is viewed as mere execution - an uninteresting consequence of intelligent, centralized processes.

Traditional task analyses decompose complex behaviors into component acts, each of which is thought to entail decision making on the part of some cognitive process because even simple actions, especially those involving hands, consist of innumerable details, and therefore require a marked level of intelligence (Rosenbaum, 2017). These approaches emphasize means-end reasoning (i.e., how the tool user conceives of the problem and possible solutions) and mechanical reasoning (i.e., knowledge of the effects of actions on objects and the interactions between objects) more than how interactions with tools create new opportunities for perception, action, and cognition (Lockman, 2000; Smitsman & Bongers, 2003).

Developmental research on tool use is representative of this asymmetrical interest. Until recently, studies of tool-use in early infancy have primarily focused on tool selection and how improvements in decision making processes contribute to increases in the frequency and complexity of infant tool use (Piaget, 1952). The guiding assumption that tool use emerges once the requisite cognitive capacities have developed has created a focus on tool selection (Bates, Carlsonluden, & Bretherton, 1980; Rat-Fischer, O'Regan, & Fagard, 2012) or grasp configuration (Conolly & Dalglish, 1989; McCarty, Clifton, & Collard, 2001; Rosenbaum, Chapman, Weigelt, Weiss, & van der Wel, 2012) at the expense of studying actual tool use (Lockman, 2000).

Even in the adult literature, substantial emphasis is placed on the neural structures or processes that are thought to facilitate body-tool assimilation, such as bimodal neurons (Maravita & Iriki, 2004) or the plasticity of representations of the body or external space (Cardinali, Brozzoli, et al., 2009). Moreover, when movement is considered, manual control has been the primary interest (Cardinali, Frassinetti, et al., 2009; Heuer & Sülzenbrück, 2009), while little consideration has been given to postural control (Bongers et al., 2004; Bongers et al., 2003) or the interactions among multiple body segments (Valk et al., 2016; van der Steen & Bongers, 2011).

Tool use is a whole-body activity that requires the coordination of multiple bodily degrees of freedom. The ability to adapt the coordination of postural and suprapostural (focal) aspects of behavior is necessary for the development of skillful tool-use. This position does not deny the role of cognition in more complex forms of tool use; nor does it suggest that neurophysiological differences between humans and other species do not influence tool-use abilities. Rather, it emphasizes that the basic ingredients for tool use are non-cognitive and preadapted through basic

perception-action routines, the exploration and discovery of behavioral solutions, and physical engagement with tools (Lockman, 2000)—all of which rely on the ability to control posture with respect to environmental surfaces and objects (Smitsman & Bongers, 2003).

This dissertation broadly addresses the question, how are postural control, postural-manual coupling, and multi-segment coordination adapted to accommodate tool use actions? To begin, I provide background on postural control and the integration of postural and suprapostural behaviors. Next, I provide overview of multi-segment coordination and its role in postural maintenance and suprapostural performance with specific focus on the uncontrolled manifold (UCM) framework. Subsequently, I highlight the current state of literature on manual adaptations to tool use followed by a review of the research on postural adaptations to tool use, which tends to focus on foot placement and body configuration more than postural stability, postural-manual coupling, or multi-segment coordination.

2.2. Postural control

Postural control, defined here as the ability to control and orient the body to itself or environmental surfaces and objects to facilitate perception and action cycles, is crucial for achieving behavioral goals (Riccio, 1993; Riccio & Stoffregen, 1988; Stoffregen & Riccio, 1988). This section outlines an ecological approach to posture control, which has been applied to a wide range of goal-directed actions.

2.2.1. The conditions for maintaining standing balance

Humans consistently adopt bipedal stance to achieve behavioral goals (e.g., walking, communication, reaching, manipulation, etc.). Bipedal stance is inherently unstable due the small base of support, high center of mass (CoM), and numerous linkages of the lower and upper body, as well as the presence of constant (e.g., gravity) and variable (e.g., a dog pulling on a leash) external forces. There are two necessary conditions to maintain upright balance: 1) prevent the vertical collapse of the body and 2) maintain the projection of the extrapolated CoM—the vertical projection of the CoM plus its velocity multiplied by $\sqrt{h_{CoM}/g}$, where h_{CoM} is the distance of the CoM to the ankle joint and g is acceleration due to gravity—within the base of support (Hof, Gazendam, & Sinke, 2005). The former is accomplished by maintaining a

sufficient support moment in the lower limb joints (Winter, 1980), while the latter is achieved via a combination of passive mechanical properties (e.g., viscoelastic properties of the muscle-tendon complex) and active neuromuscular control (Horak, 2006).

2.2.2. Models of standing posture

Mathematical models of human posture—for example, the single degree of freedom inverted pendulum model (Winter, Patla, Prince, Ishac, & Gielo-Periczak, 1998)—have provided important insights in to the regulation of standing balance. The underlying assumption of these models is that the CoM position is regulated. Control of the CoM is achieved by shifting the CoP—the point location of the ground reaction forces applied under the feet. The difference between the CoP and CoM is proportional the horizontal acceleration of the CoM. Standing balance is maintained by limiting CoM excursions about the upright position, while other orientations are maintained by counteracting the destabilizing moment due to gravity.

Relatively simple models that incorporate only passive mechanical forces accurately describe quiet standing (Gage, Winter, Frank, & Adkin, 2004; Winter, Patla, Ishac, & Gage, 2003; Winter et al., 1998; Winter, Patla, Rietdyk, & Ishac, 2001)—although there is debate about whether the apparent joint stiffness is, by itself, sufficient to maintain balance (Morasso & Schieppati, 1999). More complex models that incorporate neuromuscular feedback control (Peterka, 2002) have provided insights into sensory re-weighting (Assländer & Peterka, 2014, 2016; Carver, Kiemel, & Jeka, 2006) and mechanisms of instability in neurological populations (Chagdes, Huber, et al., 2016; Chagdes, Rietdyk, et al., 2016).

2.2.3. An ecological approach to postural control

Traditionally, research on postural control has largely been concerned with the mechanisms that stabilize upright posture (see Nashner and Mccollum (1985) or Massion (1992) for a review). Quiet stance—where people stand upright with arms by their side and look straight ahead (Lee & Lishman, 1975) or stand as still as possible (Andersen & Dyre, 1989)—has been the default paradigm. From this perspective, the assumed goal of postural control is to minimize movements of the CoM and there has been little consideration for perception-action goals other than standing upright (Nashner & Mccollum, 1985; Schöner, 1991; Winter et al., 1998). Postural

variability is normally equated with postural stability, where more variability is indicative of less stable balance. This implies that postural control represents a perception-action cycle that operates without reference to other behaviors besides maintaining a desired body configuration (Riley, Mitra, Stoffregen, & Turvey, 1997).

The ecological approach to postural control focuses on how the interaction between the actor and environment imposes constraints on opportunities for perception and action (Ricchio, 1993; Ricchio & Stoffregen, 1988; Stoffregen & Ricchio, 1988). From this perspective standing is analyzed as a means to an end because it presents opportunities for engaging in other behaviors. There are different ways to stand—both in terms of body configuration and postural dynamics—and these differences can serve as means to different ends (Bardy, Marin, Stoffregen, & Bootsma, 1999; Bernstein, 1967; Reed, 1988; Ricchio & Stoffregen, 1988). Static and dynamic properties of the actor, environment, and task constitute a set of constraints that place limitations on the potential postural strategies and patterns of sway that lead to the achievement of behavioral goals (Horak, 2006).

2.2.4. (Re)Defining posture

Postural control refers the ability to control and orient the body to itself or environmental surfaces and objects (Ricchio & Stoffregen, 1988; Stoffregen & Ricchio, 1988). Posture has traditionally been defined as a specific body configuration with respect to a reference frame, usually aligned with gravity (Latash & Zatsiorsky, 2015). But there is always some degree of postural variability. Reed (1982) defined postures as persistences in actor-environment relations, which involve the whole body or certain body parts. This definition implies that postural control consists of more than just maintaining a stationary position and configuration; there can be dynamic postures where the body configuration changes over time but specific topological relations with the environment are retained.

2.2.5. Postural control for suprapostural tasks

Standing upright is useful to the extent that is stable enough to engage in other behaviors (Bernstein, 1967; Ricchio, 1993). Coordination between standing balance and other behaviors becomes important when extraneous postural sway could interfere with task performance, such

as precise manual actions (Haddad et al., 2010) or visual fixation (Stoffregen, Smart, Bardy, & Pagulayan, 1999). In this respect, postural stability refers to the ability to suppress variability that would compromise either standing balance or other perception-action goals despite internal and external disturbances (Ricchio & Stoffregen, 1988), rather than a lack of movement.

When standing is the only goal, task success is normally measured by spatial measures of postural sway: Less sway indicates “good” postural control and more sway indicates “poor” postural control. However, the only measure of performance is whether the person fell or not. So, any amount of postural sway that does not lead to loss of balance should be considered successful. This does not imply that populations that exhibit pathological increases in postural sway are equally susceptible to loss of balance as healthy adults. Rather, it highlights the point that what constitutes “good” versus “bad” postural control depends on the task definition (Haddad et al., 2013).

Successful postural control should be defined with respect to the achievement of suprapostural goals in addition to maintaining balance (Ricchio & Stoffregen, 1988; Riley et al., 1999; Stoffregen et al., 1999). Suprapostural tasks are superordinate to the control of posture and are defined and evaluated in different terms (i.e., they are not quantified by the amount of postural sway). Minimizing postural sway may facilitate some behavioral goals, but not all possible goals. The ability to adaptively modulate standing posture with respect to the demands of concurrent behavioral goals, rather than indiscriminately reduce body movement, is a better indication of “good” postural control (Haddad et al., 2013).

Many studies have examined the role of suprapostural task constraints on postural control. For example, when looking at objects located at different distances, postural sway is modulated based on the precision demands of visual fixation (Stoffregen et al., 2000; Stoffregen et al., 1999), visual search (Prado, Stoffregen, & Duarte, 2007; Stoffregen et al., 2000), and visual tracking (Deprá et al., 2019; Stoffregen, Bardy, Bonnet, & Pagulayan, 2006). For example, decreases in postural stability during unipedal, but not bipedal, stance is associated with improved visual tracking performance, indicating that the ability to reduce postural stability is necessary to accommodate different visual task constraints (Deprá et al., 2019).

The precision demands of manual tasks also influence how postural sway is regulated. Tasks requiring greater precision are characterized by decreased postural variability, which is interpreted as evidence that postural variability is being regulated in a manner that facilitates the

completion of suprapostural tasks (Balasubramaniam et al., 2000; Haddad et al., 2010; Riley et al., 1999). These findings collectively suggest that the degree of postural variability is sensitive to the stability requirements of the suprapostural task, indicating that differences in postural sway are functionally related to task constraints.

2.2.6. Boundary-relevant postural dynamics

Variability in postural sway is often interpreted as extraneous fluctuations due to physiological noise or the inability to maintain a desired configuration. There are primarily two conditions for maintain standing balance: (1) prevent vertical collapse of the lower limbs and trunk and (2) maintain the extrapolated CoM remain within the base of support. If these two conditions are satisfied, then innumerable body configurations or postural sway dynamics can be adopted. What is crucial is that an actor is sensitive to the relationship between the movements of the CoM and stability boundaries.

Stability boundaries can be measured geometrically and functionally (Slobounov, Moss, Slobounova, & Newell, 1998). Geometric boundaries are estimated using the area contained within the spatial boundaries of the feet and mark the absolute limits of standing posture. Functional boundaries represent a reduced area within the geometric base of support that is defined based on sustained maximal leans in different directions. The functional base of support corresponds to the limit of static postural stability. Once the extrapolated CoM has passed outside the functional base of support upright stance cannot be stabilized without taking a step to re-establish a new base of support (Hasson, Van Emmerik, & Caldwell, 2008) or grasping for external support (Bateni, Zecevic, McIlroy, & Maki, 2004). Maintaining standing balance therefore consists of maintaining a spatiotemporal margin of safety between the CoM and the base of support.

The functional boundaries change if standing is not the only goal (Haddad et al., 2013). A different, more restricted, functional boundary will be defined based on the constraints placed on standing posture. For example, when performing a precision manual task while standing, people normally reduce their postural sway to reduce the influence of extraneous body movements on suprapostural task performance (Balasubramaniam et al., 2000; Haddad et al., 2010; Riley et al., 1999). However, postural variability is not completely attenuated, just decreased enough to meet concurrent task demands.

Postural control is commonly assessed using spatiotemporal measures of the CoP trajectory with the assumption that less postural variability corresponds to greater postural stability (Newell, van Emmerik, Lee, & Sprague, 1993). However, boundary-independent measures do not account for the rate and direction of postural sway with respect to stability boundaries, which are important for organizing postural responses, such as initiating a step following a perturbation (Hasson et al., 2008). Additionally, postural variability is thought to aid in the detection of task-specific stability boundaries that distinguish behavioral strategies for maintaining standing balance (Riccio, 1993; van Emmerik & van Wegen, 2002). Furthermore, the extent to which postural variability represents a threat to balance depends on how close the CoM is to the base of support.

Boundary-relevant measures have emerged as complementary method for examining postural stability (Haddad, Gagnon, Hasson, Van Emmerik, & Hamill, 2006; Hof et al., 2005; Slobounov, Slobounova, & Newell, 1997). Postural time-to-boundary measures a temporal margin that represents how long it would take the CoP or CoM to reach the base of support based on its instantaneous position, velocity, and acceleration (Haddad, van Emmerik, et al., 2006). Postural TtB has been shown to be sensitive to changes in postural control associated with motor development (Haddad et al., 2008), skeletal disorders (Gruber et al., 2011), aging (Slobounov et al., 1998; van Wegen, van Emmerik, & Riccio, 2002), neuromuscular dysfunction (Van Emmerik, Remelius, Johnson, Chung, & Kent-Braun, 2010), brain injury (Slobounov, Cao, Sebastianelli, Slobounov, & Newell, 2008), and variations in task constraints (Balasubramaniam et al., 2000; Riley et al., 1999).

2.2.7. Performatory and exploratory postural variability

Postural variability may not immediately serve the goals of maintaining standing or suprapostural behaviors. Stimulation provided by postural variability may supply information about the interaction between the actor and environment (Riccio, 1993; van Emmerik & van Wegen, 2002). This information allows the actor to adopt task-specific strategies for maintaining balance. This implies that standing posture is a behavior that is achieved based on obtained, rather than imposed, stimulation (Gibson, 1966). Postural variability may therefore be viewed as essential for adaptive control.

Postural stability not only entails maintaining balance but provides a platform for perception (Gibson, 1966, 1979). Postural variability can therefore be categorized as either performatory or exploratory. Performatory actions are directed towards the needs or goals of the actor (e.g., maintaining balance, reaching, etc.). Exploratory actions, on the other hand, serve to uncover information relevant for guiding action. Balasubramaniam et al. (2000) found that postural variability was reduced in the direction that would most influence task performance during a precision manual task requiring participants to maintain a laser pointer on a distant target. Interestingly, postural variability increased in the orthogonal direction, which had little influence on task performance, relative to quiet standing, which is consistent with the interpretation that postural variability provides a continuous source of information about actor-environment relations (Ricchio, 1993). More recently, Carpenter, Murnaghan, and Inglis (2010) showed that CoP variability does not decrease even if the body is fully immobilized. Nearly all participants demonstrated increased CoP activity when the CoM was stabilized which is not predicted by any model of standing posture. This indicates that despite the lack of need to stabilize posture, the neuromuscular system may be generating exploratory postural activity.

How can exploratory actions be undertaken without interfering with performatory actions? Ricchio (1993) postulated that exploratory behavior can be undertaken if the timescales of exploration are shorter than performatory dynamics. When people stand intermittent ballistic impulses are used to regulate movement of the CoM (Loram, Maganaris, & Lakie, 2005), indicative of a “drift-and-act” scheme of control (Milton, 2013). Exploratory information may therefore be generated between intermittent corrective impulses when posture drifts. Loram, Gollee, Lakie, and Gawthrop (2011) offer four important advantages that intermittent control offers over continuous control—all of which emphasize information-generation. First, intermittent control provides short windows where motor noise is not introduced into the system, which allows external disturbances to be identified with greater certainty. Second, intermittent control avoids the conundrum of distinguishing the source(s) of variability in behavior because only external disturbances are present in between corrective actions. This increases the observability of the system (Ricchio, 1993) and simplifies the process of determining whether further intervention is necessary. Third, less information regarding system dynamics can be observed from a closed loop system when there is low-frequency excitation. However, ballistic impulses can stimulate higher frequencies within the system and allow more information about its

behavior to be acquired. Fourth, intermittent control allows for periods of recovery between actions. Muscles, nerve fibers, and other neurophysiological mechanisms all exhibit refractoriness. Intermittent control provides windows for recovery. The advantages of intermittent control, which has only been recently examined in the context of standing posture, may prove crucial for understanding the exploratory, information-generating role of postural sway.

2.2.8. Summary

In summary, postural control promotes a variety of perception-action goals beyond standing upright. Successful postural control should therefore be defined with respect to the performance of suprapostural (focal) behaviors—in addition to maintaining balance—based on observations that the dynamics of postural sway are adaptively related to suprapostural task constraints. Postural stability should be measured using a combination of spatiotemporal and boundary-relevant measures to quantify the proximity to stability boundaries. Furthermore, consideration should be given to the role of postural variability in performatory and exploratory aspects of behavior.

2.3. Postural-manual integration

Postural and manual control are clearly important components of many actions. However, there is a tendency to focus on postural control and manual control separately. Traditionally, motor control processes have been divided into independent and opposing categories: postural control and goal-directed movement (Massion, 1992, 1994; Massion, Alexandrov, & Frolov, 2004). Postural control consists of mechanisms that stabilize the body configuration against internal and external disturbances; goal-directed control mechanisms serve to stabilize the movements of one or more body segments along a trajectory. This distinction has been propounded by findings that voluntary movements, such as raising an arm, are often immediately preceded by lower limb muscle activations that counteract potential disturbances to balance (e.g., Belenkiy, Gurfinkel, and Paltsev, 1967).

2.3.1. Trunk-arm coordination during seated reaching

When people perform seated reaching movements without or without trunk involvement, the end-point trajectory and final position remain unchanged. Ma and Feldman (1995) demonstrated that seated reaching movements to a target remained accurate when hand movements were coupled with in-phase (i.e., trunk and hand to target) or out-of-phase (i.e., trunk away from target, hand to target), leading them to suggest that trunk and arm movements are characterized by a compensatory synergy that acts to stabilize the end-point trajectory.

Seated reaches made in near space are consistently executed using a combination of shoulder flexion and elbow extension, while reaches in far space also include trunk rotation and scapular motion (Kaminski, Bock, & Gentile, 1995). Trunk rotation becomes integrated with movements at the shoulder and elbow joints, which are tightly linked during reaching (Soechting & Lacquaniti, 1981). Additionally, for distant targets, trunk rotation terminates progressively later than shoulder and elbow motion, indicating that the trunk is the primary contributor to the terminal stages of transport.

Although the trunk is normally thought to contribute to postural stability (Bouisset & Zattara, 1990; Massion, 1992), there is a strong preference for engaging axial body segments when reaching in far space despite the added energy costs and potential for inducing instability. Despite these risks, the neuromuscular system appears to readily recruit and exploit available degrees of freedom in a context-dependent manner. Moreover, posture and goal-directed movement are tightly integrated to simultaneously maintain stability while satisfying concurrent task demands (Riccio, 1993; Riccio & Stoffregen, 1988).

2.3.2. Upper and lower limb coordination while standing and reaching

Standing reaches involving both the lower and upper extremities are characterized by two distinct synergies: one contributing to postural maintenance and another moving the body towards the target (Kaminski, 2007; Kaminski & Simpkins, 2001). When reaching in near space movements of the arm occur relatively independently of the lower extremities. However, when reaching in far space lower extremities movements become coupled to arm movements and contribute to transporting the body towards the target. Regardless of reach distance, there is significant center of mass displacement towards the target, which is inconsistent with the idea

that postural control acts to minimize movements of the center of mass (Pozzo et al., 2002). The temporal coordination between the peak velocity of the hand and center of mass were conserved when reaching in microgravity despite noticeable increases in lower and upper limb joint angular variability . (Patron, Stapley, & Pozzo, 2005).

These findings indicate that there is no bright-line separating postural and goal-directed components of behavior. Moreover, the tendency to associate axial and lower body segments with postural stability and the upper limbs with goal-directed movement (Massion, 1992) fails to recognize that these designations are closely related to the task and environmental conditions. During upright standing, the joints of both the upper and lower body contribute to center of mass stabilization (Hsu et al., 2007), indicating that even postural maintenance devoid of goal-directed arm movements is a whole-body activity.

2.3.3. Postural-manual coupling

Although there is evidence to suggest that posture and goal-directed actions can be controlled relatively independently, there is a growing body of literature that demonstrates that postural and manual actions exhibit varying degrees of coordination depending on the task demands (Amado et al., 2016; Haddad et al., 2010; Huys et al., 2003). For example, postural and manual actions are tightly coordinated when the precision demands of the manual task are high (Balasubramaniam et al., 2000; Haddad et al., 2010; Riley et al., 1999). However, the coupling between postural and manual control can vary over time.

Studies examining juggling while standing have provided insights into the variable nature of the coupling between postural and manual actions during learning (Huys et al., 2003, 2004a, 2004b). Early in learning ball trajectories and postural sway were strongly coupled, likely due to mechanical reasons. Postural-manual coupling was found to decrease as learning progressed, which was thought to enhance the ability to attenuate extraneous postural fluctuations on juggling performance. Thus, the ability to flexibly alter the coupling between postural and manual actions appears to be crucial to the adaptive control of behavior.

Studies of stick balancing while standing indicate that improvements in performance are associated with intermittent changes in postural-manual coupling characterized by reduced coupling to mitigate the influence of postural fluctuations on manual performance while allowing

for rapid multi-joint postural corrections when the pole becomes unstable (Balasubramaniam, 2013; Cluff et al., 2011; Cluff et al., 2012).

Postural and task constraints can also influence the strength of the coupling. For example, when expert drummers perform a rhythmic manual task while standing the coupling between postural and manual behaviors decreases as postural (i.e., two-footed to one-footed stance) and manual (i.e., 1:1 to 2:3 rhythms) task difficulty increase (Amado et al., 2016). These findings suggest that expert performers systematically decouple postural and manual behaviors when there is a risk that postural fluctuations could interfere with manual task performance.

2.3.4. Timescales of learning in standing postural-manual tasks

There are a limited number of studies that have examined adaptations to postural-manual control over repeated performances of the same task (Cluff et al., 2011; Galgon et al., 2010; Huys et al., 2003). This is surprising because postural responses exhibit a delayed response to changes in environmental constraints, such as support surface extent (Horak & Nashner, 1986). One of the limitations of studies that examine postural responses to discrete or continuous support surface movements is that practice is limited, making it unclear how long it takes adults to converge on stable behavioral strategies. Another limitation is that the primary goal of these tasks is maintain balance. Because standing posture is normally adopted to complete other behavioral goals (Haddad et al., 2013; Riccio & Stoffregen, 1988; Stoffregen et al., 1999), previously observed postural adaptations may require differential modifications to simultaneously maintain balance and suprapostural task performance.

Galgon et al. (2010) examined changes to postural and manual control over three successive days (100 trials per day) as participants performed a serial reaching task while standing. The serial reaching task consisted of a 15-step sequence between three vertically aligned targets located away from the midline of the body with the goal of maintaining a 1 s movement duration between targets. Increases in postural stability facilitated improvements in reaching performance early in learning, while further increases to postural stability continued through late learning.

Multiple timescales of learning occur in the context of postural-manual tasks (Galgon et al., 2010; Huys et al., 2003), which is consistent with dynamical theories of learning and behavior change (Newell, Liu, & Mayer-Kress, 2001; Thelen & Smith, 1994). Postural

adaptations appear to occur at the same rate or more slowly than manual adaptations, possibly to explore alternative postural solutions that facilitate manual task performance. Increasing the challenge to standing balance may delay postural or postural-manual adaptations, which could initially interfere with or, in the limiting case, interrupt task performance.

2.3.5. Summary

In summary, posture and goal-directed movement are coordinated to maintain postural stability and suprapostural performance (Ricchio, 1993; Ricchio & Stoffregen, 1988). First, degrees of freedom are recruited and exploited in a task-dependent manner, allow lower limb and axial segments to actively contribute to goal-directed movements while ensuring postural stability. Second, postural-manual coupling varies with practice and postural-manual task constraints. Weaker postural-manual coupling is associated with better performance in expert performers, possibly to decrease the risk of postural interference with manual task performance. Third, postural adaptations support improvements manual performance, especially early in learning, providing support for the presence of multiple timescales of learning in postural-manual tasks.

2.4. Multi-segment coordination: The UCM Framework

Bernstein (1967) was one of the first to consider the vast number of independent neuromuscular components, or degrees of freedom, and the problem this poses for the control of voluntary movement (cf. Greene, 1972). Not only are there potentially many variables to control, but the redundancy of the neuromuscular system—there are more degrees of freedom than constraints associated with common tasks at any level of analysis (e.g., motor units→muscle force, muscle forces→joint torque, joint rotations→end-effector position, etc.)—guarantees that no unique motor solution exists unless additional constraints are introduced.

Dynamical systems theory views coordinated movement as an emergent property of an animal-environment system subjected to constraints, not the product of prescriptions or instructions from a motor program (Turvey & Shaw, 1995). From this perspective, the neuromuscular system controls and coordinates the degrees of freedom by providing minimal oversight while allowing lower subsystems to fine tune behavioral outcomes rather than orchestrating the behavior of each degree of freedom separately or binding them into inflexible

collectives (Greene, 1972; Turvey, 1990; van Emmerik, Rosenstein, McDermott, & Hamill, 2004)

While the degrees of freedom problem is commonly treated as a challenge for the neuromuscular system to overcome, there have been recent proposals that the problem needs to be reformulated (Gelfand & Latash, 1998; Latash, 2000, 2012, 2018). This alternative view, dubbed the principle of motor abundance, emphasizes the opportunities that having more degrees of freedom than constraints provides when performing actions under different conditions. The nervous system flexibly combines and coordinates the degrees of freedom by imposing time-varying constraints that facilitate the emergence of families of solutions that satisfy the task demands without repeating exactly—this is what Bernstein (1967) called “repetition without repetition”.

From this perspective, the nervous system does not need to solve any problems, rather it must exploit the available degrees of freedom to identify solutions that hold relevant aspects of performance invariant. The extent to which bodily degrees of freedom are coordinated to maintain task-relevant performance variables has been studied using uncontrolled manifold (UCM) analysis (Scholz & Schoner, 1999). The UCM framework has been employed to study neuromuscular synergies that stabilize one or more task-relevant variables by examining covariation among body-level variables (e.g., finger forces, joint angles, etc.). Briefly, the UCM analysis is a hypothesis-driven framework that assesses whether covariation among body-level variables (e.g., joint angles) stabilizes task-level variables (e.g., endpoint position). Variability in the n -dimensional space of elemental variables over repeated performances of a task is projected into two orthogonal subspaces or manifolds: the UCM space and orthogonal (ORT) spaces. The UCM represents variations among elemental variables that do not change in the task-level variables, while variation in the ORT subspace leads to changes in the task-level variables. By comparing the relative amount of variance in the UCM and ORT spaces, a synergy index can be computed to determine whether a task-level variable is stabilized.

UCM analysis has been applied to many different tasks: pointing (Tseng et al., 2003), reach-to-grasp movements (Jacquier-Bret et al., 2009), pistol-shooting (Scholz, Schoner, Latash, 2000), sit-to-stand movements (Scholz & Schoner, 1999), and standing posture (Hsu et al., 2007). This work has recently been extended into the domain of tool use (Valk et al., 2016; van der Steen & Bongers, 2011). These studies demonstrate greater endpoint variability (i.e., ORT

variance) when reaching with tools. Parallel increases in UCM variability led to similar endpoint stability across changes in rod length, indicating that joint angle covariation tends to stabilize the end-effector position independent of changes to arm geometry. One limitation of these studies is that they focused on seated reaching, meaning that there are no postural requirements. Part of the attraction of the UCM analysis is that it can identify multiple task-relevant variables that may be differentially stabilized throughout performance (Scholz & Schoner, 1999).

Previous studies show that joints of the lower and upper body contribute to center of mass stabilization during standing (Hsu et al., 2007), indicating that even postural maintenance is a whole-body activity. When the postural constraints are increased by having people stand on a reduced base of support, increases in center of mass motion (i.e., ORT variability) are accompanied by concurrent increases in joint angle variability that leave the stability of the center of mass position unchanged (Hsu et al., 2014). Additionally, when people perform manual task while standing, increases in joint variance does not adversely affect center of mass motion position, indicating that the nervous system exploits motor redundancy to maintain multiple performance variables (Hsu & Scholz, 2012). These findings are commensurate with the idea that “practice and repetition of behavior leads not to stereotypy of movement, but to *movement variability* along with *functional invariance*” (Reed, 1989, p. 7).

Tools introduce a disturbance to the geometry and dynamics of the arm, which has the potential to affect postural stability and postural-manual coupling. To date, no studies have examined how multi-joint coordination facilitates postural stability and suprapostural performance during tool use.

2.5. Manual Adaptations to Tool Use

Tool use is an important area of research for psychology, neurophysiology, and motor behavior because it provides insights into the organization of perception, cognition, as well as motor learning and control (Biryukova & Bril, 2012; Bongers et al., 2003). Recent research has focused on the control and coordination of manual behaviors performed with and without tools to develop a better understanding of how tools are integrated into actions. Two approaches have been adopted: 1) comparing movements performed with and without tools or 2) examining changes to movements before and after extended tool use training.

2.5.1. Comparing manual actions with and without tools

Many tool use actions are completed using the distal end of the object, but other locations may be relevant depending on the design of the tool, the target object, or the intended action. Effectively controlling tools requires shifting point of control from the hand to the tool (Arbib, Bonaiuto, Jacobs, & Frey, 2009; Heuer & Sülzenbrück, 2009). Several studies have examined changes to the endpoint trajectory with and without tools, while other studies have investigated how patterns of intersegmental coordination support tool use actions.

2.5.1.1. Endpoint trajectories

When people interact with tools, changes to the morphology and functional capabilities of their limb are typically accompanied by a distal shift in the effective point of control from the hand to the tool (Arbib et al., 2009). Reach trajectories may not be unique to the hand but may be characteristic of the end-effector of the kinematic chain (Heuer & Sülzenbrück, 2009). For example, people reliably produced curved hand motion to preserve straight cursor motion when performing point-to-point movements (Flanagan & Rao, 1995; Wolpert, Ghahramani, & Jordan, 1995), indicating a preference for straight end-effector paths.

Studies examining the operation of sliding first-order levers have found that the straightness of the hand path is transferred to the tip of the lever (Hegele & Heuer, 2010; Heuer & Sülzenbrück, 2009; Sülzenbrück & Heuer, 2010, 2012). However, the speed profile of the reach is independent of the end-effector (Verwey & Heuer, 2007). The adoption of hand-like paths when controlling the lever requires exposure to the physical lever, not a virtual one represented by a cursor (Sülzenbrück & Heuer, 2010). Increasing the mechanical transparency by presenting the orientation of the lever arm leads to faster movements and straighter paths (Hegele & Heuer, 2010), as well as faster reaction times and online corrections to displaced targets (Baugh, Hoe, & Flanagan, 2012). These findings indicate that tool use actions are facilitated by direct visual and haptic experience of the tool. Moreover, characteristics of the hand path appear to be transferred to the tool tip, which the velocity profile remains unchanged.

The transfer of features of the endpoint trajectory from the hand to the tool is not required by the task demands (Sülzenbrück & Heuer, 2013). Similar movement times and accuracy could, in principle, be achieved using straight or curved paths. These adaptations may therefore

represent a preference of the neuromuscular system when reaching under different conditions. However, one important limitation of these studies is that straight reach paths are primarily confined to movements made in the horizontal plane.

Reaches in the horizontal plane exhibit straight line paths independent of reach direction (Morasso, 1981). However, reaches made in the sagittal plane (Atkeson & Hollerbach, 1985) or three-dimensions (Breteler, Meulenbroek, & Gielen, 1998) exhibit varying degrees of curvature. For example, reach paths become increasingly curved as speed increases when three-dimensional movements across the mid-sagittal plane are made from the lower to upper area of the reaching workspace (Breteler et al., 1998). The precision demands of the reach will also influence the curvature—greater precision demands are associated with straight reaches in external space, while lower precision demands are associated with straight reaches in joint space (Breteler et al., 1998). These results suggest a compromise between producing straight reaches in external space and straight reaches in joint space depending on the direction and accuracy demands of the movement (Cruse & Brüwer, 1987). Thus, the adoption of straight-line reach paths is not obligatory when reaching with a tool that extends arm length.

Reaching movements made with pointers that extend arm length are characterized by longer durations that increase proportionally with tool length (Baird et al., 2002; Valk et al., 2016). Reaching with longer tools produces higher peak velocities and longer deceleration times, as well as more curved reach trajectories (Valk et al., 2016). Greater endpoint variability is observed for longer rods (Valk et al., 2016), which may have deleterious effects on performance depending on the target size (Baird et al., 2002). These modifications are thought to result from changes to the inertial properties of the arm and the disproportionate influence of proximal joint rotations on the end-effector position, which reduces the controllability of the tool.

Two important factors that appear to modify reach trajectories with tools are reach distance and target size—which are the fundamental parameters determining speed-accuracy tradeoffs in movement (Fitts, 1954; Woodworth, 1899). Reaching over longer distances produces slower reaches, higher peak velocities, and more asymmetric velocity profiles—such as when reach distance is adjusted for tool length (Valk et al., 2016). However, when reach distance remains constant across performance with and without tools, slower reaches are accompanied by lower peak velocities and accelerations than free hand reaching (Cardinali, Frassinetti, et al., 2009; Cardinali et al., 2012). The target size determines the asymmetry of the velocity profile.

Reach trajectories for the same index of difficulty but different distances and target widths yield identical movement times but different tangential velocity profiles (MacKenzie, Marteniuk, Dugas, Liske, & Eickmeier, 1987). Specifically, the length of the deceleration phase is inversely proportional to the target width but relatively independent of the movement distance.

In summary, the kinematic details of reach trajectories prospectively vary based on neuromechanical, environmental, and task-related constraints (Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987). In the context of tool use actions, changes to reach trajectories are an expected consequence of the geometric and dynamic changes to the arm. Reaching with a tool that extend arm's length will require greater precision depending on the location and size of the target object because small variations in body configuration will have disproportionate impact on the end-effector position.

2.5.1.2. Endpoint stability

Hand-held tools functionally alter the body and the forces required to manipulate the limb, which may require changes to the coordination among the involved degrees of freedom. van der Steen and Bongers (2011) examined the coordination of the arm degrees of freedom using uncontrolled manifold (UCM) analysis during seated reaching movements with and without rods of different length to determine whether the tool tip is stabilized to the same degree as the hand. Variation in the joint angle profiles—elbow flexion-extension, wrist abduction-adduction, and finger flexion-extension—was observed when using the tools independent of length. These changes were argued to reflect changes in coordination because the same final postures could be achieved over different rod lengths. The stability of the tool tip trajectory was similar across tool lengths and did not differ from the fingertip during free hand reaching.

One limitation of the previous study is that the end-effector kinematics were not examined, making it difficult to determine how changes to the coordination of the arm degrees of freedom influence the movement trajectory. In a follow-up study, Valk, Mouton, and Bongers (2016) examined end-effector kinematics and joint angle covariation during reaching movements made with the same rods. Reaching with longer rods produced higher peak velocities and longer deceleration times, as well as more curved reach trajectories. Greater endpoint variability was documented for longer rods, which translates to greater ORT variability. However, concurrent increases in UCM variability led to no differences in the stability of the endpoint across changes

in rod length. This indicates that joint angle covariation tends to stabilize the end-effector position independent of changes to arm geometry.

In summary, these findings demonstrate that changes in tool length are accompanied by changes in the endpoint trajectory, which depend on the characteristics of the tool and nature of the task, but do not affect the neuromuscular system's ability to stabilize the endpoint. These findings have been interpreted as evidence that similar control strategies are employed when reaching with or without a tool.

2.5.2. Comparing manual actions before and after tool use

An alternative method for studying tool use adaptations is to examine movements performed without the tool before and after an extended bout of tool use. This paradigm is reminiscent of traditional sensorimotor adaptation paradigms (Krakauer, 2009; Krakauer & Mazzoni, 2011; Shadmehr et al., 2010), which have been applied to reaching (Shadmehr & Mussa-Ivaldi, 1994), walking (Morton & Bastian, 2006), standing (Horak & Diener, 1994), and eye movements (Wallman & Fuchs, 1998).

Cardinali, Frassinetti, et al. (2009) studied how free-hand reach-to-grasp movements were affected by an extended bout of tool use. During the pre- and post-tool use phases, participants reached for and grasped a blocked using their hands. During the tool use phase, participants performed the same reach-to-grasp actions using a tool that extended arm length by 40 cm. Participants had no prior experience with the tool and were not allowed practice. Twelve trials were performed during the pre- and post-tool use phases; four blocks of twelve trials were performed during the tool use phase. The latency and amplitude of the peak acceleration, velocity, and deceleration during the transport component of the reach were measured.

Comparisons of the pre- and post-tool use phases consisting of free hand reaching movements revealed longer latencies and lower peak amplitudes following tool use. These changes also generalized to pointing movements. The results were compatible with those observed after stratifying participants into groups with short (< 75 cm) and long (≥ 75 cm) arm lengths during the pre-tool use phase. Reach kinematics did not differ between the four tool use blocks, indicating a rapid adaptation to the tool. The differences between pre- and post-tool use could not be replicated in a follow-up experiment where participants performed the same tasks with a wrist-worn load.

These findings were attributed to changes to the Body Schema—the multisensory neural representation of the body dimensions and configuration (Holmes & Spence, 2004). This hypothesis received some support from a follow-up experiment where participants performed an implicit arm length estimation task following tool use. Following tool use, participants overestimated their arm length—measured from the elbow to the tip of the middle finger. The authors concluded that their results provide evidence that the Body Schema—specifically the represented arm length—was modified following tool use and produced the tool-use-dependent aftereffects (Cardinali, Frassinetti, et al., 2009).

To identify some of the principles guiding the ability to incorporate tools into body representations, Cardinali et al. (2016) examined whether changes to free hand reaching kinematics following tool use were depended on morpho-functional congruences between the tool and body. There is evidence suggesting representations of specific body parts are altered by tool use based on implicit hand- and arm-length estimation tasks (Miller, Longo, & Saygin, 2014). For example, tools that enlarge the hand (e.g., a baseball mitt) alter the hand, but not arm, representations, while tools that extend arm length (e.g., mechanical grabber) alter arm but not hand representations.

When aspects of the hand (i.e., finger length) are altered during a similar reach-to-grasp task, grasping parameters but not transport parameters changed following tool use. Maximum grip aperture decreased following tool use for both tools, which was interpreted as evidence for an increase in finger length representation based on previous results (Karak & Newport, 2010). These results support the idea that different aspects of the body representation are modified based on morpho-functional congruencies between the modified body part and tool.

In summary, reaches made with tools that extend arm length produce changes to subsequent free hand reaching and pointing movements (Cardinali, Frassinetti, et al., 2009). Tool-use-dependent reaching adaptations occur rapidly—requiring only a few trials, even when participants are not familiar with the tool—and do not emerge when participants are trained to reach with a wrist-worn load of similar weight (Cardinali, Frassinetti, et al., 2009; Lacquaniti et al., 1982). The nature of the tool-use actions, specifically, whether the tool causally interacts with a target object or surface, influences the strength of the aftereffects (Cardinali et al., 2012). Furthermore, the morpho-functional characteristics of the tool determine which component of the reaching movement is affected—a tool that increases arm length produces aftereffects restricted

to transport parameters, whereas a tool that modifies finger length only impacts prehensile parameters (Cardinali et al., 2016; Cardinali, Frassinetti, et al., 2009; Cardinali et al., 2012).

2.6. Postural Adaptations to Tool Use

Less attention has been given to postural adaptations that support tool use. Previous studies have primarily focused on how changes to the tool characteristics and task constraints influence the final standing position (i.e., distance from the feet to the object) and postural configuration (i.e., joint angles) when displacing an object (Bongers et al., 2004; Bongers et al., 2003). Stance location and postural configuration depend on the geometric and dynamic properties of the body + tool system (Bongers et al., 2003). For example, standing position increases for longer rods but when the mass of the rod increases standing position decreases and the arm is held closer to the body. By altering the accuracy demands of the task, it is possible to examine how the controllability of the tool—which depends on the geometric and dynamic properties of the rod—influences the stance location and postures adopted to satisfy the task requirements. When the accuracy constraints are high, closer standing positions are adopted for longer and lighter rods. Body posture is affected by rod length with less forward lean observed for longer rods, while the arm is held closer to the body for smaller target objects and heavier rods. These findings are consistent with the idea that body and arm postures are adapted to mitigate threats to balance and improve the controllability of the tool (Bongers et al., 2004).

While these studies have provided useful information about the sensitivity of posture to characteristics of the tool and task demands, there are several limitations. First, task performance was not measured, meaning that associations between postural control and manual performance cannot be established. Second, postural measures were limited to the static configuration of body segments prior to object manipulation. This leaves it unclear whether different postures were adopted to improve postural stability, support manual task performance, or both. For this reason, these studies cannot provide information about tool- and task-specific changes in postural control, postural-manual coupling, and multi-segment coordination.

2.7. Conclusion

Studies of motor control and learning strongly suggest that multiple dimensions of postural-manual control are adapted to simultaneously maintain postural stability and manual task performance. To date, studies of tool use have independently examined postural and manual control while overlooking the integration of postural-manual control.

CHAPTER 3 – METHODS

3.1. Participants

Forty healthy adults between the ages of 18 and 30 years were recruited from the Purdue University West Lafayette campus. Participants were free of neurophysiological impairments and orthopedic injuries affecting balance, prehension, vision, or tool use (see Appendix A for screening form). Participants were assigned one of two groups: Normal BoS or Reduced BoS. The Normal BoS group was collected first, followed by the Reduced BoS group. Demographic and anthropometric information for the two groups is found in Table 3.1.

Previous studies did not report means and standard errors (Cardinali, Frassinetti, et al., 2009). However, effect sizes—partial eta squared and Cohen’s d —were recovered from the reported F-values and statistical degrees of freedom. The estimated effect sizes are large— $\eta_p^2 \geq 0.13$ and $d \geq 0.8$ —suggesting that the recorded sample size should provide sufficient statistical power.

Table 3.1. Participant demographics and anthropometrics for the Normal and Reduced BoS groups. Means \pm standard deviations and statistical tests are presented where appropriate.

	Normal BoS	Reduced BoS	$t_{,975}(35)$	p
Age (yrs)	20.4 \pm 1.1	20.5 \pm 2.2	0.13	.89
Gender	15 F, 5 M	15 F, 5 M	N/A	N/A
Height (cm)	169.9 \pm 13.5	165.1 \pm 10.1	1.28	.21
Mass (kg)	69.2 \pm 16.7	66.9 \pm 12.6	0.50	.62
l_{arm} (cm) *	64.2 \pm 6.8	59.3 \pm 4.5	2.67	.01
l_{tool} (cm) *	32.2 \pm 3.4	29.9 \pm 2.3	2.53	.02
Handedness	18 R, 2 L	20 R, 0 L	N/A	N/A

* l_{arm} - arm length measured from the acromion process to the 3rd metacarpophalangeal joint.

* l_{tool} - $0.5 l_{arm}$ measured to the nearest cm.

3.2. Equipment

Participants stood on an adjustable support surface mounted on top of a force plate (AMTI OR6-7; Advanced Mechanical Technology, Inc., Watertown, MA, USA). Ground reaction forces and moments were collected at 1000 Hz and the width of support surface was

adjusted to foot length. Three-dimensional kinematics were collected at 200 Hz from ten Vicon Vero cameras (Vicon Motion Systems Ltd., Oxford, UK). Data from the force plate and motion capture system were synchronized and collected using The MotionMonitor (Innovative Sports Training, Inc., Chicago, IL, USA). A digital video camera (Sony HandyCam, HDR-CX05) was used for offline coding of task performance.

3.3. Instrumentation

Participants wore shorts or leggings, a tight-fitting t-shirt or tank top, and tennis shoes. Reflective material and logos were covered with tape prior to data collection. Participants were instrumented with retroreflective markers attached to rigid body clusters, each containing four markers (green circles, Figure 3.1). Each cluster had a unique marker configuration, allowing

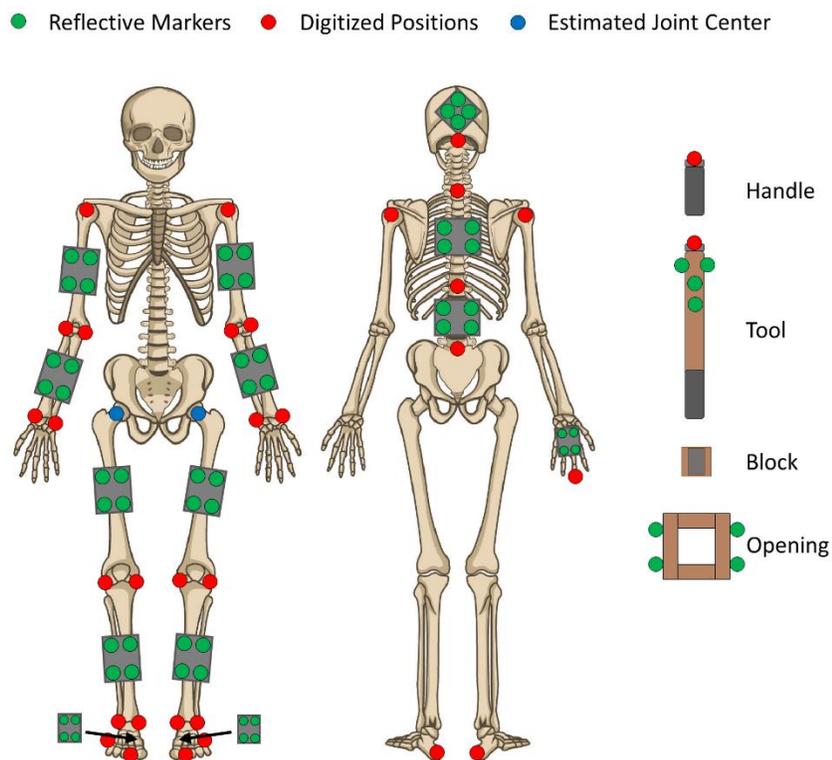


Figure 3.1. Depiction of the marker setup. Retroreflective markers and marker clusters were placed on various body segments and objects (green circles). A calibrated stylus was used to digitize relevant anatomical landmarks and locations on the objects (red circles). The only exceptions are the hip joint centers, which were estimated using external anatomical landmarks (blue circles).

them to be auto identified in real-time. No-slip bands were wrapped around each body segment and the clusters were secured using Velcro straps.

Joint centers and other anatomical landmarks were digitized using a calibrated stylus with a positional error less than 0.5 mm (red circles, Figure 3.1). Joint centers were estimated as the centroid of multiple measurements. For example, measurements taken from the medial and lateral epicondyles of the humerus were used to estimate the elbow joint center. The hip joints were estimated from external landmarks—the left and right anterior and posterior superior iliac spines (Davis III, Ounpuu, Tyburski, & Gage, 1991)—and were the only exception to this procedure (blue circles, Figure 3.1). The tools and opening were instrumented with retroreflective markers and the tip of the tools were digitized.

3.4. Experimental task

The experimental task was modeled after precision fitting tasks used in previous studies (Haddad et al., 2012; Liddy et al., 2019; Simon-Kuhn, Haddad, & Huber, 2019). The fitting task consists of acquiring and transporting a block to an opening using the dominant hand and holding the block in place for 5 s (Figure 3.2). This experimental paradigm was selected because it requires integrated postural and manual control. The task consists of two distinct behavioral subphases related to movement (i.e., transporting the block to the opening) and posture (i.e., holding the block in the open), allowing aspects of static and dynamic postural-manual control to be examined.

Two manual conditions were performed: No Tool and Tool (Figure 3.3, top left). During the No Tool condition, participants manipulated a 10 cm handle that did not extend arm length. During the Tool condition, participants manipulated a tool that extended arm length—the distance between the acromion and third metacarpophalangeal joint—by 50%. The handle length was also 10 cm, similar to the No Tool condition. The length of the tool body varied from 25-40 cm. This ensured that the tool body was within ± 0.5 cm of 50% of arm's length—see Appendix B for information related to tool design. Handles were wrapped in overgrip tape to make them easier to grasp.

Previous studies that have compared reach-to-grasp actions completed with the hand versus a mechanical grabber (e.g., Cardinali et al., 2009). The tools designed for this study were selected to control for potential differences that may arise due changes to the sensorimotor

consequences between conditions. Previous studies have found differences in movement characteristics based on both the morphofunctional congruence between the tool and limb/hand, as well as the sensorimotor constraints imposed by the tool (Cardinali et al., 2016). For example, differences between actions performed with and without a tool could arise because one task requires performing a precision grip with the hand to grasp the block while the other condition requires performing a power grip to grasp the tool, squeeze the trigger, and grasp the block with the mechanical fingers. The only difference between the No Tool and Tool conditions in this study is the changes to the arm geometry and dynamics, allowing the tool-specific rather than grasp-specific adaptations to be studied. Because the tools do not allow for grasping, the experimental analysis is limited to the transport and fitting components of the task, eliminating the prehensile component related to block acquisition.

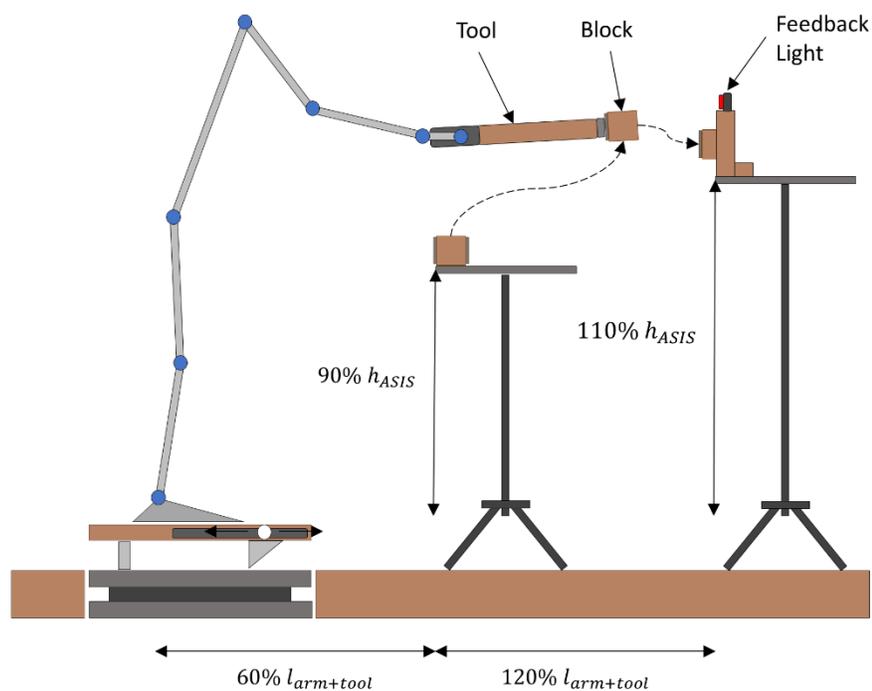


Figure 3.2. Depiction of the experimental setup. Participants stood on an adjustable support surface placed on top of a force plate while performing a precision fitting task. The fitting task consists of manipulating a hand-held object (No Tool: 0% arm extension; Tool: 50% arm extension) to acquire and transport a block to an opening and then hold it in place for 5s. See text for more details.

The objects used in the No Tool and Tool conditions were wooden dowels with a magnet attached to the tip. The block was a 3.8 cm³ piece of wood with a strip of magnetic tape attached to the front (Figure 3.3, top right). This allowed the block to be attach to the magnet without grasping. The block was positioned on a pedestal at height of 90% of anterior superior iliac spine and 60% of arm + tool length from the ankle joint in the AP direction. The block was fitted through a wood frame with a 5.5 cm² opening (Figure 3.3, top right). The interior of the opening was lined with conductive tape that was wired to a red LED positioned on top of the frame. A second wire ran from the red LED to the block, which had conductive tape on its exterior surfaces. This allowed the red LED to turn on when the block contacted any side of the opening, which provided feedback that an error had been committed.

Previous studies have either examined a single tool (Cardinali et al., 2016; Cardinali, Frassinetti, et al., 2009; Cardinali et al., 2012) or multiple tools with fixed lengths in absolute units (Valk et al., 2016; van der Steen & Bongers, 2011). This means that the relative tool length varied between 61% and 80% of arm length based on normative measures (Tilley, Dreyfuss, & Wilcox, 2001). Variation in relative tool length was avoided to derive a clearer picture of postural-manual adaptations when the tool properties are normalized to the user. Furthermore, because this study examined standing and reaching, the relative distance to the target was held constant across participants because people normally begin to engage their trunk at when reaching beyond 95% of arm's length (Mark et al., 1997). The postural requirements of reaching may therefore vary across participants when using a fixed tool length or absolute target distance. Reach distances and tool lengths were therefore scaled to body dimensions. The opening was positioned on a pedestal at height a 110% of anterior superior iliac spine and 120% of arm + tool length from the ankle joint in the AP direction. The block and opening were both aligned with the dominant shoulder in the ML direction. The purpose of placing the opening beyond arm's length was to increase the difficulty of the task and ensure the involvement of joints other than the arm (e.g., scapular protraction, trunk flexion, ankle dorsiflexion, etc.).

Participants stood on an adjustable support surface mounted on top of the force plate (Figure 3.3., bottom). The area of the support surface was the same as the force plate (50.8 cm × 46.4 cm). The support surface height was 8 cm. A rectangular steel block of the same width was fixed 20 cm from the back of the support surface. A triangular steel block of the same width was attached to two steel rods could be adjusted AP direction. Changing the distance between the

rectangular and triangular steel blocks allowed the base of support width in the AP direction to be manipulated. If the base of support width is as long, or longer than, the feet, then it will not tip forward under any circumstances. However, if the base of support width is shorter than the feet, then displacing the center of mass beyond the anterior boundary—defined by the edge of the triangular steel block—would cause the support surface to tip forward.

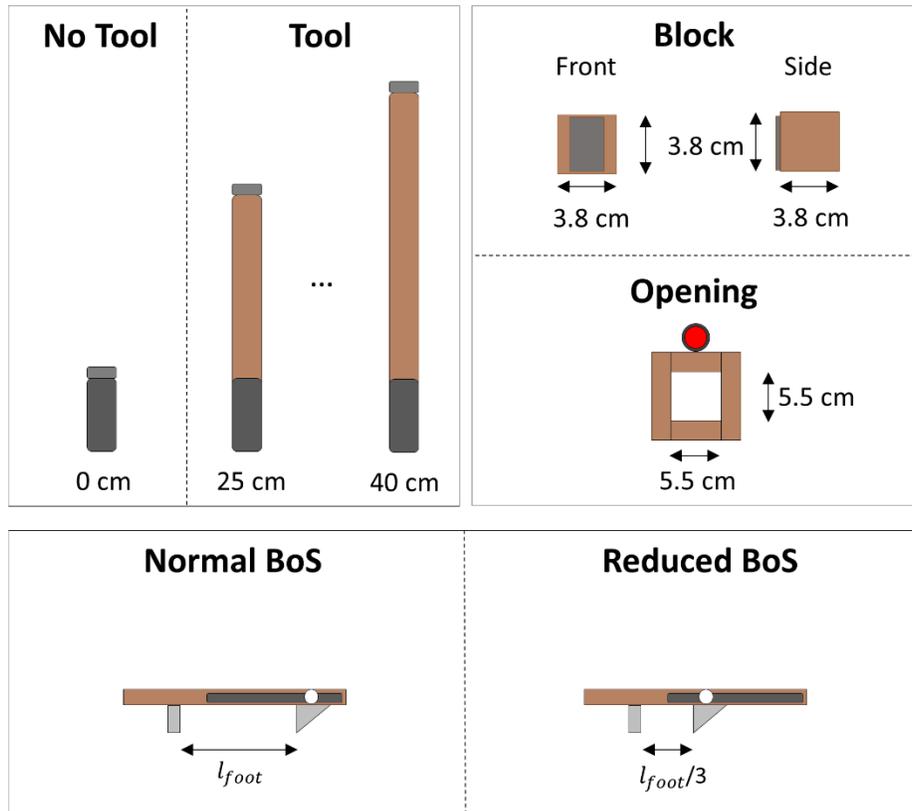


Figure 3.3. Depiction of the experimental conditions and task details. Participants performed the fitting task with the short handle that does not extend arm length (No Tool condition) or a longer tool that extended arm length by 50% (Tool condition). The goal of the task was to acquire, transport, and fit the block through the opening and hold it in place for 5 s without contacting the sides. There were two experimental groups: Normal and Reduced BoS. The Normal BoS group performed the experimental tasks while standing on a support surface the same length as their feet, while the Reduced BoS group performed the same tasks while standing on a support surface that was 33% of foot length.

Two postural conditions were performed: Normal and Reduced BoS. The Normal BoS condition required participants to stand on the support surface with the width adjusted to foot length. The Reduced BoS condition required participants to stand on the support surface with the width adjusted to 33% of foot length and centered at the ankle joint. Participants were randomly

assigned to either the Normal or Reduced BoS group. A between-participants design was selected to avoid burdening participants with performing twice as many trials, needing to return for a second session, or contaminating the results with carryover effects. Reducing the base of support is a reliable method for increasing the difficulty of maintaining standing balance because the projection of the center of mass must be confined to a smaller region to prevent the platform from tipping. This manipulation is expected provide information about how postural constraints influence tool use adaptations.

3.5. Experimental procedure

Upon arrival, participants provided written informed consent to procedures approved by the Purdue University Institutional Review Board (Appendix C). If needed, the participant was provided time to change clothing in locker rooms adjacent to the laboratory. The experimenter then provided an overview of the research goals, experimental setup, instrumentation practices, and study procedures. The experimenter subsequently administered the screening form, assessed handedness with a modified Edinburgh Handedness Inventory (see Appendix D), and recorded anthropometric information to prepare the experimental setup (Table 2.2).

Table 3.2. Anthropometric measurements. These measurements were used to adjust the experimental setup to participants' body dimensions. The height of the anterior superior iliac spine, arm length, and foot length were recorded on the same side of the body as the dominant hand.

Abbreviation	Units	Description
h_{body}	m	Height of the body measured from the floor to the crown of the head
m_{body}	kg	Mass of the body
h_{ASIS}	cm	Height of the anterior superior iliac crest measured from the floor
l_{arm}	cm	Length of the arm measured from the acromion process to the third metacarpophalangeal joint
l_{foot}	cm	Length of foot measured from the posterior aspect of the calcaneus to the tip of the second distal phalanx

Afterwards, participants were instrumented according to the procedures outlined above. Once instrumentation was complete, the digitization procedure was conducted to build a biomechanical model of the participant (Figure 2.4). This procedure uses rigid body clusters and

a calibrated stylus (RMS error < 2 mm) to identify joint centers and other relevant anatomical landmarks (see section 3.3 for details).

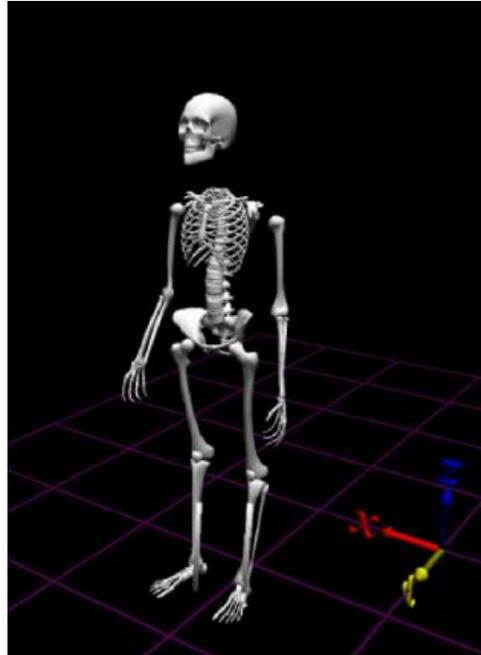


Figure 3.4. Biomechanical model. An example of the biomechanical model constructed using the The MotionMonitor digitization procedure.

Once the digitization procedure was complete, the experimental setup was adjusted and participants were provided instructions about the fitting task and support surface. These instructions did not differ between the Normal and Reduced BoS groups. For the fitting task, participants were instructed to use the handle or tool to acquire the block, transport it as quickly and accurately as possible to the opening, and hold it in place for five seconds. Participants were told to avoid making fitting errors—defined as any contact as the block was entering or being held in the opening—to the best of their ability. Participants were also informed that they would receive a \$.10 reward on trials when no fitting errors were committed. For the support surface, participants were instructed to avoid destabilizing or tipping the platform. If the platform did tip forward, participants were instructed to continue performing the fitting task, leaving the platform tipped forward. The platform was repositioned on the force plate when the trial was completed. The experimenter then demonstrated the task to the participant several times. Participants were

provided five trials of practice in the No Tool condition to ensure that they understood the task instructions.

The experimental procedure was the same for the Normal and Reduced BoS groups. First, participants performed 20 trials of the No Tool condition to establish a baseline. Next, participants performed an extended bout of tool use training consisting of 40 trials of the Tool condition. No practice was provided before the Tool condition and participants were not allowed to hold or manipulate the tool beforehand. Last, participants performed an additional 20 trials of the No Tool condition, which was intended to serve as a washout. A total of 80 trials was performed during the testing session. Thirty second rest breaks were enforced every 5 trials, allowing participants to stretch or adjust their stance. Three minutes of enforced seated rest was provided between conditions.

Blocks of five trials were performed in sequence to reduce the time needed for data collection and allow the experimenter to save the data. At the beginning of each block, the experimenter asked the participant if they were ready to proceed. After receiving confirmation, the experimenter provided a verbal “go” command to signal the participant to begin the task. The participant then acquired the block and transported it to the opening. Once the block crossed the threshold of the opening, the experimenter started a five second timer. After the five seconds had elapsed, the experimenter provided a verbal “return” command to signal the participant to remove the block and return it to the pedestal. The participant then removed the block from the handle or tool with their non-dominant hand and placed it back in the starting location. The participant then returned to a “ready” posture with their dominant arm relaxed by their side. The experimenter then continued to inform the participant when to “go” and “return” until five trials were completed. Meanwhile, a second experimenter was recording digital video for offline coding of fitting performance. Once experimental protocol was complete, the experimenter removed the reflective markers from the participant, counted the number of successful trials, and compensated the participant for their participation and performance.

3.6. Data analysis

Dependent variables related to each specific aim are described in the following sections. Preprocessing procedures are described within the section dedicated to each specific aim. All analyses were conducted during the transport and fitting stages of the task. The transport stage

represents the duration from when the block was acquired to when crossed the frontal plane of the opening. The initiation and termination of the transport stage were identified using position and velocity constraints. The positional constraint was related to the proximity of the end-effector to the AP position of the opening. The end-effector had to be within 3.8 cm of the opening, which corresponds to the width of the block. The velocity constraints were related to the tangential velocity of the end-effector exceeding and falling below 2.5% of maximum velocity for initiation and termination, respectively. The fitting stage represents the 5 s duration following the termination of the transport stage. The middle 3 s of the fitting stage were retained to remove any transient behaviors associated with entering the opening and preparing to remove the block.

3.6.1. Specific Aim 1: Characterize adaptations to postural control during tool use under different levels of postural constraint and how these adaptations support manual task performance.

Kinematic and kinetic data were preprocessed prior to conducting the analyses described below. The three-dimensional positions of the end-effector and support surface were filtered with a zero-lag, low-pass Butterworth filter at a cutoff frequency of 10 Hz. Forces and moments recorded from the force plate were also filtered with a zero-lag, low-pass Butterworth filter at a cutoff frequency of 10 Hz before computing the center of pressure (CoP).

3.6.1.1. Task performance

The goal of the fitting task to fit the block and hold in its position for five seconds while avoiding contact with edges of the opening. To measure task performance, the number of errors committed when fitting the block through the opening and holding it in place was recorded. Errors were identified from video recordings when the red LED was illuminated. Only contacts made when entering or holding the block in the opening were counted. The number of fitting errors identified in the first and last two blocks of each condition were recorded due to the relatively sparse error distribution.

3.6.1.2. Postural performance

The goal of standing on the support surface is to avoid tipping it during the fitting task. To measure postural performance, the maximum angular deviation of the support surface relative to the horizontal in the sagittal plane were measured. Maximum angular deviation represents a continuous measure of postural performance. Small deviations correspond to wobbling of the support surface and were not categorized as postural errors. This is consistent with the quantification of task performance described above where endpoint variability without contacting the sides of the opening does not constitute a fitting error. Large deviations correspond to substantial movements of the support surface and, in some cases, complete loss of balance. Maximum angular deviations greater than 1° were considered postural errors. Trials with postural errors were removed from subsequent analyses due to the corruption of the center of pressure measurements.

3.6.1.3. Manual control

During the transport stage, manual control will be quantified using normalized mean squared jerk. Jerk—the time-derivative of acceleration—is a common measure for quantifying reach smoothness, which has traditionally been regarded as a signature of skilled, coordinated movement (Hogan & Sternad, 2009). Measures of jerk are sensitive to movement duration and amplitude. Dimensionless jerk measures are preferable for quantifying changes in movement smoothness across participants and experimental conditions. Normalized mean squared jerk was computed for the three-dimensional endpoint path (Eq. 1), where r is the endpoint position, x is the ML coordinate, y is the AP coordinate, z is the vertical coordinate, t_1 and t_2 are the respective reach initiation and termination times, T is the reach duration, and A is the three-dimensional reach amplitude.

$$J(r) = \frac{T^6}{A^2} \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} [\ddot{r}_x(t)^2 + \ddot{r}_y(t)^2 + \ddot{r}_z(t)^2] dt \quad \text{Eq. (1)}$$

During the fitting stage, manual control will be quantified by measuring the sum of the endpoint variances in the mediolateral and vertical directions (Eq. 2), where $r_{x,z}$ represents the frontal plane endpoint position, x represents the mediolateral coordinate, z represents the vertical coordinate, and N represents the number of data points in the 3 s fitting interval. Failure to

constrain movement in either of these directions increases the likelihood of bringing the block into contact with the opening. Thus, measuring endpoint variability during the fitting stage provides information about the extent to which people mitigate the risk of committing fitting errors.

$$Var(r_{x,z}) = \sum_{i=1}^N (x_i - \bar{x})^2 + \sum_{j=1}^N (z_j - \bar{z})^2 \quad \text{Eq. (2)}$$

3.6.1.4. Postural control

Postural control will be measured using spatiotemporal and boundary-relevant measures during the transport and fitting stages of the task. During the transport stage, postural sway was quantified by the CoP excursion from reach initiation to termination. To account for transient behaviors at the beginning and end of the reach, the initial and terminal positions were determined by averaging across the first and last 25 ms (i.e., 5 data points at 200 Hz). CoP excursion was then measured as the distance between these positions. Additionally, the maximum CoP velocity was measured from reach initiation to termination. ML and AP CoP position time series were numerically differentiated using a three-point central difference method. Maximum CoP velocity was then measured as the maximum of the norm of the CoP velocity vector. Both measures take in account the ML and AP components of postural sway. Because the fitting task primarily consists of sagittal plane movements, these measures were nearly identical to the AP CoP excursion and velocity.

During the fitting stage, postural sway was quantified by fitting a 95% confidence ellipse to the ML and AP CoP path during the middle 3 s of fitting. This technique uses principle component analysis to fit an ellipse to the two-dimensional CoP path that encompasses 95% of the data points (Oliveira, Simpson, & Nadal, 1996). The area of the best-fit ellipse is then used to quantify the magnitude of postural sway. Additionally, the mean absolute CoP velocity was measured during the middle 3 s of fitting. ML and AP CoP position time series were numerically differentiated using a three-point central difference method. Mean CoP velocity was then measured as the mean of the norm of the CoP velocity vector. Again, these measures take in account the ML and AP components of postural sway. Both components were included because ML and AP sway are particularly relevant during the fitting stage because postural excursions in

either direction may induce end-effector movements bring the block into contact with the opening.

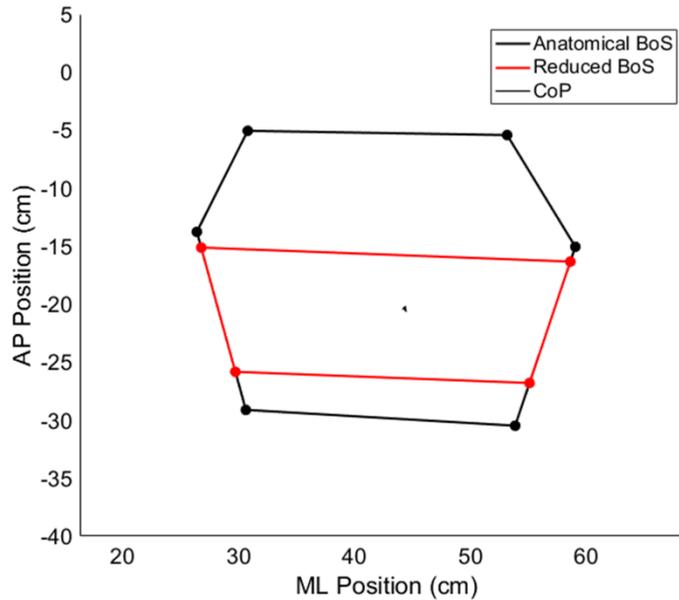


Figure 3.5. Example of the anatomical and reduced base of support. The anatomical base of support consists of the perimeter of the feet was used for the Normal BoS group (black lines). Because the Reduced BoS group was standing on a narrow support surface, the anatomical boundaries and ankle positions were used to redefine the base of support with an AP width of $1/3$ foot length while retaining the lateral boundaries (red lines).

Postural TtB was measured during the transport and fitting phases. Postural TtB is computed at each instant in time by creating an extrapolated trajectory based on the instantaneous position, velocity, and acceleration of the CoP and estimating the amount of time it would take to contact each boundary of the base of support. The base of support was defined by the 2nd metatarsal, 5th metatarsal, and calcaneus for the Normal BoS group, yielding a six-sided boundary. For the Reduced BoS group, the base of support was adjusted to account for the narrow support surface width, which was scaled to $1/3 l_{foot}$ and centered at the ankle joint. Points were projected a distance $1/6 l_{foot}$ forward and backward of the ankle position along the lines connecting the toe and heel for the left and right feet, yielding four new points located within the anatomical base of support. These points were shifted to the intersection of the lateral anatomical boundaries and the lines connecting the two front and back temporary positions,

yielding four points that determined the reduced base of support, which consisted of a four-sided boundary (Figure 3.5).

Shorter TtB indicates a closer spatiotemporal proximity to the limits of stability in the absence of any corrective response and therefore provides instantaneous information regarding the current postural state. TtB is a useful complementary measure of postural control for three reasons. First, because TtB is measured with respect to the base of support, it is a useful measure for assessing postural sway during dynamic tasks where the CoP is translated within the base of support, such as reaching. Second, because TtB is evaluated at each point in time, it is sensitive to instantaneous changes in the dynamics of postural sway. Third, quantifying the temporal proximity of the CoP to the base of support provides a useful measure of how liberally or conservatively postural sway is being modulated relative to the stability boundaries.

There are several approaches to quantifying TtB during a single trial. Some studies compute the mean (Slobounov et al., 1998) or mode (Liddy et al., 2019) of the TtB distribution over the entire trial duration. Others have opted to examine the average of the n lowest values or minima (van Wegen et al., 2002) or within different phases of a movement (Haddad et al., 2010). Here, the minimum 10 TtB values were averaged during the transport and fitting stages within each trial to quantify the spatiotemporal proximity of the CoP to the base of support.

3.6.2. Specific Aim 2: Examine postural-manual coupling under different levels of postural constraint during and following an extend bout of tool use.

3.6.2.1. Postural-manual coupling

Postural-manual coupling was assessed using average mutual information. Average mutual information quantifies linear and nonlinear correlations between two times series. Average mutual information indicates how much information (measured in bits) about one time series at time t can be learned from measurements of a second time series at time t . Average mutual information for two time series $x = x_1, x_2, \dots, x_m, \dots, x_M$ and $y = y_1, y_2, \dots, y_n, \dots, y_N$ is measured as:

$$I_{x,y} = \sum_{x_m, y_n} P_{x,y} \log_2 \left(\frac{P_{x,y}(x_m, y_n)}{P_x(x_m)P_y(y_n)} \right) \quad \text{Eq. (3)}$$

where I is the average mutual information between measurements of x and y , $P_{x,y}(x_m, y_n)$ is the joint probability density of x and y , and $P_x(x_m)$ and $P_y(y_n)$ are the marginal probability densities of x and y , respectively. This metric indicates how much information can be learned about x_m from the measurement of y_n . Average mutual information is a symmetric measure such that $I_{x,y} = I_{y,x}$. The advantage of average mutual information as a measure of coupling is that it is model-free, meaning that no assumptions need to be made regarding the nature of the correlations between the time series (e.g., linear, nonlinear, etc.).

Average mutual information can also be measured over different time lags, which indicates how much information can be learned about x_m from the measurement of $y_{n+\tau}$, where τ is the time lag. This method—referred to as time-lagged average mutual information—was not employed because it would require including an additional factor in the statistical analyses, which already contain factors related to group, experimental condition, and time.

Average mutual information was computed between the ML and AP components of the CoP and end-effector positions during the transport and fitting stages. Average mutual information varies between 0 and 1 bits, where 0 bits means the variables are independent and 1 bits means the two variables are perfectly coupled.

3.6.3. Specific Aim 3: Determine how multi-segment coordination supports postural control and suprapostural task performance under normal and challenging postural conditions with and without tools.

3.6.3.1. Segment lengths

The following sagittal plane segment lengths, l_i , were computed: (1) shank, (2) thigh, (3) pelvis, (4) trunk, (5) head, (6) sternoclavicular, (7) upper arm, (8) forearm, and (9) hand + tool. Segment lengths were computed as the Euclidean distance between adjacent joint centers. Segment lengths showed small variations due to frontal and transverse plane movements but remained nearly constant throughout each trial.

3.6.3.2. Joint angles

The following sagittal plane joint angles were computed: (1) ankle, (2) knee, (3) hip, (4) lumbosacral junction (LSJ), (5) cervical-thoracic junction (CTJ), (6) scapular, (7) shoulder, (8)

elbow, and (9) wrist (Figure 3.6). Joint angles were measured counterclockwise relative to the long axis of the preceding segment. For example, the wrist angle was computed as the counterclockwise angle of the hand + tool segment relative to the forearm. Joint angles were computed as follows:

$$\theta_i = \text{mod}(\tan^{-1} 2d \left(\frac{z_2 y_1 - y_2 z_1}{y_1 y_2 + z_1 z_2} \right) + 360, 360) \quad \text{Eq. (4)}$$

where y_i and z_i are components of the unit vectors $\bar{v}_1 = \begin{bmatrix} y_1 \\ z_1 \end{bmatrix}$ and $\bar{v}_2 = \begin{bmatrix} y_2 \\ z_2 \end{bmatrix}$ for the distal and proximal segments, respectively. The four-quadrant arc tangent function yields angles between $[-180^\circ, 180^\circ)$, which were corrected to $[0^\circ, 360^\circ)$ using the modulo operation with a dividend of $\theta_i + 360$ and a divisor of 360.

3.6.3.3. Center of mass

The location of the whole-body CoM was approximated using the sagittal plane joint angles, θ_i , segment lengths, l_i , the distances from distal end of the segment to its CoM, d_i , and segment masses, m_i , and total body mass, M (Eq. 5).

$$\bar{r}_{com} = \begin{bmatrix} r_y \\ r_z \end{bmatrix} = \begin{bmatrix} \left(\frac{m_1}{M}\right) d_{1,y} & \left(\frac{m_2}{M}\right) d_{2,y} & \dots & \left(\frac{m_n}{M}\right) d_{n,y} \\ \left(\frac{m_1}{M}\right) d_{1,z} & \left(\frac{m_2}{M}\right) d_{2,z} & \dots & \left(\frac{m_n}{M}\right) d_{n,z} \end{bmatrix} \quad \text{Eq. (5)}$$

3.6.3.5. Uncontrolled manifold analysis

UCM analysis was used to examine motor variability over repeated performances of the fitting task exhibited using a redundant set of inputs (θ_i) to quantify the stability of task relevant outputs (CoM and end-effector positions). The geometric model of standing and reaching is shown in Figure 3.8. The task relevant variables examined in this task were the AP and vertical positions of the CoM (Eq. 5) end-effector (Eq. 6).

$$\bar{r}_{end} = \begin{bmatrix} r_y \\ r_z \end{bmatrix} = \begin{bmatrix} l_1 \cos(\theta_1) + l_2 \cos(\theta_1 + \theta_2) + \dots + l_n \cos(\theta_1 + \dots + \theta_n) \\ l_1 \sin(\theta_1) + l_2 \sin(\theta_1 + \theta_2) + \dots + l_n \sin(\theta_1 + \dots + \theta_n) \end{bmatrix} \quad \text{Eq. (5)}$$

Multiple body segments including the shank, thigh, pelvis, trunk, scapula, upper arm, forearm, and hand + tool contribute to changes in the end-effector position. These segments also contribute to changes in whole-body CoM, which also included the head. There are eight joint angles for the end-effector position and nine segments for the CoM position so the task is redundant because there are more inputs (n) than outputs (m). Joint angles and segment CoMs

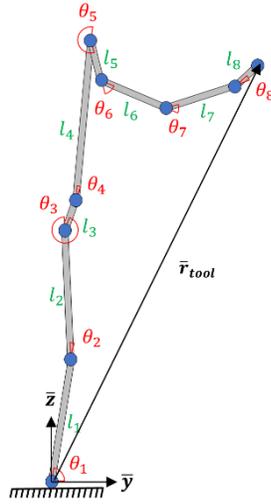


Figure 3.6. Geometric model of standing and reaching. Sagittal plane joint angles and segment lengths were determined as shown.

across 20 repetitions were examined. This corresponds to pre-tool-use, early tool use, late tool use, and post-tool use. Deviations from the mean joint angle configuration or segment CoM position were computed and projected onto two orthogonal manifolds. The first manifold—the uncontrolled manifold (UCM)—is the null space of the Jacobian relating small changes in the inputs to small changes in the outputs (Eq. 7).

$$\mathbf{J} = \frac{d\bar{\mathbf{r}}}{dt} = \begin{bmatrix} \frac{\partial \bar{\mathbf{r}}}{\partial \theta_1} & \dots & \frac{\partial \bar{\mathbf{r}}}{\partial \theta_n} \end{bmatrix} \quad \text{Eq. (7)}$$

Variance within the UCM has no influence on the outputs. The dimension of UCM is $n-m$. Variation within the manifold orthogonal to the UCM (ORT) leads to changes in the outputs. The dimension of ORT is the number of constraints m . The variances of the projected inputs within the UCM and ORT subspaces, V_{UCM} and V_{ORT} , was quantified. This allowed the synergy index ΔV to be computed (Eq. 8).

$$\Delta V = \frac{(V_{\text{TOT}}/n-m)-(V_{\text{ORT}}/m)}{V_{\text{TOT}}/n} \quad \text{Eq. (8)}$$

where $V_{\text{TOT}} = V_{\text{UCM}} + V_{\text{ORT}}$. A positive ΔV indicates covariation among the input variables that stabilizes the task-level output variable, a negative ΔV indicates that the input variables lead to changes in (i.e., destabilize) the output variable, and $\Delta V = 0$ indicates that the input variables are

independent of one another. The synergy index is bounded: $-n \leq \Delta V \leq n/m$. As such, ΔV values were transformed using the Fisher z-transform (Eq. 9)

$$\Delta Vz = 0.5 \log \frac{n+\Delta V}{n-\Delta V} \quad \text{Eq. (9)}$$

Setting $\Delta V = 0$ provides a limit for determining whether there is task-specific covariation among inputs that stabilizes the output.

3.7. Statistical analysis

Statistical analyses were varied across specific aims and dependent variables. All analyses are described in detail below. Transformations to improve adherence to assumptions of constant variance and normality are also described, where applicable. All statistical analyses were conducted in SAS 9.4 (SAS Institute, Cary, NC, USA).

3.7.1. Specific Aim 1: Characterize adaptations to postural control during tool use under different levels of postural constraint and how these adaptations support manual task performance.

3.7.1.1. Task performance

Fitting errors were analyzed with a general linear mixed model with a negative binomial distribution and logarithmic link function. Fixed factors included Group (Normal BoS and Reduced BoS), Condition (Pre-Tool-Use, Tool-Use, and Post-Tool-Use), and Time (Early and Late). Participants was treated as a random factor with a compound symmetric variance-covariance structure. Significance was assessed at $\alpha = 0.05$. Multiple comparisons were made using Tukey-Kramer adjustments. Standardized effects sizes—Cohen's d —were also computed.

3.7.1.2. Postural performance

Only the Reduced BoS group was included in the statistical analyses. The number of postural errors were computed for the transport and fitting stages during the first and last two blocks of each condition. The first and last three maximum angular deviations of the support surface were analyzed with a generalized linear mixed model. The transport maximum angular deviations were log transformed while the fitting maximum angular deviations were Fixed

factors included Condition (Pre-Tool-Use, Tool-Use, and Post-Tool-Use) and Time (Early and Late). Participants was treated as a random factor with a compound symmetric variance-covariance structure. Significance was assessed at $\alpha = 0.05$. Multiple comparisons were made using Tukey-Kramer adjustments. Standardized effects sizes—Cohen's d —were also computed.

3.7.1.3. Manual control

The first and last three reaches of each condition were analyzed with a generalized linear mixed model. Normalized mean squared jerk and endpoint variance were log transformed prior to statistical analysis. Fixed factors included Group (Normal and Reduced BoS), Condition (Pre-Tool-Use, Tool-Use, and Post-Tool-Use), and Time (Early and Late). Participants was treated as a random factor with a compound symmetric variance-covariance structure. Significance was assessed at $\alpha = 0.05$. Multiple comparisons were made using Tukey-Kramer adjustments. Standardized effects sizes—Cohen's d —were also computed.

3.7.1.4. Postural control

The first and last three reaches of each condition were analyzed with a generalized linear mixed model. CoP sway area and mean velocity were log transformed prior to statistical analysis. Fixed factors included Group (Normal and Reduced BoS), Condition (Pre-Tool-Use, Tool-Use, and Post-Tool-Use), and Time (Early and Late). Participants was treated as a random factor with a compound symmetric variance-covariance structure. Significance was assessed at $\alpha = 0.05$. Multiple comparisons were made using Tukey-Kramer adjustments. Standardized effects sizes—Cohen's d —were also computed.

3.7.1.4. Associations between postural and manual control

Fisher-transformed Pearson correlations and 95% confidence limits were computed to examine the associations between measures of postural and manual control during the transport and fitting stages of the task. No significant deviations from linearity were observed for any pairwise comparisons.

3.7.2. Specific Aim 2: Examine postural-manual coupling under different levels of postural constraint during and following an extend bout of tool use.

The first and last three reaches of each condition were analyzed with a generalized linear mixed model. No variables were transformed prior to statistical analysis. Fixed factors included Group (Normal and Reduced BoS), Condition (Pre-Tool-Use, Tool-Use, and Post-Tool-Use), and Time (Early and Late). Participants was treated as a random factor with a compound symmetric variance-covariance structure. Significance was assessed at $\alpha = 0.05$. Multiple comparisons were made using Tukey-Kramer adjustments. Standardized effects sizes—Cohen's d —were also computed.

3.7.3. Specific Aim 3: Determine how multi-segment coordination supports postural control and suprapostural task performance under normal and challenging postural conditions with and without tools.

3.7.3.1. Transport Stage

V_{UCM} , V_{ORT} , and DV_z were analyzed with a generalized linear mixed model. V_{UCM} and V_{ORT} were log transformed prior to all statistical analyses. Fixed factors included Group (Normal and Reduced BoS), Condition (Pre-Tool-Use, Tool Use, and Post-Tool-Use), and Time (5%, 50%, and 95% of movement duration). Participants was treated as a random factor with a compound symmetric variance-covariance structure. Significance was assessed at $\alpha = 0.05$. Multiple comparisons were made using Tukey-Kramer adjustments. Standardized effects sizes—Cohen's d —were also computed.

3.7.3.1. Fitting Stage

V_{UCM} , V_{ORT} , and DV_z were analyzed with a generalized linear mixed model. V_{UCM} and V_{ORT} were log transformed prior to all statistical analyses. Fixed factors included Group (Normal and Reduced BoS), Condition (Pre-Tool-Use, Early Tool Use, Late Tool Use, and Post-Tool-Use). Participants was treated as a random factor with a compound symmetric variance-covariance structure. Significance was assessed at $\alpha = 0.05$. Multiple comparisons were made using Tukey-Kramer adjustments. Standardized effects sizes—Cohen's d —were also computed.

CHAPTER 4 – RESULTS

4.1. Specific Aim 1

4.1.1. Task Performance

Fitting errors were observed in both groups across all conditions. The average percent accuracy across groups and conditions was 93.8%. Table 4.1 contains the accuracy scores for each group and experimental condition. Both groups rarely made errors pre- and post-tool-use. However, accuracy was lower during tool use, especially for the Reduced BoS group. Statistical analyses of the error counts revealed a significant main effect of Condition ($F_{1,196}=71.96, p<.01$). Post-hoc comparisons revealed a greater number of errors in the tool use condition compared to the pre- (mean difference=2.84, $t_{.975}(76)=8.73, p<.01, d=1.00$) and post-tool-use conditions (mean difference=2.91, $t_{.975}(76)=8.70, p<.01, d=.99$). These findings indicate that fitting errors occurred more frequently during the tool use condition independent of the base of support width (Figure 4.1).

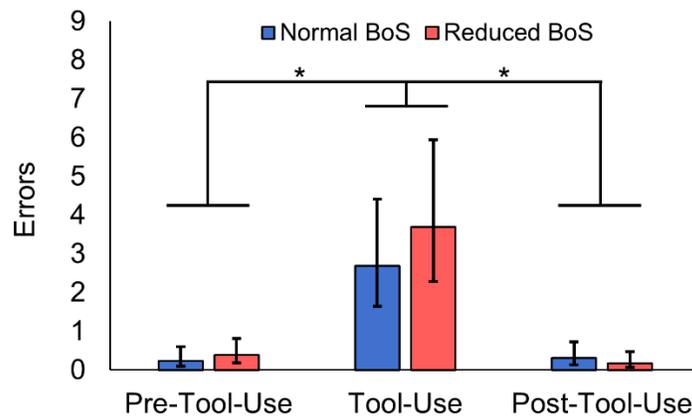


Figure 4.1. Fitting errors. Means and 95% confidence limits for the number of fitting errors for the Normal and Reduced BoS groups across the experimental conditions. Greater numbers of errors were observed during the tool use condition compared to pre- and post-tool-use. Note: All values were back-transformed from logarithmic scale, which creates asymmetric confidence limits. * $p<.01$

Table 4.1. Fitting task accuracy. Accuracy—the percentage of trials without errors—for the Normal and Reduced BoS groups during pre-tool-use, tool-use, and post-tool-use.

Group	Pre-Tool-Use	Tool-Use	Post-Tool-Use
Normal BoS	98.8%	86.9%	98.1%
Reduced BoS	98.5%	81.6%	99.1%

4.1.2. Postural Performance

4.1.2.1. Postural Errors

No postural errors were observed in the Normal BoS group, as expected due to the width of the base of support in the AP direction being longer than the feet. Only 42 postural errors—2.6% of the 1600 trials—were observed in the Reduced BoS group, indicating that participants were able to modify their standing behavior to accommodate the reduced base of support. Table 4.1 shows how postural errors were distributed by Condition and Time during the transport and fitting stages of the task for the Reduced BoS group. More postural errors occurred during tool use than pre- and post-tool-use. However, almost no postural errors occurred during post-tool-use. Additionally, more postural errors were observed while fitting than during object transport.

Table 4.2. Postural errors for the Reduced BoS group. Error counts (percentages) are shown for the transport and fitting stage for each experimental condition. Postural errors were categorized as occurring early or late within each condition based on whether they occurred in the first or last two blocks.

Stage	Time	Pre-Tool-Use	Tool-Use	Post-Tool-Use
Transport	Early	1 (2.4%)	4 (9.5%)	1 (2.4%)
	Late	1 (2.4%)	9 (21.4%)	0 (0.0%)
Fitting	Early	4 (9.5%)	5 (11.9%)	0 (0.0%)
	Late	7 (16.7%)	9 (21.4%)	1 (2.4%)

4.1.3.2. Maximum Angular Deviation

The maximum angular deviation of the support surface was examined during the transport and fitting stages of the task to assess postural performance. The Normal BoS group did not show any changes in the support surface orientation and was therefore excluded from the analysis. During the transport stage, statistical analyses revealed significant effects of Condition ($F_{2,335}=33.36, p<.01$). Comparisons among conditions showed reduced maximum angular deviation during tool-use compared to pre- (mean difference=.02°, $t_{.975}(335)=4.37, p<.01, d=.24$)

and post-tool-use (mean difference=.03°, $t_{.975}(335)=8.16, p<.01, d=.45$). Additionally, maximum angular deviations were greater during pre- compared to post-tool-use (mean difference=.01°, $t_{.975}(335)=3.79, p<.01, d=.21$).

During the fitting stage, statistical analyses indicated a significant main effect of Condition ($F_{2,335}=6.16, p<.01$) and Condition \times Time ($F_{2,335}=3.29, p<.01$). Comparisons among conditions showed reduced maximum angular deviation during post-tool-use compared to pre-tool-use (mean difference=.004°, $t_{.975}(335)=2.72, p=.02, d=.15$) and tool-use (mean difference=.005°, $t_{.975}(335)=8.16, p<.01, d=.45$). Comparisons of the Condition \times Time means showed greater support surface deviations during early tool-use compared to late tool-use (mean difference=.008°, $t_{.975}(335)=2.94, p=.04, d=.16$), early post-tool-use (mean difference=.01°, $t_{.975}(335)=4.13, p<.01, d=.23$), and late post-tool-use (mean difference=.009°, $t_{.975}(335)=3.44, p<.01, d=.19$). These results indicate reduced support surface deviations during tool-use with these reductions being maintained following tool-use (Figure 4.2b).

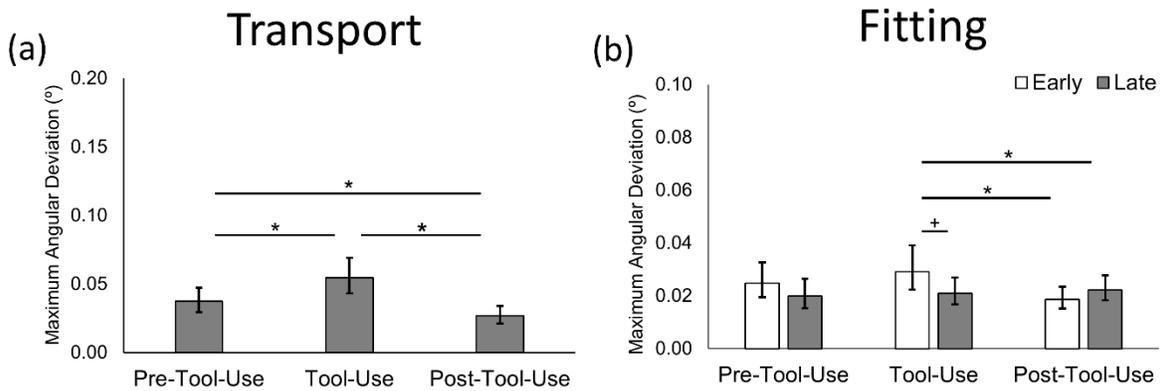


Figure 4.2. Maximum angular deviation of the support surface for the Reduced BoS group. Means and 95% confidence limits for the maximum angular deviation during transport (a) and fitting (b). See text for details regarding mean differences. Note: Means and confidence limits were back-transformed from following following statistical analysis for ease of interpretation, leading to asymmetric confidence intervals.

4.1.3. Manual Control

4.1.3.1. Transport Stage

Normalized Mean Squared Jerk

Normalized mean squared jerk was examined to assess the smoothness of the three-dimensional reach path during object transport (Figure 4.3). Greater normalized mean squared jerk measures correspond to less smooth movements. Statistical analyses revealed significant main effects of Condition ($F_{2,670}=6.99, p<.01$) and Time ($F_{1,670}=48.51, p<.01$) as well as significant interactions of Group \times Condition ($F_{2,670}=4.76, p<.01$) and Condition \times Time ($F_{2,670}=6.99, p=.04$). Smoother reaches were found post-tool-use compared to pre-tool-use (mean difference $=.28, t_{.975}(670)=2.82, p=.01, d=.11$) and tool-use (mean difference $=.36, t_{.975}(670)=3.54, p<.01, d=.14$). Less smooth reaches occurred early compared to late within conditions (mean difference $=.57, t_{.975}(670)=6.97, p<.01, d=.22$).

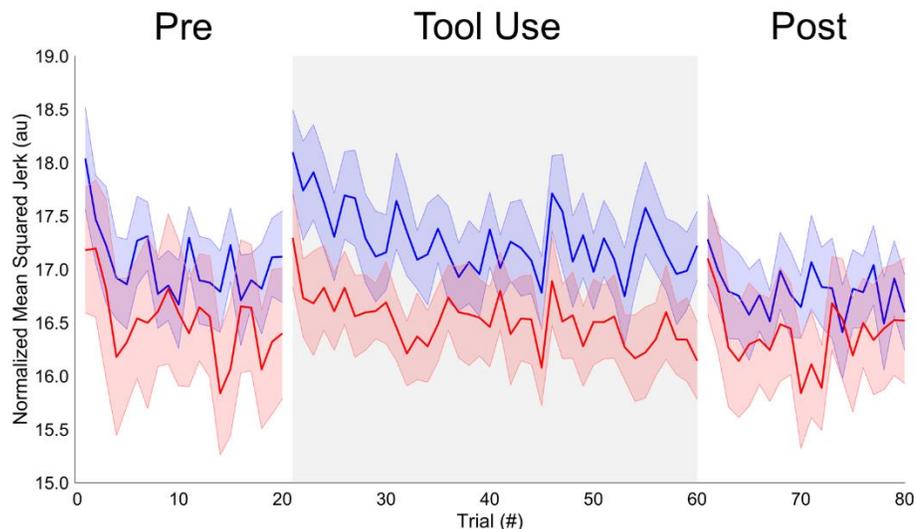


Figure 4.3. Normalized mean squared jerk during the transport stage. Means and 95% confidence limits across participants for the normalized mean squared jerk of the reach path during object transport for the Normal BoS (blue) and Reduced BoS (red) groups during Pre-Tool-Use, Tool-Use, and Post-Tool-Use.

Post-hoc analysis of the Condition \times Time effect showed that reach smoothness was reduced during early pre-tool-use compared to late pre-tool-use (mean difference $=.68, t_{.975}(670)=4.80, p<.01, d=.19$), late tool-use (mean difference $=.62, t_{.975}(670)=4.41, p<.01, d=.17$),

early post-tool-use (mean difference=.47, $t_{.975}(670)=3.28$, $p=.01$, $d=.13$), and late post-tool use (mean difference=.79, $t_{.975}(670)=5.51$, $p<.01$, $d=.21$). Reach smoothness was greater during late pre-tool-use relative to early tool-use (mean difference=.77, $t_{.975}(670)=5.42$, $p<.01$, $d=.21$). Reach smoothness also improved from early to late tool use (mean difference=.72, $t_{.975}(670)=5.02$, $p<.01$, $d=.19$). Reach smoothness was higher during early (mean difference=.55, $t_{.975}(670)=3.89$, $p<.01$, $d=.15$) and late post-tool-use (mean difference=.87, $t_{.975}(670)=6.13$, $p<.01$, $d=.24$) compared to early tool-use. These findings collectively indicate that 1) reach smoothness improved during pre-tool-use and tool-use and 2) smoother reaches were observed during post-tool-use compared to early pre-tool-use and tool-use but did not change over time (Figure 4.4a).

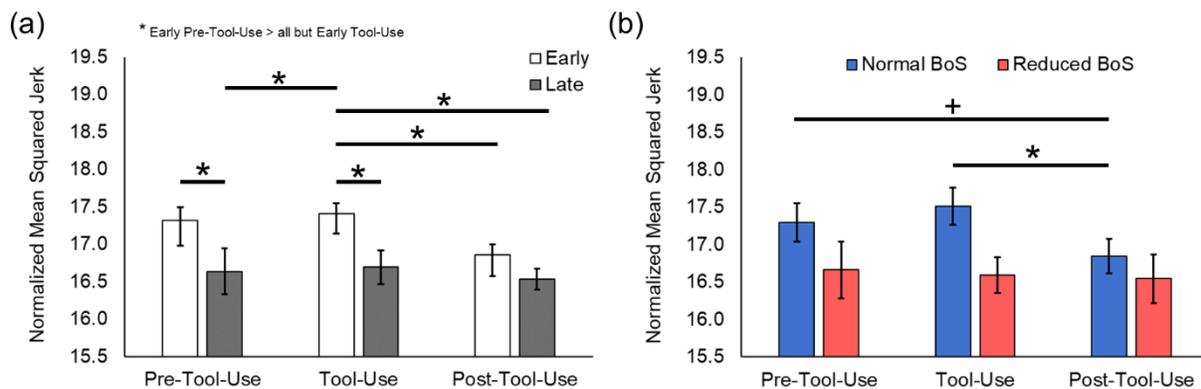


Figure 4.4. Normalized mean squared jerk during the transport stage. Means and 95% confidence limits for the (a) Condition \times Time and (b) Group \times Condition interaction effects. See text for details regarding mean differences (* $p < .01$; + $p < .05$). Note: The displayed confidence limits were computed from the means and standard errors of the observations. The standard errors from the statistical analysis were inflated for effects containing the between-participant factor of group.

Post-hoc comparisons of the Group \times Condition effect showed greater smoothness post-tool-use compared to pre-tool-use (mean difference=-.45, $t_{.975}(670)=-3.15$, $p=.02$, $d=.12$) and tool-use (mean difference=-.67, $t_{.975}(670)=-4.68$, $p<.01$, $d=.18$) for the Normal BoS group. No differences were observed between the Normal and Reduced BoS groups. These findings indicate that reach smoothness improved following tool-use but only for the Normal BoS group (Figure 4.4b).

4.1.3.2. Fitting Stage

Endpoint Variability

Endpoint variance—the sum of the variances in the ML and vertical directions—was examined to assess the variability of the end-effector while the block was being fitted (Figure 4.5). Statistical analyses revealed a significant main effect of Condition ($F_{1,670}=34.88, p<.01$) and an interaction effect of Group \times Condition ($F_{2,670}=3.45, p=.03$). Greater endpoint variability was observed during tool-use than pre- (mean difference=.04 $\text{cm}^2, t_{.975}(670)=5.27, p<.01, d=.20$) and post-tool-use (mean difference=.06 $\text{cm}^2, t_{.975}(670)=8.25, p<.01, d=.32$). Endpoint variability decreased from pre- to post-tool-use (mean difference=.02 $\text{cm}^2, t_{.975}(670)=2.98, p<.01, d=.12$).

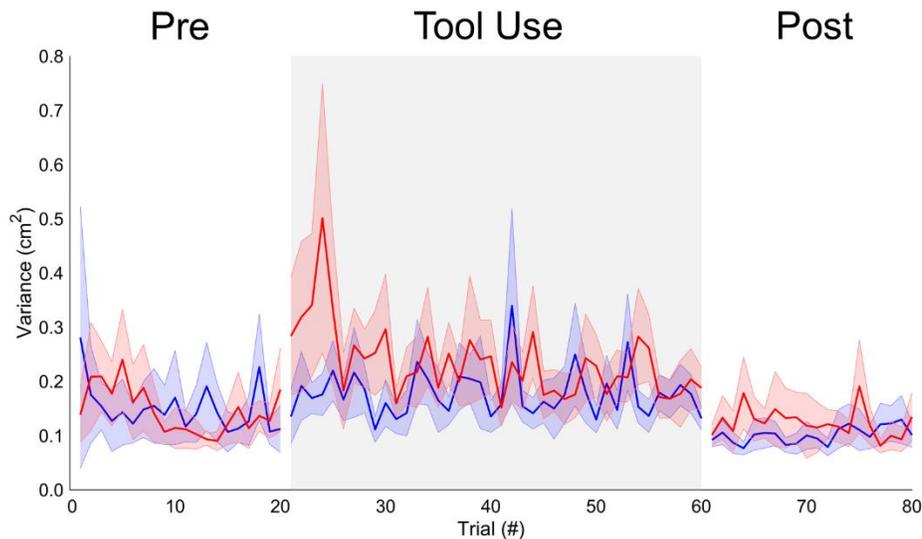


Figure 4.5. Endpoint variability during the fitting stage. Means and 95% confidence limits across participants for the endpoint variance when the object was fitted through the opening for the Normal BoS (blue) and Reduced BoS (red) groups during Pre-Tool-Use, Tool-Use, and Post-Tool-Use.

Post-hoc comparisons of the Group \times Condition effect revealed greater endpoint variability during tool-use than pre- (mean difference=.03 $\text{cm}^2, t_{.975}(670)=3.04, p=.03, d=.12$) and post-tool-use (mean difference=.04 $\text{cm}^2, t_{.975}(670)=4.37, p<.01, d=.17$) for the Normal BoS group. Similarly, greater endpoint variability was observed during tool-use compared to pre- (mean difference=.05 $\text{cm}^2, t_{.975}(670)=4.40, p<.01, d=.17$) and post-tool-use (mean difference=.08 $\text{cm}^2, t_{.975}(670)=7.29, p<.01, d=.28$) for the Reduced BoS group. Both the pre- (mean difference=.06 $\text{cm}^2, t_{.975}(670)=3.53, p<.01, d=.14$) and post-tool-use (mean difference=.08 $\text{cm}^2,$

$t_{.975}(670)=4.37, p<.01, d=.17$) endpoint variability for the Normal BoS group was lower than the Reduced BoS group during tool use. Post-tool-use endpoint variability was also lower than pre-tool-use for the Reduced BoS group (mean difference=.03 cm², $t_{.975}(670)=2.89, p=.04, d=.07$).

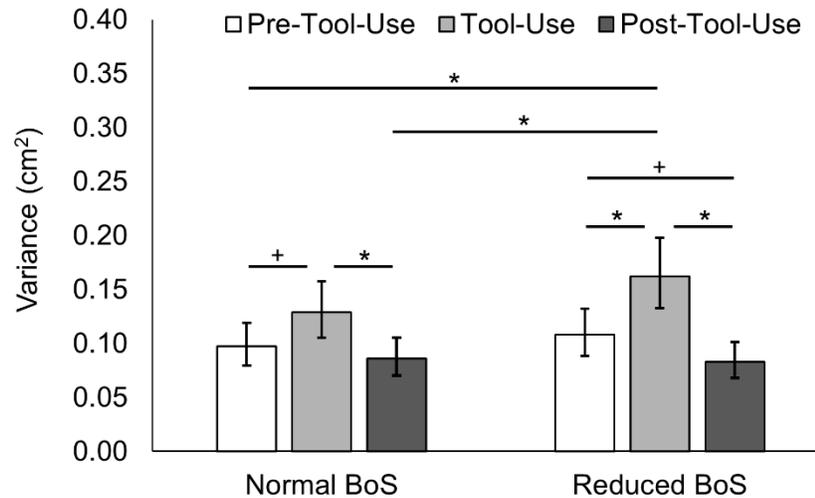


Figure 4.6. Endpoint variability during the fitting stage. Means and 95% confidence limits by group and experimental condition. Greater endpoint variability was observed during tool use for both groups compared to pre- and post-tool-use. The Normal BoS group also exhibited reduced endpoint variability during pre- and post-tool-use relative to the Reduced BoS group during tool-use. Additionally, the Reduced BoS showed decreased endpoint variability following tool-use compared to pre-tool-use. See text for details regarding mean differences (* $p < .01$; + $p < .05$).

4.1.4. Postural Control

4.1.4.1. Transport Stage

CoP Excursion

CoP excursion was examined to assess postural sway during reaching (Figure 4.7). Statistical analyses revealed significant effects of Group ($F_{1,670}=64.04, p<.01$), Condition ($F_{2,670}=142.81, p<.01$), Time ($F_{1,670}=82.29, p<.01$), Group \times Condition ($F_{2,670}=28.96, p<.01$), Group \times Time ($F_{2,670}=39.52, p<.01$), and Group \times Condition \times Time ($F_{2,335}=3.01, p=.04$). Greater CoP excursion was observed for the Normal BoS group (mean difference=3.66 cm, $t_{.975}(670)=8.06, p<.01, d=.31$). Greater CoP excursion occurred during tool use than pre- (mean

difference=1.31 cm, $t_{.975}(670)=15.13$, $p<.01$, $d=.58$) and post-tool-use (mean difference=1.29 cm, $t_{.975}(670)=14.94$, $p<.01$, $d=.58$). Greater CoP excursion was observed late within conditions (mean difference=.66 cm, $t_{.975}(670)=9.31$, $p<.01$, $d=.36$).

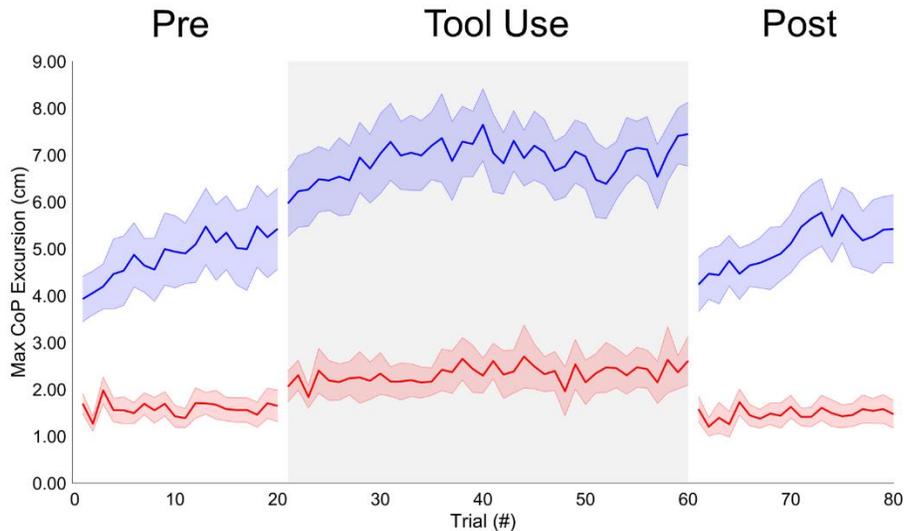
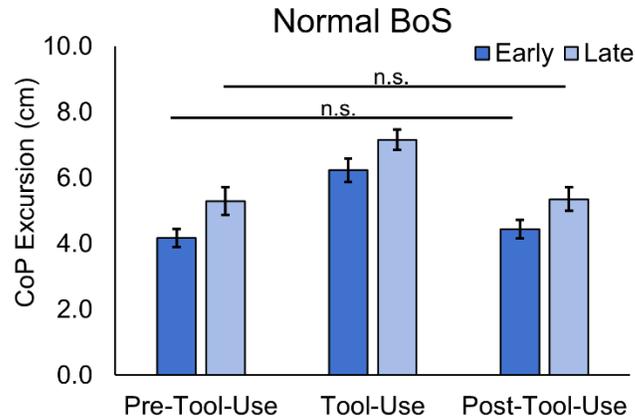


Figure 4.7. Maximum CoP excursion during the transport stage. Means and 95% confidence limits across participants for maximum CoP excursion during object transport for the Normal BoS (blue) and Reduced BoS (red) groups during Pre-Tool-Use, Tool-Use, and Post-Tool-Use.

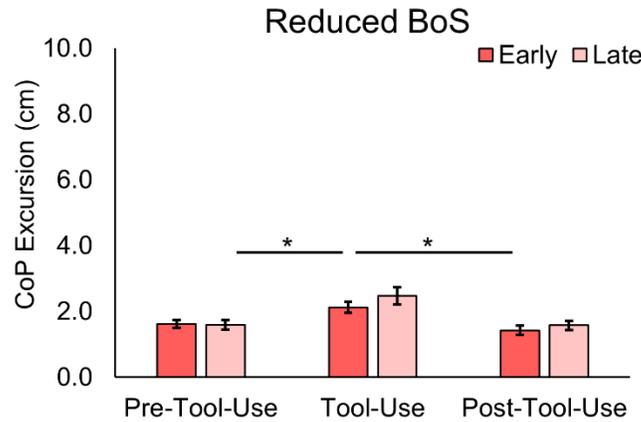
The Group \times Condition effect indicated greater CoP excursion in the Normal BoS group under all circumstances. Additionally, CoP excursion increased during tool use but did not differ between pre- and post-tool-use for both groups. The Group \times Time effect showed that greater CoP excursion in the Normal BoS group for all comparisons. Increases in CoP excursion were observed from early to late within conditions for the Normal BoS group (mean difference=.66 cm, $t_{.975}(670)=9.31$, $p<.01$, $d=.44$) but not the Reduced BoS group.

To reduce the difficulty of reporting the Group \times Condition \times Time effect, specific details regarding mean differences are reported in Figure 4.8. Greater Cop excursion was found for the Normal BoS group with the only exception being a lack of differences between early pre-tool-use in the Normal BoS group and late tool-use in the Reduced BoS group. CoP excursion increased within each condition for the Normal BoS group but did not change for the Reduced BoS group. In general, both groups exhibited increased postural sway during the tool use compared to pre- and post-tool-use, with only a few exceptions for the Reduced BoS group. During early post-tool-use, the maximum CoP excursion returned to similar levels as early pre-

tool-use in both groups. Similar increases in the CoP excursion also occurred from early to late pre- and post-tool-use for the Normal BoS group.



Note:
 All other Normal means are different ($p < .01$).
 Normal Early Pre not different than Reduced Late Tool.
 All other Normal means are greater than all Reduced means ($p < .01$).



Note:
 Reduced Pre and Post < Reduced Late Tool at $p < .01$ level.

Figure 4.8. CoP excursion during the transport stage. Means and 95% confidence limits for by group, experimental condition, and time. Greater sway was observed in the Normal BoS group. Greater sway was observed during tool use. Postural sway increased within each condition but only in the Normal BoS group. See text for additional information and figure notes for details regarding mean differences ($*p < .01$).

These results demonstrate continued adaptation of postural sway when reaching with and without tools. Greater postural sway was observed during tool use despite the relative reach distance remaining constant. However, when postural constraints were increased, no changes in postural sway were observed within conditions and only small increases were observed during

tool use. The adaptations to postural sway documented under normal standing conditions is protracted—taking approximately 10 trials—but appears to increase when the task is performed with a tool (Figure 4.7).

Maximum CoP Velocity

Maximum CoP velocity—measured using both the ML and AP components of the CoP—was also examined to assess postural sway during reaching (Figure 4.9). Similar to maximum CoP excursion, there were several significant statistical effects: Group ($F_{1,670}=16.85, p<.01$), Condition ($F_{2,670}=82.06, p<.01$), Time ($F_{1,670}=32.93, p<.01$), Group \times Condition ($F_{2,670}=3.09, p=.04$), Group \times Time ($F_{1,670}=31.97, p<.01$), and Group \times Condition \times Time ($F_{2,335}=6.20, p<.01$).

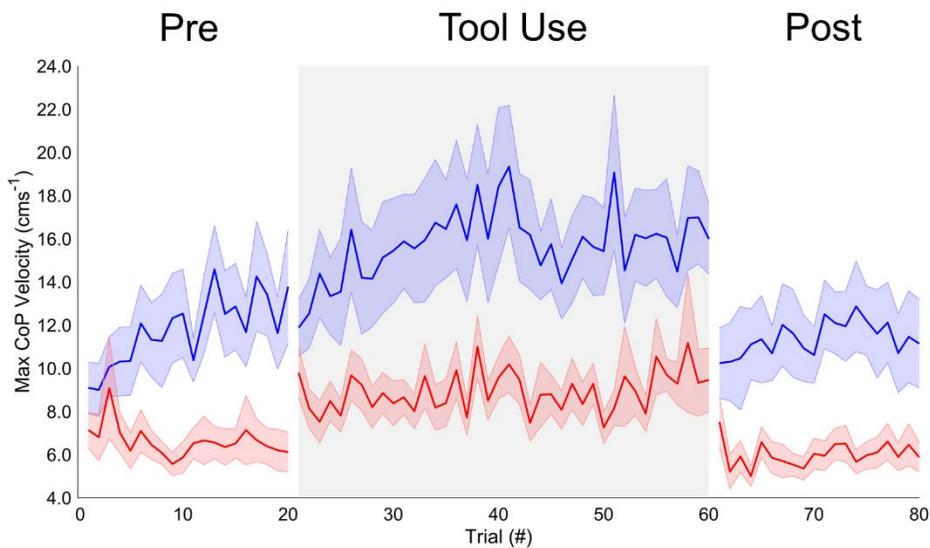
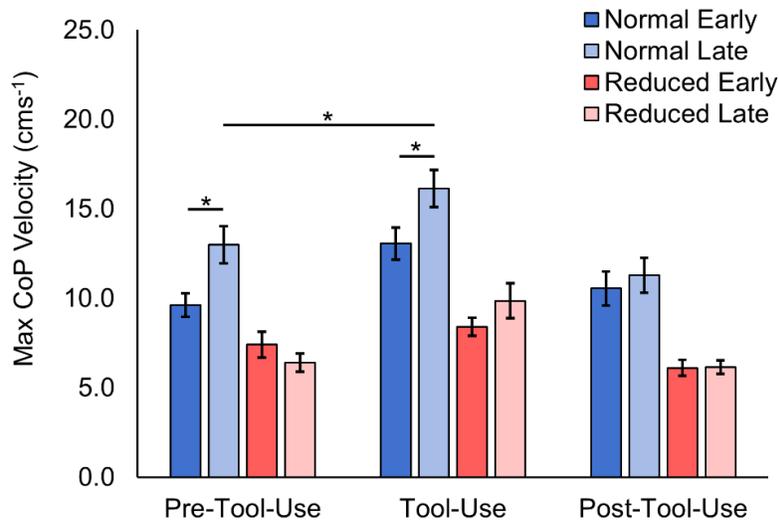


Figure 4.9. Maximum CoP velocity during the transport stage. Means and 95% confidence limits across participants for maximum CoP velocity during object transport for the Normal BoS (blue) and Reduced BoS (red) groups during Pre-Tool-Use, Tool-Use, and Post-Tool-Use.

Slower postural sway was observed in the Reduced BoS group (mean difference=4.95 cms⁻¹, $t_{.975}(670)=4.11, p<.01, d=.16$). Faster postural sway was observed during tool use compared to pre- (mean difference=2.81 cms⁻¹, $t_{.975}(670)=9.86, p<.01, d=.38$) and post-tool-use (mean difference=3.43 cms⁻¹, $t_{.975}(670)=12.02, p<.01, d=.46$). Faster postural sway was observed late within conditions (mean difference=1.33 cms⁻¹, $t_{.975}(670)=5.74, p<.01, d=.22$).

The Group \times Condition effect indicated faster postural sway within-conditions for the Normal BoS group. Faster postural sway was observed during tool use compared to pre- and post-tool-use for both groups. No differences in sway velocity were observed between pre- and post-tool-use for either group. However, sway velocity during pre- and post-tool-use for the Normal BoS group did not differ from the Reduced BoS group during tool use. The Group \times Time effect showed that postural sway was faster in the Normal BoS group for all comparisons. Increases in CoP velocity were observed from early to late trials for the Normal BoS group (mean difference=2.65 cms⁻¹, $t_{.975}(670)=8.06$, $p<.01$, $d=.31$) but not the Reduced BoS group.



Note:

- Normal Pre Early less than Normal Tool Early and Late at $p < .01$ level.
- Normal Pre Early not different from any Reduced means.
- Normal Pre Late greater than Normal Post Early at $p < .01$ level.
- Normal Pre Late greater than all Reduced at $p < .01$ level except Reduced Tool Late.
- Normal Tool Early greater than Normal Post Early at $p < .01$ level.
- Normal Tool Early greater than Reduced Pre and Post at $p < .01$ level.
- Normal Tool Late greater than all other means at $p < .01$ level.
- Normal Post Late greater than Reduced Pre Late, Post Early and Late at $p < .05$ level.
- Reduced Pre Early less than Reduced Tool Late at $p < .05$ level.
- Reduced Pre Late less than Reduce Tool at $p < .05$ level.
- Reduced Tool Early greater than Reduced Post at $p < .05$ level.
- Reduced Tool Late greater than Reduced Post at $p < .05$ level.

Figure 4.10. Maximum CoP velocity during the transport stage. Means and 95% confidence limits for by group, experimental condition, and time. Greater sway velocity was observed in the Normal BoS group. Greater sway velocity was observed during tool use. Postural sway velocity increased within the pre-tool-use and tool-use conditions but only in the Normal BoS group. See text for additional information and figure notes for details regarding mean differences ($*p < .01$).

For the Group \times Condition \times Time effect, the Normal BoS group exhibited greater sway velocity than the Reduced BoS group under most circumstances. There was also a consistent tendency for sway velocity to be greater during tool use, independent of group. Within conditions, the Normal BoS tended to increase sway velocity over time with the one exception being post-tool-use, whereas the Reduced BoS group showed no changes in sway velocity within any condition. For details regarding mean differences, see Figure 4.10. In large part, these findings mirror those reported for maximum CoP excursion with primary difference being the lack of changes during post-tool-use in the Normal BoS group. The increases in maximum sway velocity in the Normal BoS group occur over similar timescales as those observed for maximum CoP excursion—approximately 10 trials for the pre-tool-use and 20 trials for tool-use (Figure 4.11).

Minimum TtB

Minimum TtB was computed to assess the spatiotemporal proximity of the CoP to the base of support during object transport (Figure 4.11). Statistical analyses revealed significant effects of Group ($F_{1,670}=36.19, p<.01$), Condition ($F_{2,670}=76.24, p<.01$), Time ($F_{1,670}=5.59, p=.02$), Group \times Time ($F_{2,670}=23.41, p<.01$), and Group \times Condition \times Time ($F_{2,335}=6.61, p<.01$).

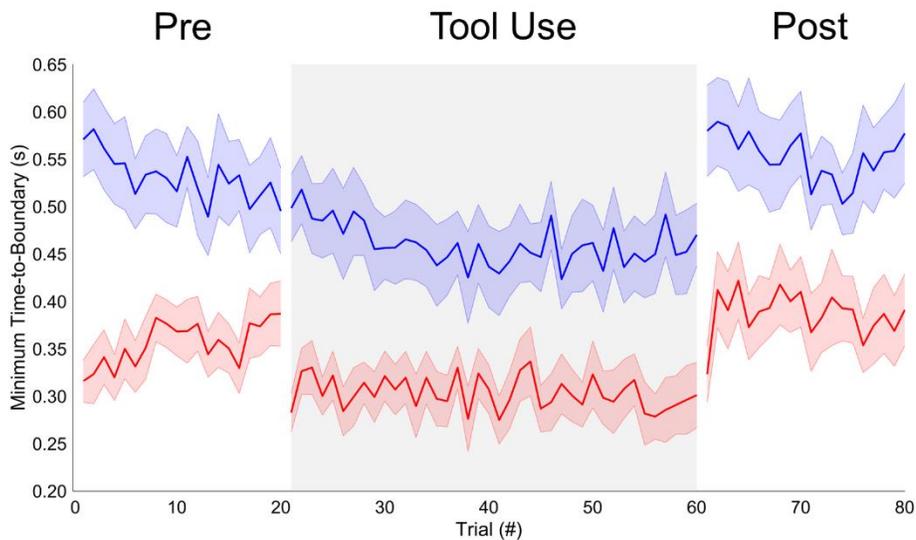
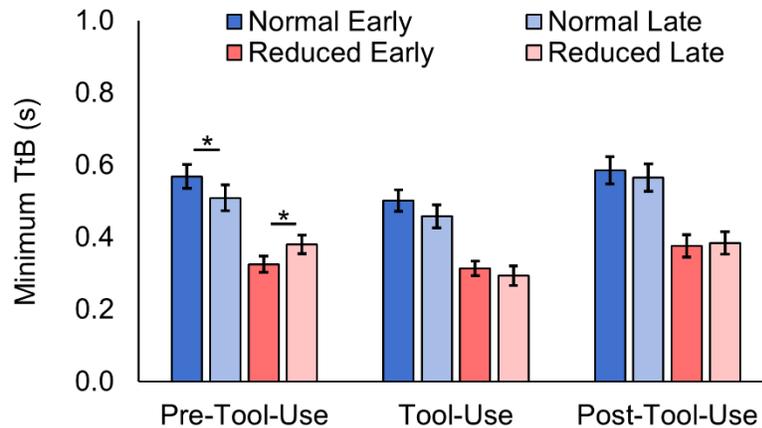


Figure 4.11. Minimum TtB during the transport stage. Means and 95% confidence limits across participants for minimum TtB during object transport for the Normal BoS (blue) and Reduced BoS (red) groups during Pre-Tool-Use, Tool-Use, and Post-Tool-Use.

Longer TtB was found for the Normal BoS group (mean difference=.19 s, $t_{.975}(670)=6.02, p<.01, d=.23$). Shorter TtB was found during tool use compared to pre- (mean difference=.05 s, $t_{.975}(670)=7.66, p<.01, d=.30$) and post-tool-use (mean difference=.09 s, $t_{.975}(670)=12.22, p<.01, d=.47$) but longer TtB was observed post-tool-use compared to pre-tool-use (mean difference=.03 s, $t_{.975}(670)=4.56, p<.01, d=.18$). TtB was longer early than late within conditions (mean difference=.01 s, $t_{.975}(670)=2.36, p=.02, d=.09$).

Multiple comparisons for the Group \times Time effect showed longer TtB for the Normal BoS group. TtB was shorter late within conditions for the Normal BoS group (mean difference=.04 s, $t_{.975}(670)=5.09, p<.01, d=.20$) but not the Reduced BoS group. These results provide further support for shorter TtB in the Reduced BoS group and indicate that longer TtB early compared to late within conditions is primarily attributable to the Normal BoS group.



Note:

- All Normal greater than all Reduced ($p < .01$).
- Normal Pre Early greater than Normal Tool ($p < .01$).
- Normal Pre Late greater than Normal Tool Late ($p < .05$).
- Normal Pre Late less than Normal Post ($p < .01$).
- Normal Tool less than Normal Post ($p < .01$).
- Reduced Pre Early less than Reduced Post ($p < .01$).
- Reduced Pre Late greater than Reduced Tool ($p < .01$).
- Reduced Tool less than Reduced Post ($p < .01$).

Figure 4.12. Minimum TtB during the transport stage. Means and 95% confidence limits for by group, experimental condition, and time. Longer TtB was observed in the Normal BoS group. Shorter TtB was generally observed during tool use. Within condition changes in TtB were only observed during pre-tool-use with the Normal BoS group showing decreased TtB and the Reduced BoS group showing increased TtB. See text for additional information and figure notes for details regarding mean differences ($*p < .01$).

Post-hoc analysis of the Group \times Condition \times Time effect revealed several significant differences (see Figure 4.13 for details). The Normal BoS group exhibited longer minimum TtB. Under most circumstances, both groups had shorter TtB during tool use compared to pre- and post-tool-use. Within condition changes to minimum TtB were limited to the pre-tool-use. Minimum TtB decreased and increased from early to late pre-tool-use for the Normal BoS group (mean difference=.06 s, $t_{.975}(670)=4.25$, $p<.01$, $d=.16$) and Reduced BoS group (mean difference=.05 s, $t_{.975}(670)=3.89$, $p<.01$, $d=.15$), respectively.

4.1.4.2. Fitting Stage

Sway Area

Sway area—the area of the 95% confidence ellipse of the CoP position—was examined to assess postural variability while during fitting (Figure 4.13). Statistical analyses revealed significant effects of Condition ($F_{2,670}=25.88$, $p<.01$), Time ($F_{1,670}=4.65$, $p=.03$), and Group \times Condition \times Time ($F_{2,670}=3.58$, $p=.03$). Greater sway was observed during tool use compared to pre- (mean difference= .06 cm², $t_{.975}(670)=6.98$, $p<.01$, $d=.27$) and post-tool-use (mean difference= .08 cm², $t_{.975}(670)=4.99$, $p<.01$, $d=.19$). Greater sway was also observed late within conditions (mean difference=.02 cm², $t_{.975}(670)=2.56$, $p=.01$, $d=.10$).

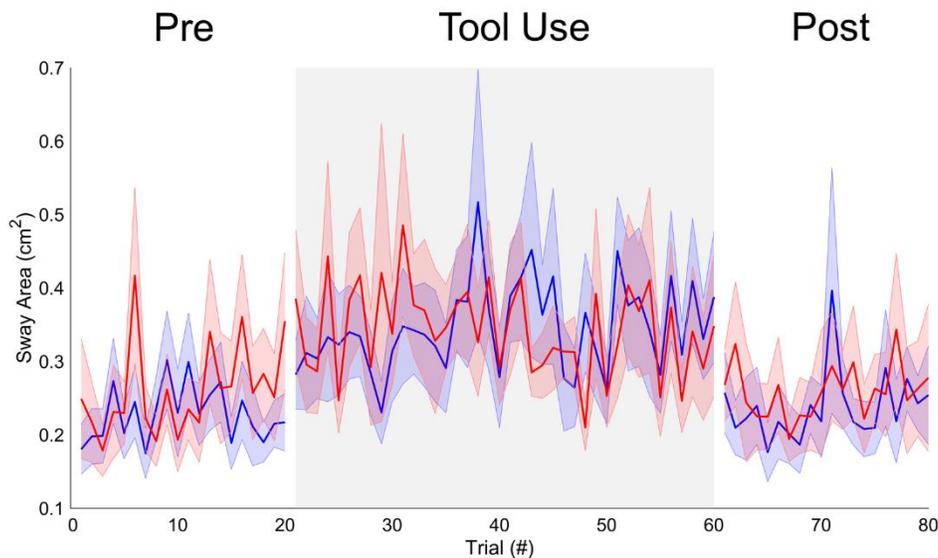
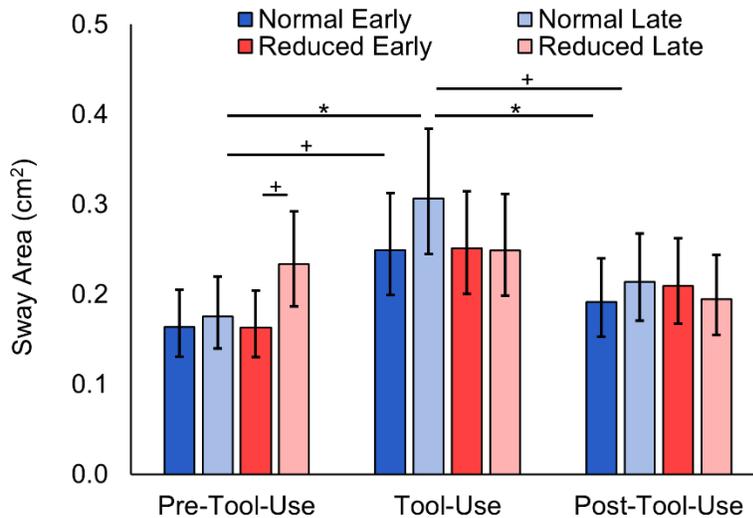


Figure 4.13. CoP sway area during the fitting stage. Means and 95% confidence limits across participants for the CoP sway area while the object was held in the opening for the Normal BoS (blue) and Reduced BoS (red) groups during Pre-Tool-Use, Tool-Use, and Post-Tool-Use.

Post-hoc comparisons of the Group \times Condition \times Time effect revealed that sway area was elevated during tool-use compared to pre- and post-tool-use tool-use for the Normal BoS group. Sway area was greater during late tool-use in the Normal BoS group compared to early pre-tool-use for the Reduced BoS group. Otherwise, there were no differences between the Normal and Reduced BoS groups. Within the Reduced BoS group, postural sway increased from early to late pre-tool-use. The Condition effect was therefore driven by increases in postural sway in the Normal BoS group, while the Time effect was driven by pre-tool-use differences in the Reduced BoS group and non-significant changes during tool use in the Normal BoS group. See Figure 4.14 for specific details regarding mean differences. These findings indicate that 1) postural sway increased during tool-use only in the Normal BoS group, 2) postural sway increased during pre-tool-use in the Reduced BoS group but did not change thereafter, and 3) postural sway was otherwise not different between groups.



Note:

Normal Pre Early less than Normal Tool at $p < .01$ level.
 Normal Tool Late greater than Reduced Pre Early at $p < .01$ level.
 Reduced Pre Early less than Reduced Tool at $p < .01$ level.

Figure 4.14. CoP sway area during the fitting stage. Means and 95% confidence limits by group and experimental condition. Greater postural variability was observed during tool-use in the Normal BoS group. Greater postural variability was observed during pre-tool-use for the Reduced BoS group. See text for additional details and the figure notes for details regarding mean differences ($*p < .01$, $+ p < .05$).

Mean Velocity

Mean CoP velocity—measured using the ML and AP components of the CoP velocity—was also examined to assess postural sway during fitting (Figure 4.15). There were significant statistical effects of Condition ($F_{2,670}=30.68, p<.01$) and Group \times Condition \times Time ($F_{2,670}=3.45, p=.03$). Faster postural sway was observed during tool-use compared to pre- (mean difference= .14 cm s^{-1} , $t_{.975}(670)=6.08, p<.01, d=.24$) and post-tool-use (mean difference= .17 cm^2 , $t_{.975}(670)=7.32, p<.01, d=.28$).

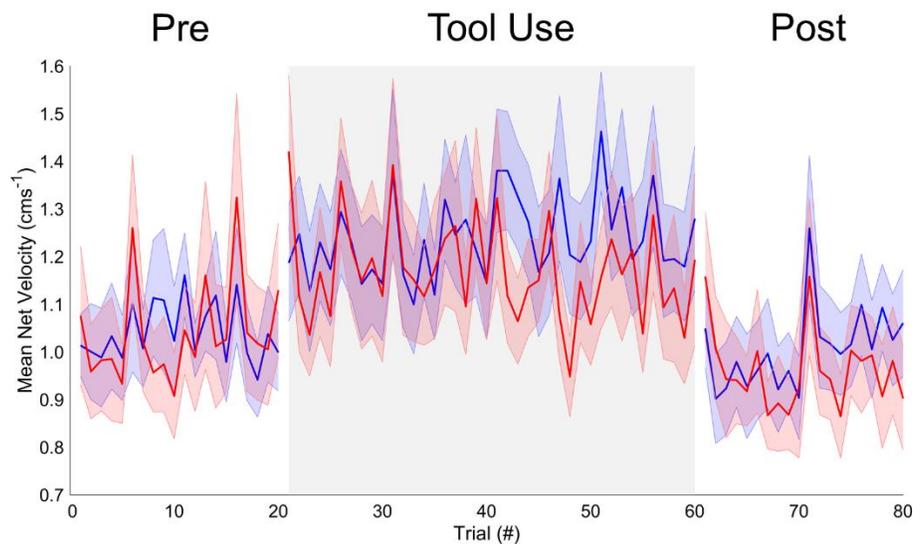
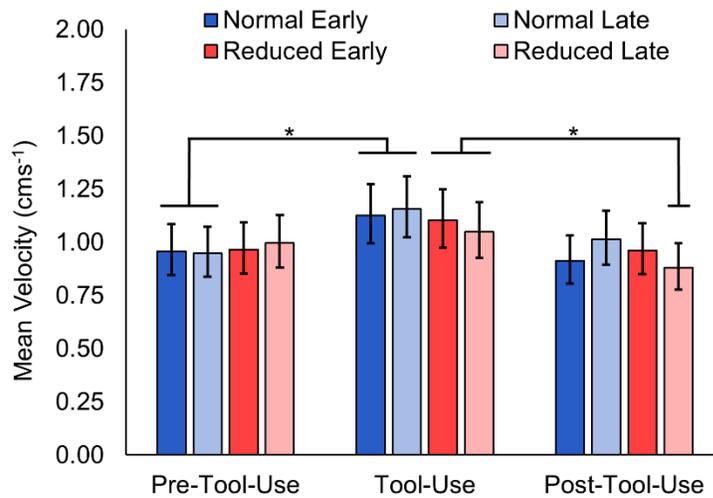


Figure 4.15. Mean CoP velocity during the fitting stage. Means and 95% confidence limits across participants for the mean CoP velocity while the object was held in the opening for the Normal BoS (blue) and Reduced BoS (red) groups during Pre-Tool-Use, Tool-Use, and Post-Tool-Use.

Post-hoc comparisons of the Group \times Condition \times Time effect revealed reduced sway velocity during early and late pre-tool-use compared to early and late tool-use in the Normal BoS group. Additionally, reduced sway velocity was observed during early post-tool-use, but not late post-tool-use, in the Normal BoS group. The Reduced BoS group showed reduced sway velocity late post-tool-use compared to early and late tool-use. However, no between-group differences were found (Figure 4.16). Thus, within-group differences between tool-use and pre- and post-tool use contributed to the condition effect described above.



Note:
Normal Post Early less than Normal Tool at $p < .01$ level.

Figure 4.16. CoP sway velocity during the fitting stage. Means and 95% confidence limits by group and experimental condition. In general, greater sway velocity was observed during the tool-use condition compared to pre- and post-tool-use. See text for additional details and the figure notes for details regarding mean differences ($*p < .01$).

Minimum TtB

Minimum TtB was computed to assess the spatiotemporal proximity of the CoP to the base of support while the object was held in the opening (Figure 4.17). Statistical analyses revealed significant effects of Group ($F_{1,670}=56.47, p<.01$), Condition ($F_{2,670}=30.72, p<.01$), Time ($F_{1,670}=6.39, p=.02$), Group \times Condition ($F_{2,670}=4.65, p<.01$), and Group \times Time ($F_{2,670}=7.52, p<.01$).

Longer TtB was found for the Normal BoS group (mean difference=.26 s, $t_{.975}(670)=7.51, p<.01, d=.29$). Shorter TtB was found during tool use compared to pre- (mean difference=.05 s, $t_{.975}(670)=5.67, p<.01, d=.22$) and post-tool-use (mean difference=.09 s, $t_{.975}(670)=7.52, p<.01, d=.29$). TtB was longer early than late within conditions (mean difference=.02 s, $t_{.975}(670)=2.53, p=.01, d=.10$).

Examination of the Group \times Condition effect showed longer TtB for the Normal BoS group (Figure 4.18). Shorter TtB was observed during tool use compared to pre- (mean difference=.08 s, $t_{.975}(670)=6.03, p<.01, d=.23$) and post-tool-use (mean difference=.09 s,

$t_{.975}(670)=6.99, p<.01, d=.27$) for the Normal BoS group. These results provide further evidence for shorter TtB in the Reduced BoS group and indicate that the condition effect was only consistently observed in the Normal BoS group.

Post-hoc analysis of the Group \times Time effect showed longer TtB for the Normal BoS group. TtB was shorter late within conditions for the Normal BoS group (mean difference $=.04$ s, $t_{.975}(670)=3.73, p<.01, d=.14$) but not the Reduced BoS group. These results provide further support for shorter TtB in the Reduced BoS group and indicate that longer TtB early compared to late within conditions is primarily attributable to Normal BoS group.

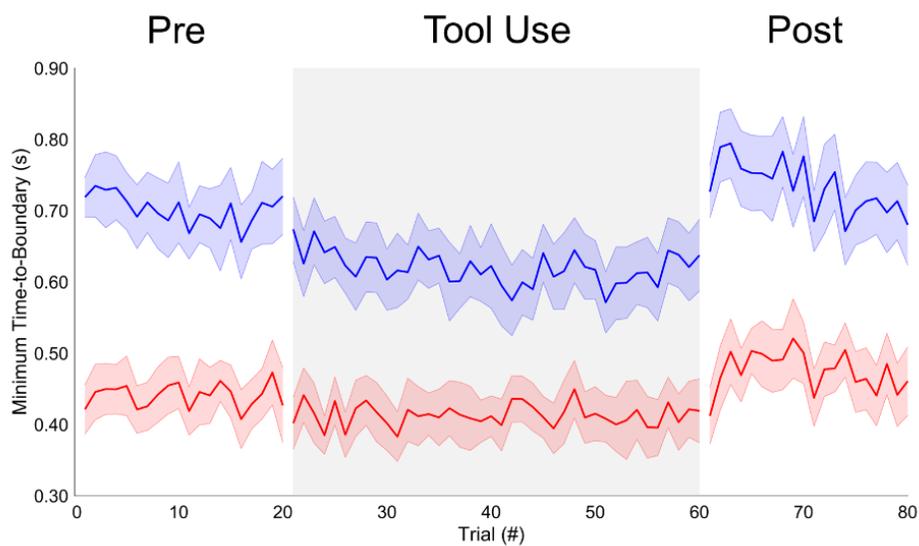
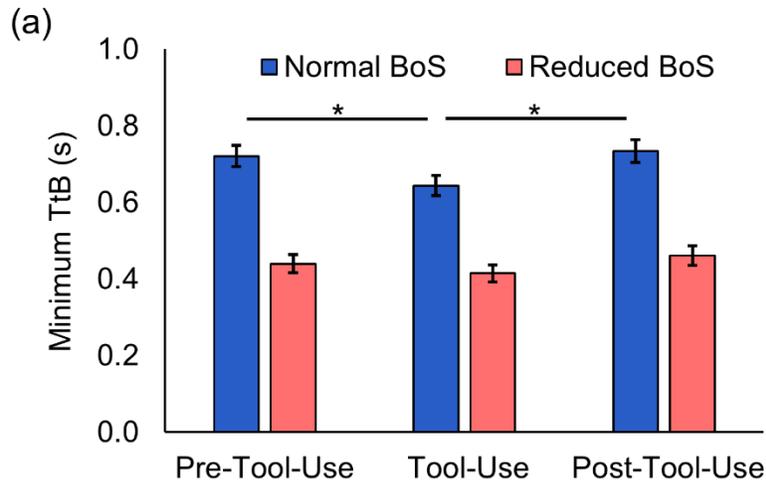
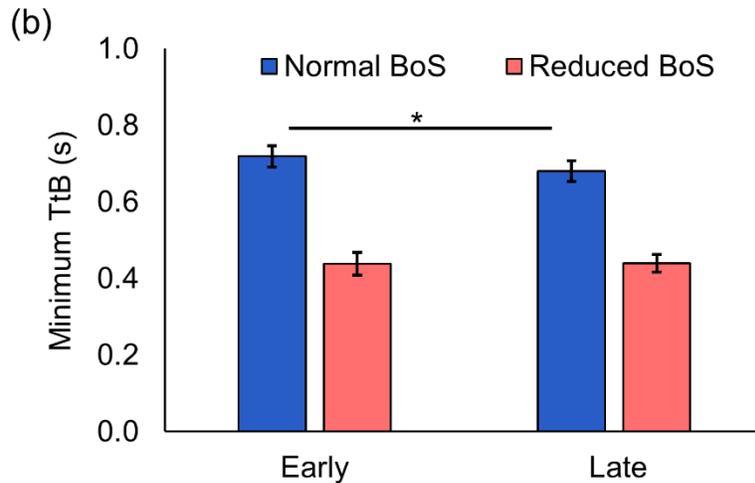


Figure 4.17. Minimum TtB during the fitting stage. Means and 95% confidence limits across participants for the minimum TtB while the object was held in the opening for the Normal BoS (blue) and Reduced BoS (red) groups during Pre-Tool-Use, Tool-Use, and Post-Tool-Use.



Note:
All Normal greater than all Reduced ($p < .01$).



Note:
All Normal greater than all Reduced ($p < .01$).

Figure 4.18. Minimum TtB during the fitting stage. Means and 95% confidence limits by (a) group and experimental condition and (b) group and time. Longer TtB was observed for the Normal BoS group. Shorter TtB was observed during tool-use compared to pre- and post-tool-use but only for the Normal BoS group. Shorter TtB was observed late within conditions but only for the Normal BoS group. See text for additional details and the figure notes for details regarding mean differences ($*p < .01$).

4.1.5. Relationship between Postural and Manual Control

The associations between postural and manual variables during the transport (Table 4.3) and fitting stages (Table 4.4) were measured to examine concurrent changes in postural and manual control before, during, and after tool use. No significant associations were observed between postural and manual control in the Reduced BoS group during the transport and fitting stages across all conditions.

During the transport stage of pre-tool-use, CoP excursion and maximum CoP velocity were negatively correlated with normalized mean squared jerk in the Normal BoS group. This indicates that increases in the displacement and speed of postural sway were associated with improvements in reach smoothness. A similar trend was observed during tool use with increases in postural displacements and sway velocity being associated with improved reach smoothness.

During the fitting stage of tool use, minimum TtB was negatively associated with end-effector variability in the Normal BoS group. This indicates that longer minimum TtB was associated with less end-effector variability while fitting the object through the opening. A similar trend was observed post-tool-use with longer minimum TtB associated with reduced end-point variability.

Table 4.3. Correlations between measures of postural and manual control during the transport stage. Fisher-transformed Pearson r correlations with 95% confidence limits between normalized mean squared jerk (manual control) and CoP excursion, maximum CoP velocity, and minimum TtB (postural control) by group and condition. Significant correlations are bolded.

		CoP Excursion	Maximum CoP Velocity	Minimum TtB
Normal BoS	Pre-Tool-Use	-.54 [-.79, -.13] <i>p</i> = .01	-.56 [-.80, -.16] <i>p</i> < .01	.39 [-.06, .71] <i>ns</i>
	Tool Use	-.45 [-.67, -.16] <i>p</i> < .01	-.48 [-.69, -.20] <i>p</i> < .01	.27 [-.03, .54] <i>ns</i>
	Post-Tool-Use	-.12 [-.54, .34] <i>ns</i>	-.13 [-.54, .33] <i>ns</i>	.17 [-.30, .57] <i>ns</i>
Reduced BoS	Pre-Tool-Use	-.14 [-.55, .32] <i>ns</i>	.06 [-.40, .49] <i>ns</i>	-.33 [-.67, .13] <i>ns</i>
	Tool Use	-.17 [-.46, .14] <i>ns</i>	.07 [-.24, .38] <i>ns</i>	-.14 [-.44, .17] <i>ns</i>
	Post-Tool-Use	.06 [-.39, .49] <i>ns</i>	.08 [-.37, .51] <i>ns</i>	-.31 [-.66, .15] <i>ns</i>

Table 4.4. Correlations between measures of postural and manual control during the fitting stage. Fisher-transformed Pearson r correlations with 95% confidence limits between end-effector variability (manual control) and sway area, mean CoP velocity, and minimum TtB (postural control) by group and condition. Significant correlations are bolded.

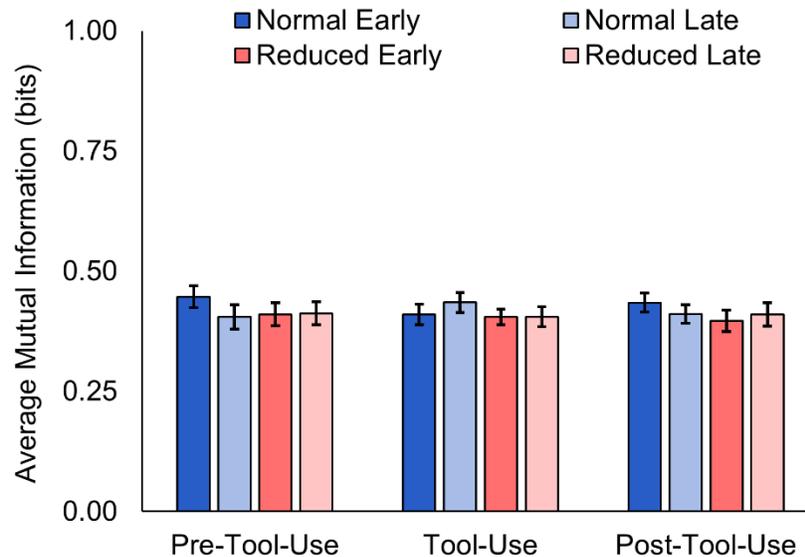
		Sway Area	Mean CoP Velocity	Minimum TtB
Normal BoS	Pre-Tool-Use	-.36 [-.69, .09] <i>ns</i>	-.27 [-.63, .20] <i>ns</i>	.00 [-.44, .44] <i>ns</i>
	Tool Use	.26 [-.05, .53] <i>ns</i>	.28 [-.04, .54] <i>ns</i>	-.33 [-.58, .02] <i>p</i> = .03
	Post-Tool-Use	.02 [-.43, .45] <i>ns</i>	.20 [-.27, .59] <i>ns</i>	-.46 [-.74, -.01] <i>p</i> = .04
Reduced BoS	Pre-Tool-Use	.19 [-.28, .58] <i>ns</i>	.26 [-.21, .63] <i>ns</i>	.05 [-.40, .48] <i>ns</i>
	Tool Use	.13 [-.19, .42] <i>ns</i>	.11 [-.21, .40] <i>ns</i>	-.08 [-.38, .24] <i>ns</i>
	Post-Tool-Use	-.30 [-.65, .17] <i>ns</i>	-.06 [-.49, .39] <i>ns</i>	.29 [-.18, .65] <i>ns</i>

4.2. Specific Aim 2

4.2.1. Transport Stage

4.2.1.1. ML Coupling

Average mutual information was computed to assess the coupling of the CoP and end-effector positions in the ML direction during object transport (Figure 4.19). Statistical analyses revealed a significant interaction of Group \times Condition \times Time ($F_{2, 670}=3.36, p=.04$). Post-hoc comparisons revealed that there were no differences between any pairs of means after applying Tukey-Kramer adjustments. There was a moderate degree of coupling between the CoP and end-effector position in the ML direction, but postural-manual coupling did not depend on any of the experimental factors.



Note:

No means were significantly different after Tukey-Kramer adjustments.

Figure 4.19. Average mutual information of the CoP and end-effector positions in the ML direction during object transport. Means and 95% confidence limits by group, experimental condition, and time. No differences were observed between any pairs of means. See text for additional details.

4.2.1.2. AP Coupling

Average mutual information was computed to assess the coupling of the CoP and end-effector positions in the AP direction during object transport (Figure 4.20). Statistical analyses revealed significant effects of Group ($F_{1, 670}=125.79, p<.01$), Condition ($F_{2, 670}=6.10, p<.01$), and Group \times Condition ($F_{2, 670}=3.56, p=.03$). Stronger postural-manual coupling was observed in the Normal BoS group (mean difference=.13 bits, $t_{.975}(670)=11.22, p<.01, d=.43$). Stronger postural-manual coupling was observed during pre-tool-use than tool use (mean difference=.03 bits, $t_{.975}(670)=3.47, p<.01, d=.13$).

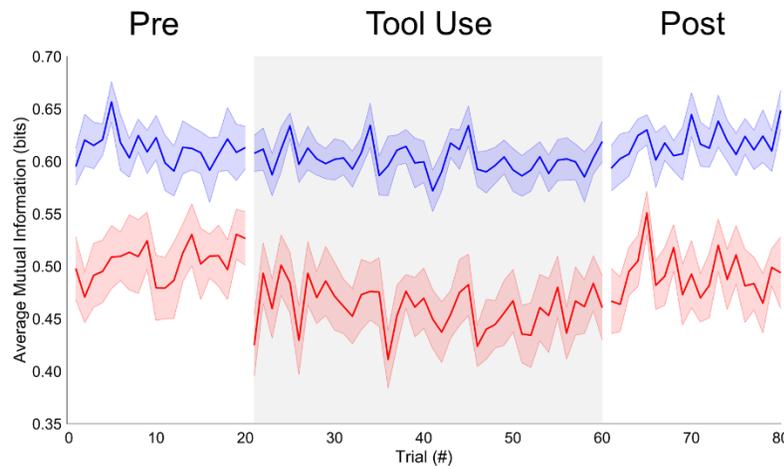
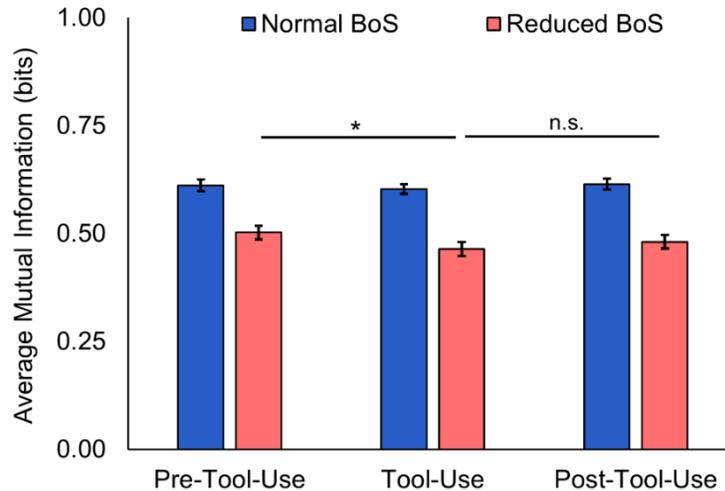


Figure 4.20. Average mutual information of the CoP and end-effector positions in the AP direction during object transport. Means and 95% confidence limits across participants for the minimum TtB while the object was held in the opening for the Normal BoS (blue) and Reduced BoS (red) groups during Pre-Tool-Use, Tool-Use, and Post-Tool-Use.

Examination of the Group \times Condition revealed that all Normal BoS means were greater than all Reduced BoS means at the $p < .01$ level (Figure 4.21). No differences were observed across conditions for the Normal BoS group. Postural-manual coupling decreased from pre-tool-use to tool use (mean difference=.04 bits, $t_{.975}(670)=4.03, p<.01, d=.16$). However, no differences were found between tool use and post-tool-use. Overall, there was substantially stronger postural-manual coupling in the AP direction for the Normal BoS group but only a marginal decrease for the Reduced BoS group.



Note:
 All Normal greater than all Reduced ($p < .01$).
 No differences between Normal means.

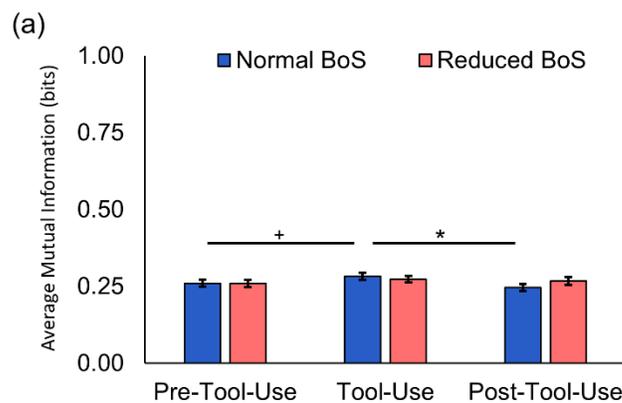
Figure 4.21. Average mutual information of the CoP and end-effector positions in the AP direction during object transport. Means and 95% confidence limits by group and experimental condition. Greater postural-manual coupling was observed in the Normal BoS group. No differences were found across conditions for the Normal BoS group; reductions to postural-manual coupling were observed from pre-tool-use to tool use in the Reduced BoS group. See text for additional details and the figure notes for details regarding mean differences ($*p < .01$).

4.2.2. Fitting Stage

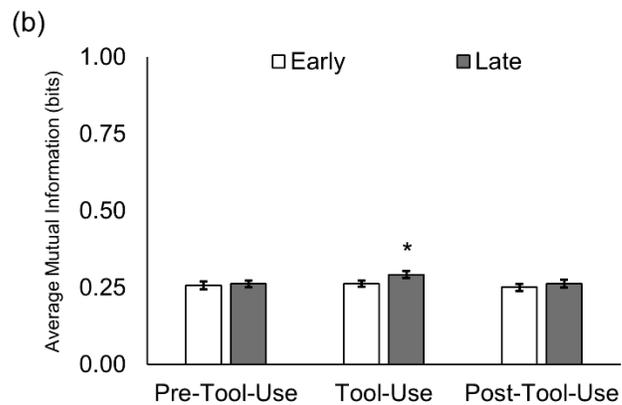
4.2.2.1. ML Coupling

Average mutual information was computed to assess the coupling of the CoP and end-effector positions in the ML direction while the object was held in the opening. Statistical analyses revealed significant effects of Condition ($F_{2, 670}=8.04, p<.01$), Time ($F_{1, 670}=11.74, p<.01$), Group \times Condition ($F_{2, 670}=4.01, p=.02$), and Condition \times Time ($F_{2, 670}=3.42, p=.03$). Stronger postural-manual coupling was observed during tool use compared to pre- (mean difference=.02 bits, $t_{.975}(670)=3.15, p<.01, d=.12$) and post-tool-use (mean difference=.02 bits, $t_{.975}(670)=3.72, p<.01, d=.14$). Weaker postural-manual coupling was observed late compared to early within conditions (mean difference=.02 bits, $t_{.975}(670)=3.43, p<.01, d=.13$).

Examination of the Group \times Condition effect revealed an increase in postural-manual coupling during tool use for the Normal BoS group compared to pre- (mean difference=.02 bits, $t_{.975}(670)=3.07$, $p=.04$, $d=.11$) and post-tool-use (mean difference=.04 bits, $t_{.975}(670)=4.57$, $p<.01$, $d=.18$). No differences across conditions were found for the Reduced BoS group. There was also no evidence of between-group differences (Figure 4.22a). Post-hoc comparisons of the Condition \times Time effect showed that postural-manual coupling was greater during late tool use compared to all other means (Figure 4.22b). Compared to object transport, ML postural-manual coupling was notably weaker when the object was being held in the opening.



Note:
No between group differences.
No differences across conditions for the Reduced BoS group.



Note:
Tool Late greater than all other means ($p < .01$).

Figure 4.22. Average mutual information of the CoP and end-effector positions in the ML direction while the object was held in the opening. Means and 95% confidence limits by (a) group and experimental condition and (b) experimental condition and time. Greater postural-manual coupling was observed during tool use in the Normal BoS group. Greater postural-manual coupling was observed late tool use compared to all other times. See text for additional details and the figure notes for details regarding mean differences ($^{\dagger} p < .05$, $*p < .01$).

4.2.2.2. AP Coupling

Average mutual information was computed to assess the coupling of the CoP and end-effector positions in the AP direction while the object was held in the opening. Statistical analyses revealed a significant effect of Condition ($F_{2,335}=8.04, p<.01$). Postural-manual coupling was greater during tool use compared to pre- (mean difference=.04 bits, $t_{975}(670)=5.46, p<.01, d=.21$) and post-tool-use (mean difference=.04 bits, $t_{975}(670)=4.76, p<.01, d=.18$)—see Figure 4.23.

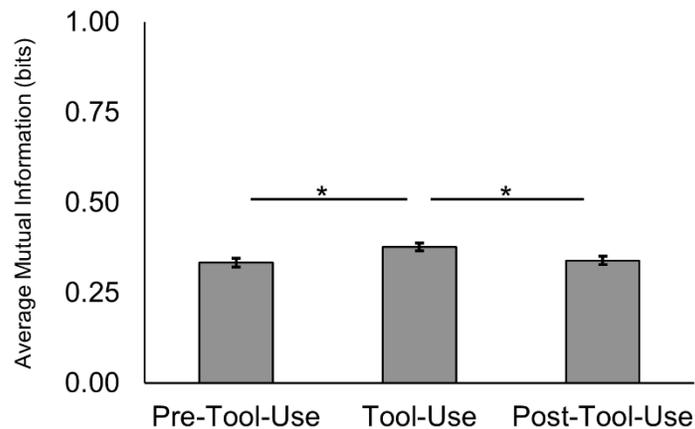


Figure 4.23. Average mutual information of the CoP and end-effector positions in the AP direction while the object was held in the opening. Means and 95% confidence limits by experimental condition. Greater postural-manual coupling was observed during tool use. See text for additional details and the figure notes for details regarding mean differences ($*p < .01$).

4.3. Specific Aim 3

4.3.1. UCM - Fitting Stage

4.3.1.1. Manual Control

4.3.1.1.1. Endpoint AP Position

V_{UCM}

Statistical analyses showed a significant effect of Group \times Condition ($F_{3, 314}=3.96$, $p<.01$). Post-hoc comparisons of the Group \times Condition effect revealed that V_{UCM} was lower during late tool use compared pre-tool-use (mean difference=5.74 deg²/df, $t_{.975}(314)=5.06$, $p<.01$, $d=.29$), early tool use (mean difference=3.74 deg²/df, $t_{.975}(314)=3.70$, $p<.01$, $d=.21$), and post-tool-use (mean difference=3.50 deg²/df, $t_{.975}(314)=3.51$, $p<.01$, $d=.20$), but only in the Normal BoS group (Figure 4.24). This shows that joint covariation leaving the AP endpoint position unchanged was lowest during late tool use and decreased throughout tool use in the Normal BoS group.

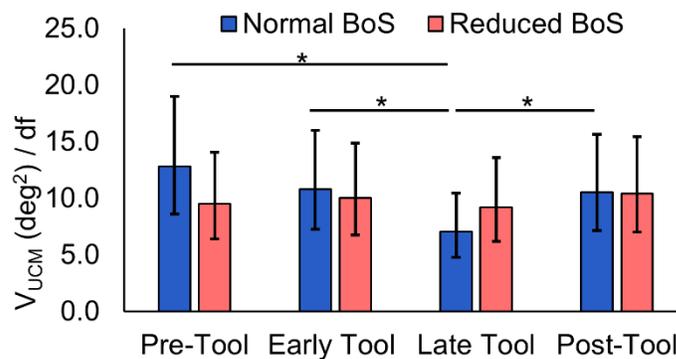


Figure 4.24. V_{UCM} of the AP endpoint position while fitting. UCM variance was lower during late tool use than all other conditions but only in the Normal BoS group. (* $p < .01$).

V_{ORT}

Statistical analyses revealed a significant effect of Condition ($F_{3, 314}=3.15$, $p=.03$). V_{ORT} was lower post-tool-use compared to late tool use (mean difference=.06 deg²/df, $t_{.975}(314)=3.80$,

$p < .01$, $d = .21$) (Figure 4.25). This indicates reduced endpoint variability in the AP direction following tool use.

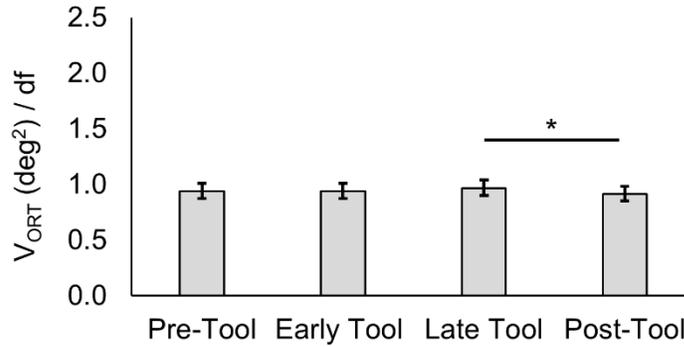


Figure 4.25. V_{ORT} of the AP endpoint position while fitting. ORT variance was greater during late tool use than post-tool-use. (* $p < .01$).

DV_z

Statistical analyses showed a significant effect of Group \times Condition ($F_{3,314} = 3.22$, $p = .02$). AP endpoint stability was lower during late tool use compared pre-tool-use (mean difference = .14, $t_{.975}(314) = 2.25$, $p = .03$, $d = .13$) and early tool use (mean difference = .19, $t_{.975}(314) = 3.03$, $p < .01$, $d = .17$) in the Normal BoS group. AP endpoint stability was also lower post-tool-use compared early tool use (mean difference = .15, $t_{.975}(314) = 2.42$, $p = .01$, $d = .14$).

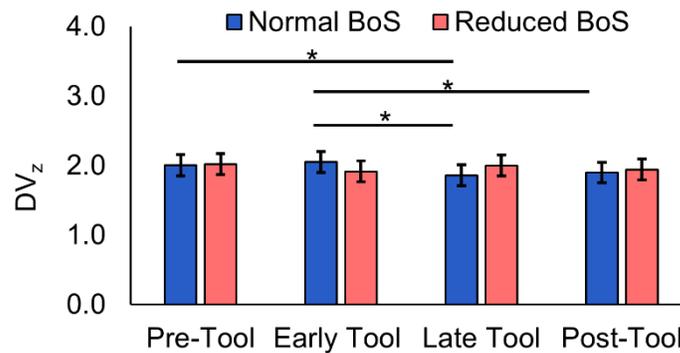


Figure 4.26. DV_z of the AP endpoint position while fitting. AP endpoint position was stabilized by joint covariation across both groups and all conditions. Endpoint stability was lower during late tool use compared to early tool use and pre-tool-use, as well as post-tool-use compared to tool use. These changes were limited to the Normal BoS group. (* $p < .01$).

Changes in AP endpoint stability were limited to the Normal BoS group which showed that AP endpoint stability decreased throughout tool-use and following tool use (Figure 4.26).

4.3.1.1.2. Endpoint Vertical Position

V_{UCM}

Statistical analyses showed a significant effect of Group \times Condition ($F_{3, 314}=3.96$, $p<.01$). Post-hoc comparisons of the Group \times Condition effect revealed that V_{UCM} was lower during late tool use compared pre-tool-use (mean difference=4.63 deg²/df, $t_{.975}(314)=4.30$, $p<.01$, $d=.24$), early tool use (mean difference=3.26 deg²/df, $t_{.975}(314)=3.70$, $p<.01$, $d=.19$), and post-tool-use (mean difference=2.51 deg²/df, $t_{.975}(314)=2.67$, $p<.01$, $d=.15$), but only in the Normal BoS group (Figure 4.27). This shows that joint covariation leaving the vertical endpoint position unchanged was lowest during late tool use and decreased throughout tool use in the Normal BoS group.

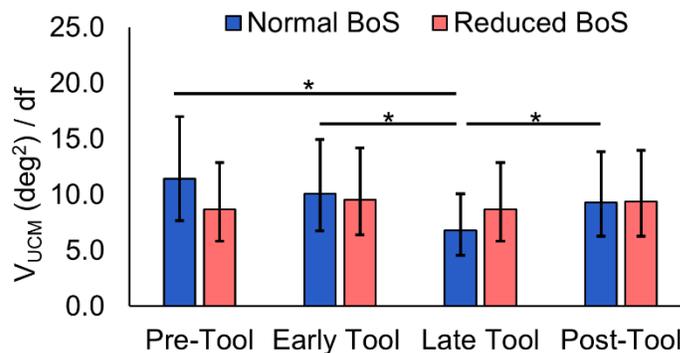
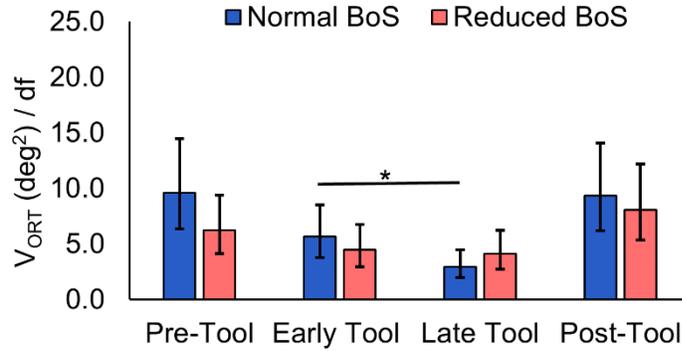


Figure 4.27. V_{UCM} of the vertical endpoint position while fitting. UCM variance was lower during late tool use than all other conditions but only in the Normal BoS group. (* $p < .01$).

V_{ORT}

Statistical analyses showed a significant effect of Group \times Condition ($F_{3, 314}=7.86$, $p<.01$). Post-hoc comparisons of the Group \times Condition effect revealed that V_{ORT} was lower during early late tool use compared pre- and post-tool-use in both groups (all $p < .01$). Vertical endpoint variability decreased throughout tool use in the Normal BoS group (tool-use (mean difference=2.69 deg²/df, $t_{.975}(314)=5.65$, $p<.01$, $d=.32$) but not the Reduced BoS group. This shows that vertical endpoint variability was consistently lower during tool use independent of

support surface constraints. Endpoint variability decreased throughout tool use in but not when the support surface width was decreased (Figure 4.28).



Note:
Early and Late Tool less than Pre- and Post-Tool-Use for both groups ($p < .01$)

Figure 4.28. VORT of the vertical endpoint position while fitting. VORT variance was lower during tool use in both groups. Vertical endpoint variability decreased throughout tool use in the Normal, but not Reduced, BoS group (* $p < .01$).

DV_z

Statistical analyses revealed a significant effect of Condition ($F_{3, 314}=44.92, p=.03$).

Vertical endpoint stability was greater during early and late tool use compared to pre- and post-

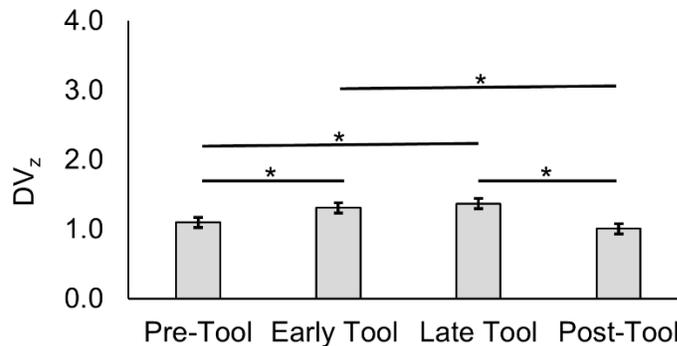


Figure 4.29. DV_z of the vertical endpoint position while fitting. Vertical endpoint position was stabilized by joint covariation across all conditions. Endpoint stability was greater during early and late tool use compared to pre- and post-tool-use (* $p < .01$).

tool use (all $p < .01$). This indicates that the stability of the vertical endpoint position was enhanced during tool use (Figure 4.29).

4.3.1.2. Postural Control

4.3.1.2.1. CoM AP Position

V_{UCM}

Statistical analyses showed a significant effect of Condition ($F_{3, 314}=18.39, p<.01$). Post-hoc comparisons of the revealed that V_{UCM} was greater during early and late tool use compared to pre- and post-tool-use (all $p < .01$). This shows that joint covariation leaving the AP CoM position unchanged was elevated during tool use independent of the support surface constraints (Figure 4.30).

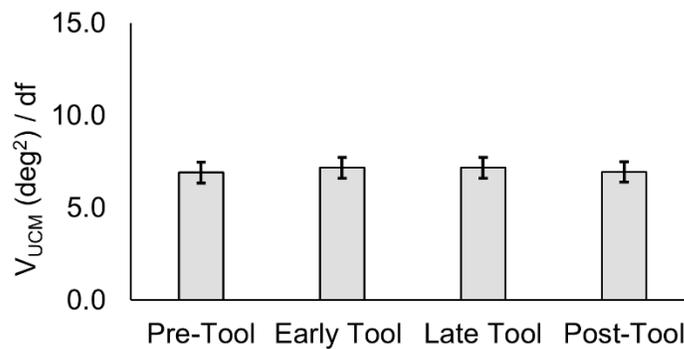


Figure 4.30. V_{UCM} of the AP CoM position while fitting. UCM variance was greater during tool use.

V_{ORT}

Statistical analyses showed a significant effect of Group \times Condition ($F_{3, 314}=5.83, p<.01$). Post-hoc comparisons of the Group \times Condition effect revealed that V_{ORT} greater during early and late tool use in the Reduced BoS group compared to pre- and post-tool-use in both groups (all $p < .01$). Greater V_{ORT} (all $p < .01$) was observed during early (mean difference=2.69 deg^2/df , $t_{.975}(314)=5.65, p<.01, d=.32$) and late tool use (mean difference=2.69 deg^2/df , $t_{.975}(314)=5.65, p<.01, d=.32$) in the Reduced BoS group compared to the Normal BoS group. This shows that the AP CoM variability increased during tool use when the support surface

extent was reduced. No changes in AP CoM variability were detected for the normal support surface extent (Figure 4.31).

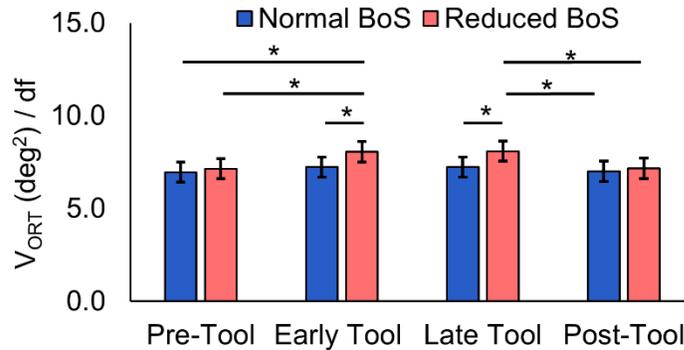


Figure 4.31. VORT of the AP CoM position while fitting. ORT variance was greater during tool use in the Reduced BoS group compared to the Normal BoS group and pre- and post-tool-use (* $p < .01$).

DVz

Statistical analyses revealed no significant effects for DVz. All DVz values were below the predetermined stability threshold, indicating that the AP CoM position was not stabilized over trials. These findings indicate that the degree of AP CoM stability while fitting was uninfluenced by tool use or support surface constraint (Figure 4.32).

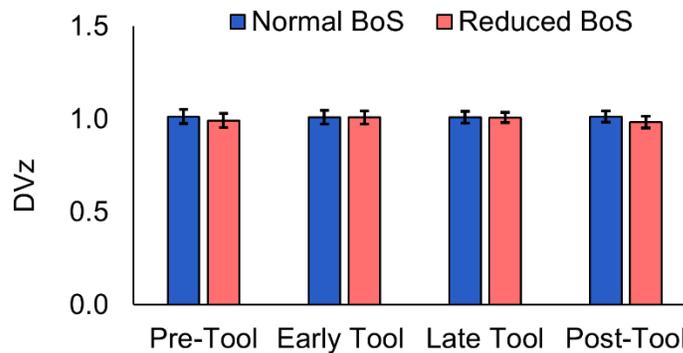


Figure 4.32. DVz of the AP CoM position while fitting. AP CoM position was not stabilized by joint covariation across any conditions. No differences were observed across groups or conditions.

4.3.1.2.1. CoM Vertical Position

V_{UCM}

Statistical analyses showed a significant effect of Group \times Condition ($F_{3, 314}=5.83$, $p<.01$). Post-hoc comparisons revealed that V_{UCM} was greater during early tool use compared to pre- (mean difference=.69 deg²/df, $t_{.975}(314)=5.05$, $p<.01$, $d=.28$) and post-tool-use (mean difference=.74 deg²/df, $t_{.975}(314)=5.47$, $p<.01$, $d=.31$) as well as late tool use compared to pre- (mean difference=.86 deg²/df, $t_{.975}(314)=6.17$, $p<.01$, $d=.35$) and post-tool-use (mean difference=.90 deg²/df, $t_{.975}(314)=6.61$, $p<.01$, $d=.37$). This shows joint covariation that leaves the vertical CoM position unchanged was elevated during tool use in the Reduced BoS group (Figure 4.33).

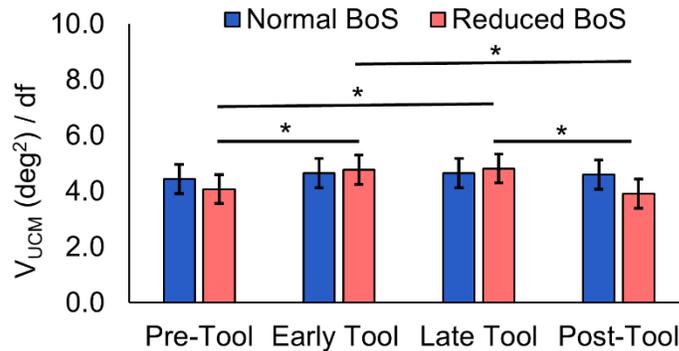


Figure 4.33. V_{UCM} of the vertical CoM position while fitting. UCM variance was greater during tool use in the Reduced BoS group (* $p < .01$). No changes were found in the Normal BoS group. No group differences were observed.

V_{ORT}

Statistical analyses showed a significant effect of Group \times Condition ($F_{3, 314}=5.83$, $p<.01$). Post-hoc comparisons revealed that V_{ORT} was greater during early tool use compared to pre- (mean difference=.72 deg²/df, $t_{.975}(314)=5.22$, $p<.01$, $d=.29$) and post-tool-use (mean difference=.76 deg²/df, $t_{.975}(314)=5.65$, $p<.01$, $d=.37$) as well as late tool use compared to pre- (mean difference=.89 deg²/df, $t_{.975}(314)=6.35$, $p<.01$, $d=.38$) and post-tool-use (mean

difference=.93 deg²/df, $t_{.975}(314)=6.80$, $p<.01$, $d=.).$ This vertical CoM variability was elevated during tool use in the Reduced BoS group (Figure 4.34).

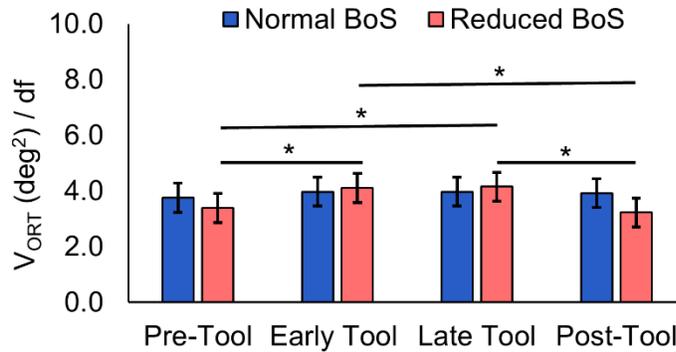


Figure 4.34. V_{ORT} of the vertical CoM position while fitting. ORT variance was greater during tool use in the Reduced BoS group (* $p < .01$). No changes were found in the Normal BoS group. No group differences were observed.

DV_z

Statistical analyses revealed no significant effects for DV_z. All DV_z values were above the predetermined stability threshold, indicating that the vertical CoM position was stabilized over trials. These findings also indicate that the degree of vertical CoM stability while fitting was uninfluenced by tool use or support surface constraint (Figure 4.35)

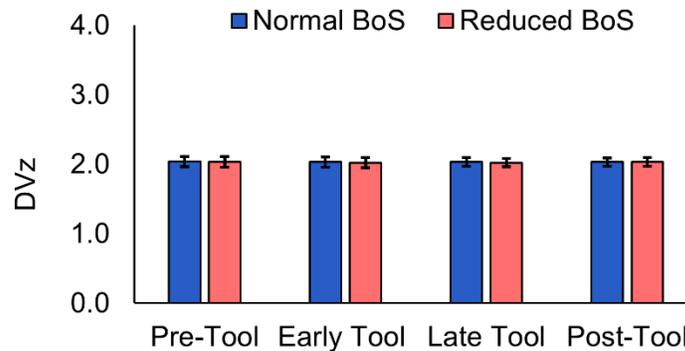


Figure 4.35. DV_z of the vertical CoM position while fitting. Vertical CoM position was stabilized by joint covariation across any conditions. No differences were observed across groups or conditions.

CHAPTER 5 – DISCUSSION

5.1. Specific Aim 1

Tool use is a whole-body activity that requires the ongoing adaptation of postural and suprapostural behaviors and the coordination of multiple bodily degrees of freedom. Previous studies examining manual control during tool use have shown that movements are modified during and following an extended bout of tool use (Baird et al., 2002; Cardinali, Frassinetti, et al., 2009; Cardinali et al., 2012; Valk et al., 2016). These studies examined seated reaching and did not consider the role of postural control or postural-manual integration in tool use. Because manipulating tools alters the arm geometry and dynamics, adaptive modifications of postural control were expected facilitate manual task performance. Consequently, we anticipated that if postural adaptations are important for tool use, then increasing constraints on standing posture would attenuate tool-use-related postural adaptations and interfere with manual task performance. The purpose of this study was to characterize adaptations to postural control during and following an extended bout of tool use under different levels of postural constraint and assess their relation to manual task performance.

5.1.1. Postural adaptations to tool use

Transport

People prefer to stand closer to the target object when manipulating a tool that extends arm length, which allows the tool be held closer to the body and presumably enhances endpoint control (Bongers et al., 2004; Bongers et al., 2003). In this study, standing distance from the target was adjusted to arm + tool length, not self-selected. To accommodate these constraints, increased forward postural displacements were expected during tool use to increase the postural contributions to the transport phase of reaching. However, reducing the base of support was expected to attenuate these postural adaptations. Consistent with these expectations, both groups increased forward postural sway when reaching with the tool but substantially smaller displacements occurred when standing on a reduced base of support. These findings indicate a greater contribution of postural sway to object transport when using a tool that extends arm

length with constraints on standing balance modulating the degree of postural involvement, anticipated.

Postural and manual behaviors exhibit strong temporal coordination when standing and reaching (Haddad et al., 2012; Patron et al., 2005). Increasing postural displacements without also increasing sway velocity would disrupt the coordination between postural and manual movements during object transport. Concurrent increases in maximum CoP velocity were expected to occur to maintain the timing of the postural contributions to reaching. Both groups increased sway velocity when the task was performed with the tool, although substantially slower sway was observed when standing on a reduced base of support. These modifications indicate coordinated changes to postural displacements and sway velocity, which may have preserved postural-manual coordination when reaching with the tool.

Shorter TtB indicates a smaller spatiotemporal margin of safety, which is thought to reflect reduced postural stability (Haddad et al., 2010). Greater forward displacement and faster sway velocity of the CoP leads to shorter TtB to the anterior boundary of the base of support. Shorter TtB was observed during tool use in both groups, which reflects the changes to postural displacement and sway velocity described above. TtB was longer in the when standing on a normal base of support, as anticipated, because the computation of TtB explicitly considers the base of support dimensions. Reducing the base of support leads to shorter TtB independent of changes in postural sway or sway velocity. However, TtB could remain the same or become longer if people modify their postural dynamics with respect to the narrower stability boundaries.

Increased postural stability is generally associated with improved suprapostural performance, particularly when precision demands are high (Haddad et al., 2010; Riley et al., 1999; Stoffregen et al., 1999). The finding that both groups exhibited shorter TtB during tool use indicates a willingness to tradeoff postural stability in exchange for suprapostural performance even when standing balance was challenged. Interestingly, recent findings suggest that reducing postural stability facilitates visual tracking (Deprá et al., 2019). The current study provides additional support for the notion that task-dependent postural control—consisting of the capability to increase *and* decrease postural stability—provides a means to modify postural responses to changing suprapostural task demands (Haddad et al., 2013), such as reaching with or without tools.

In summary, multiple dimensions of postural control were adapted when reaching with a tool that extended arm length. Previous studies have documented changes to seated reaching characteristics when using a tool (Baird et al., 2002; Cardinali, Frassinetti, et al., 2009; Cardinali et al., 2012; Valk et al., 2016). When standing posture has been examined during tool use, the focus has been how tool characteristics and task constraints influence standing position and postural configuration *prior* to tool use (Bongers et al., 2004; Bongers et al., 2003). This study provides some initial evidence of adaptations to dynamic postural control during tool use when transporting an object to a target. Decreased postural stability—as evidenced by greater forward displacement, faster sway velocity, and shorter TtB—was found when reaching with a tool beyond arm length. Furthermore, increasing the constraints on standing posture diminished, but did not fully attenuate, postural adaptations to tool use during object transport.

Fitting

Decreased postural variability and longer minimum TtB have been found during precision manual tasks (Haddad et al., 2010). Decreases in postural variability were expected to occur during tool use compared to pre- and post-tool-use to compensate for the challenges of controlling the tool. Contrary to this hypothesis, postural sway and sway velocity increased and TtB decreased in both groups when using the tool to perform the fitting task. Another counterintuitive result was the similarities in spatiotemporal measures of postural sway across variations in support surface extent. Reduced postural sway and lower sway velocity was expected when standing on a reduced base of support, which was anticipated to lead to similar TtB to the normal base of support group. TtB was nearly 250 ms shorter when participants stood on the reduced base of support, indicating that postural sway was not modified while fitting to counteract the narrower stability limits.

Previous research has suggested that the degree of postural stabilization is a function of the precision requirements for the suprapostural task (Stoffregen et al., 1999). Although there is emerging evidence that better manual performance does not always follow from reducing postural sway (Amado et al., 2016), there is a strong consensus that more precise manual tasks are normally accomplished by reducing extraneous postural variability (Balasubramaniam et al., 2000; Haddad et al., 2013; Haddad et al., 2010; Riley et al., 1999). One interesting finding was that longer TtB—indicating greater postural stability—was associated with reduced end-point variability during tool use, but only when standing on the normal base of support. This suggests a

tendency to increase postural stability in response to the challenge of performing a precision manual task using a tool. The lack of association between postural stability and endpoint variability under the restricted base of support condition may be due to the inherently challenging nature of maintaining upright balance in this configuration.

Why did people adopt a less stable posture during tool use? One plausible explanation is that the postural adaptations undertaken during object transport inadvertently interfered with fitting performance. Both groups exhibited greater forward postural displacements during tool use. These adaptations increased the postural contributions to object transport and were associated with improvements in reach smoothness. But, maintaining a substantial forward lean while fitting may be detrimental to manual performance because it requires maintaining the CoM closer to the stability limits. When people are allowed to select how close to stand to a target object when interacting with a tool, closer standing positions are adopted when the precision demands are high or the tool body is long (Bongers et al., 2004; Bongers et al., 2003). Participants adopted forward leaning postures during object transport and subsequently maintained forward postural displacement while fitting. The increased difficulty of controlling the end-effector coupled with greater proximity to the limits of stability may explain why fitting performance was markedly worse during tool use compared to pre- and post-tool-use.

5.1.2. Exploration, failure boundaries, and postural adaptations during tool use

Postural adaptations during object transport continued throughout tool use when standing on the normal base of support. Postural displacements and sway velocity systematically increased and appeared to asymptote approximately half way through the tool use condition—although this was not directly quantified. At the same time, TtB became shorter, indicating that participants were incrementally approaching their stability limits. These findings may indicate the adoption of a conservative, ‘posture first’ strategy (Shumway-Cook et al., 1997) where postural stability was initially prioritized when adjusting to using the tool and gradually decreased over time to increase the contributions of postural sway to object transport. This suggests that postural stability is not necessarily prioritized while reaching. Rather, if balance is not substantially threatened, then decreasing the spatiotemporal margin of stability may represent a behavioral strategy that serves to maintain or improve manual performance (Amado et al., 2016).

Postural variability serves multiple functions, such as maintaining standing balance and facilitating suprapostural performance, but also providing information about actor-environment relations to inform current or future behaviors (Riccio, 1993; van Emmerik & van Wegen, 2002). The adaptive modifications of postural sway observed throughout tool use may serve both pragmatic (i.e., goal-directed) and epistemic (i.e., information-related) functions (Kirsh & Maglio, 1994). Riccio (1993) postulated that exploratory behavior can be undertaken if the timescales of exploration are shorter than the performatory task dynamics. This implies that postural variability occurring on shorter timescales provides stimulation that may aid postural regulation over longer timescales. But, the exploratory, information gathering role of postural variability may not be limited to this situation. Participants consistently increased postural displacements during object transport on a trial-by-trial basis, which is an important performance component of the fitting task. These findings are interpreted as preliminary evidence that postural exploration can also take place over timescales longer than the performatory task dynamics—more specifically, in this study, across trials. This suggests that exploratory postural dynamics may occur over a wider range of timescales than previously assumed.

Postural adaptations occurred over repeated performances, possibly indicating a systematic exploration of failure boundaries. Failure boundaries represent the limit of safe behavioral characteristics based on the current task demands and environmental challenges (Rietdyk, under review). Acting near or at failure boundaries may facilitate the identification of stability limits as well as behavioral strategies that prevent loss of balance, improve recovery, or avoid injury. The information gained from probing failure boundaries presumably allows people to identify behavioral solutions that afford upright stance and suprapostural performance. The asymptotic convergence of postural behaviors documented in this study are consistent with—but do not provide firm evidence of—the exploration and identification of failure boundaries as people became adjusted to performing the fitting task with the tool.

Increasing the constraints on standing posture reduces opportunities for exploratory postural behaviors. Restricting the base of support width was expected to attenuate tool-use-related postural adaptations. Support for this prediction was provided by the lack of postural adaptations when standing on the reduced base of support. Although these participants were willing to increase postural displacement during object transport, there was little incentive for further exploration due to the prospect of becoming unstable. Importantly, this indicates a

properly calibrated sensitivity to discrepancies between action capabilities and environmental conditions. Furthermore, it highlights the flexibility with which postural control is adapted to meet concurrent goals of maintaining balance and facilitating suprapostural performance.

5.1.3. Postural adaptations support improvements in manual control during tool use

Prolonged adaptations to reach smoothness and postural stability were documented during object transport when using a tool. Reach smoothness is considered a signature of skilled, coordinated movement (Hogan & Sternad, 2009). Increases in reach smoothness were interpreted as improvements in manual control because transporting the object to the opening is a key component of successful fitting performance. Postural adaptations were associated with concurrent improvements in manual control, providing some initial support for the importance of adapting postural control when learning to manipulate and control tools. Postural control has received comparatively little attention in developmental studies of tool use, future research may benefit from examining how independent as well as integrated changes to postural and manual control support the emergence and refinement of tool use behaviors in infancy and childhood.

Decreased postural stability—quantified by greater postural displacement, faster sway velocity, and shorter TtB—was associated with smoother reach paths. These results provide additional support for the idea that reduced postural stability is not universally associated with degraded task performance (Deprá et al., 2019). Increased postural stability is usually associated with precision demanding suprapostural tasks (Balasubramaniam et al., 2000; Haddad et al., 2010; Stoffregen et al., 2000). However, the fitting task consists of two distinct behavioral components: transporting the object to the opening (i.e., reaching) and holding it in place (i.e., fitting). While increased postural stability is important for the fitting component of the task, decreased postural stability and exploration of failure boundaries may provide people with information about how much postural sway can be tolerated during the reaching component. This information may be useful for establishing whether and to what extent axial and lower limb segments can contribute to transporting the object.

Although decreasing postural stability seem like a counterintuitive strategy for improving manual control, engagement of the trunk and lower limbs reduces the dependence of endpoint motion on variability of the arm segments. Recruiting additional degrees of freedom rather than prioritizing postural stability may enhance certain aspects of suprapostural task performance,

such as reach smoothness. These findings are therefore commensurate with the ideas that standing upright facilitates suprapostural behaviors (Bernstein, 1967; Riccio, 1993; Riccio & Stoffregen, 1988) and “good” postural control permits adaptive modifications of standing balance to meet concurrent task demands, rather than minimizing body movements (Haddad et al., 2013).

5.1.4. Manual control during tool use improved independent of support surface constraints

Increasing the postural constraints by reducing the width of the base of support was expected to negatively impact reach smoothness, particularly during tool use. The current findings are at odds with this expectation because reach smoothness improved in both groups throughout tool use. This indicates that reaches made with tools became smoother and more coordinated with repeated practice, independent of constraints on standing balance.

Postural adaptations were strongly associated with improvements in reach smoothness when standing on the normal base of support, which suggests that changes in postural sway contributed to concurrent changes in manual control. However, postural outcomes were not associated with improvements in reach smoothness when standing on a reduced base of support. This suggests that each group converged on distinct behavioral adaptations that led to concurrent improvements in reach smoothness throughout tool use.

When standing on a normal base of support, postural adaptations appear to provide an effective means of enhancing manual control. By contrast, standing on a reduced base of support limits the effectiveness of this strategy and may have led to the identification of alternative solutions, such as modifying patterns of multi-segment coordination. This possibility could be verified by identifying behavioral modifications underlying the reaching-related improvements between groups and determining whether manual adaptations during tool use were realized by convergent or divergent means.

5.1.5. Contextual switching induces postural ‘resetting’ with and without tools

One unexpected finding was that postural and manual adaptations were found when the task was performed without the tool. Initial and final measures of postural control did not differ between pre- and post-tool-use, indicating a lack of transfer between exposures to the same task

conditions. Postural control also adapted throughout tool use, suggesting that changes in task context induce postural ‘resetting’. In this context, postural ‘resetting’ refers to the adoption of conservative behavioral response following changes to task context to avoid threats to balance or interference with suprapostural performance.

Previously, postural ‘resetting’ has been previously documented following changes to environmental conditions, such as support surface extent (Horak & Nashner, 1986), leading to the adoption of conservative mixed ankle and hip strategies. Over time, people converge on a postural strategy that is best-suited to the current context, leading to improvements in balance. Here, we show that tool-use-induced alterations to arm geometry lead to similar effects. Postural control therefore appears to operate in a state of constant recalibration when switching between environmental and task contexts.

5.1.6. Extended tool use did not produce manual or postural aftereffects

Prior research has documented consistent changes to reach trajectories following extended tool use (Cardinali, Frassinetti, et al., 2009; Cardinali et al., 2012). These findings have led to the proposal that tool-use-induced morphological and functional modifications of the body are rapidly compensated for by the plasticity of the Body Schema—the action-oriented, multisensory, neural representation of the body—to preserve movement accuracy (Cardinali et al., 2016; Cardinali, Frassinetti, et al., 2009; Cardinali et al., 2012). By contrast, in this study, reach smoothness did not differ before or after tool-use, indicating a lack of evidence for tool-use-dependent aftereffects. Our findings demonstrate that the ability to produce smooth reach paths is unaffected by extended tool use and is supported by evidence that reach path characteristics are load-independent (Bock, 1990)—that is, changing the inertial properties of the end-effector has no immediate effects on the reach path. This suggests that a limited number of reach parameters are affected when switching between performing a task with and without a tool.

Previous studies have reported tool-use-dependent aftereffects in a restricted set of movement characteristics related to the end-effector tangential velocity profile, including unnormalized measures of the magnitude and latency of peak acceleration, velocity, and deceleration (Cardinali, Frassinetti, et al., 2009; Cardinali et al., 2012). Latency measures are sensitive to movement duration. Changes to latency measures do not provide univocal evidence for modifications to the Body Schema. For example, people may produce slower movement and

exhibit longer peak velocity latencies to reduce errors while re-acclimating to reaching without the tool. Longer peak velocity latencies following tool use are compatible with the adoption of a behavioral strategy intended to conserve relevant performance variables—similar to the postural ‘resetting’ postulated above.

Although previous studies have only examined tool-use-dependent aftereffects during reaching, there was reason to suspect that similar postural aftereffects may occur following tool use. The premise underlying this expectation was the degree of integration between postural and manual control under various conditions. Because postural control provides support for manual performance, modifications to the arm geometry and controllability during and following tool use were anticipated to manifest in postural outcomes. This study found no evidence of postural aftereffects following tool use. Rapid changes to postural sway occurred during the first trial following tool use, but the direction of change was incompatible with an aftereffect. Furthermore, post-tool-use adaptations to postural sway paralleled those observed before tool use, suggesting that changes in task context elicited behavioral adjustments that were only superficially related to tool use. Together, the current findings suggest that the association between tool use and movement aftereffects is tenuous and requires further investigation.

5.1.7. Limitations

There are several important limitations of the current study. First, it is important to consider how data are sampled in adaptation paradigms where a subset of trials at the beginning and end of adaptation are selected to characterize learning. This is a common procedure in adaptation studies, which normally include hundreds of adaptation trials but substantially fewer baseline and washout trials. However, this means that the trials sampled during adaptation represent a smaller proportion of the total trials compared to baseline and washout. This problem also applies to the present study where the first and last three trials from each condition were submitted to the statistical analyses. Examining the same relative number of trials within each condition could potentially remedy this pitfall. Alternatively, quantifying how unequal sampling influences the interpretation of the results could be valuable for determining whether alternative sampling procedures should be adopted in future studies.

Second, the current analysis does not provide information regarding the timescales of adaptation. Multiple timescales of learning occur in postural-manual tasks (Galgon et al., 2010;

Huys et al., 2003), which is consistent with dynamical theories of learning and behavior change (Newell et al., 2001; Thelen & Smith, 1994). Previous studies have found that relatively fast improvements in manual performance but prolonged postural adaptations throughout learning (Galgon et al., 2010). In this study, improvements in reach smoothness appeared delayed—taking approximately 20 trials—when performing the task with the tool. Postural adaptations appeared to occur over roughly the same timescale. Modeling the postural and manual adaptations—for example, using two-process, state-space models (Smith, Ghazizadeh, & Shadmehr, 2006)—would help to characterize the timescales of adaptation, generate predictions regarding savings and de-adaptation, and further elucidate the neuromotor processes underlying tool use adaptations.

Third, there are limitations on the generalizability of the current findings with respect to tool use. These limitations are not restricted to the present study but extend to many behavioral studies examining tool use. There is a background assumption that behavioral adaptations documented in tool use studies apply across contexts. However, tool use behaviors vary considerably depending on factors such as the task goals and constraints tool, the environmental context, the actor's action capabilities, and the tool properties. This makes it unlikely that many of the behavioral changes found in tool use studies are broadly applicable. For example, the present study highlights the importance of considering postural control for reaching behaviors involving tools. But, the relative significance of postural control in tool use is likely to vary substantially. The present experimental design was selected to emphasize the facilitatory role of postural control for engaging in tool use. This should not however lead to suggestions that specific behavioral modifications are required for successful tool use. With this in mind, it is worth pointing out that the adaptations described in this study may be of limited relevance when examining tool use behaviors in other populations and contexts.

5.1.8. Conclusions

Previous studies have found that reaches made with tools that extend arm length produce changes to free hand reaching (Cardinali, Frassinetti, et al., 2009). This study documented adaptations to postural and manual control during and following an extend bout of tool use. Tool-use-dependent adaptations were not confined to the end-effector. Notable changes adaptations to postural sway were documented before, during, and after tool use. Postural

adaptations were attenuated when the postural constraints of the task were increased, but reach-related adaptations were consistently observed. Changes to body and arm postures during tool use have been interpreted as adaptive modifications to reduce threats to balance and improve the controllability of the tool (Bongers et al., 2004). Here, we provide initial evidence that similar modifications of postural control also occur during tool use and supports improvements in manual performance, particularly during object transport. Constraints on standing balance—reducing the support surface extent—limit task-specific adaptations to standing posture.

5.2. Specific Aim 2

The purpose of this study was to examine postural-manual coupling under different levels of postural constraint before, during, and following an extend bout of tool use. Postural and manual actions exhibit varying degrees of coordination depending on the task demands (Amado et al., 2016; Balasubramaniam, 2013; Cluff et al., 2011; Haddad et al., 2010; Huys et al., 2003). Postural and manual control become decoupled when postural and manual constraints are imposed (Amado et al., 2016) and weaker postural-manual coupling occurs over extended practice (Huys et al., 2003). Tools that extend arm length are challenging to control because of changes to the arm geometry and dynamics as well as the disproportionate influence of proximal joint rotations on the end-effector position. Reducing postural-manual coupling may provide a viable strategy for improving endpoint control during tool use by reducing the influence of postural fluctuations on manual performance. Learning to control the tool may result in further decoupling of postural and manual control with practice (Cluff et al., 2011; Huys et al., 2003). Increasing the difficulty of maintaining standing balance may further weaken postural-manual coupling to prevent immediate threats to balance and disruptions to manual performance (Amado et al., 2016). However, this may impair the ability to make the postural corrections needed to compensate for reductions in manual control when using tools.

5.2.1. Postural-manual coupling during object transport is modulated by postural constraints

Postural-manual coupling was expected to be stronger during object transport as the body and hand were transported towards the target. Stronger coupling was found in the AP direction during object transport, consistent with the study hypotheses. Postural contributions to object transport increased during tool use when standing with a normal base of support. Concurrent increases in coupling were expected to reflect more stable coordination between postural and manual control. However, coupling strength remained constant across experimental conditions. Given these results, it is possible that the degree of coordination between postural and manual control is unaffected by changes in task context associated with tool use.

Another expectation was that postural-manual coupling would increase throughout tool use when standing with a normal base of support due to the adaptive increases in the postural contributions to object transport. However, postural-manual coupling remained steady

throughout the duration of tool use. The invariance of postural-manual coupling within and across conditions may reflect a tendency to maintain coordination between postural and manual behaviors during reaching. This interpretation is partially supported by the concurrent changes in postural displacements and sway velocity, which were hypothesized to maintain the timing of the postural contributions to object transport. The preservation of postural-manual coupling over time may result from these concurrent postural adaptations.

5.2.2. Postural constraints disrupt the timing of postural-manual coordination

Placing constraints on standing balance impedes the ability to generate postural sway while reaching. During tool use, greater postural contributions to object transport occurred when standing with a normal base of support. Reductions to the support surface extent were expected to reduce postural-manual coupling and prevent adaptations over time. Postural-manual coupling was substantially weaker when standing with a the reduced base of support, consistent with previous findings (Amado et al., 2016), and no adaptations were observed throughout tool use. The results of Aim 1 showed that constraints on standing balance prevented postural adaptations, which were associated with improvements in manual control during tool use when standing on a normal base of support. The limitations placed on postural control under this condition were speculatively assumed to have a disruptive effect on postural-manual coordination. We discovered that this was, in fact, the case by performing a secondary analysis examining cross-correlations between the center of pressure and endpoint position.

This analysis confirmed the finding that postural constraints reduced postural-manual coupling independent of tool use. However, by looking at the time-delay between the peak velocity of postural sway and endpoint movement, we found that the timing of postural-manual coordination was substantially perturbed when standing on a reduced base of support during tool use. By contrast, timing remained invariant when standing on a normal base of support, suggesting that postural adaptations to tool use served a secondary function: namely, preserving the coordination between posture and manual control. This suggests that the inability to adapt posture during tool use significantly affects natural patterns of coordination among postural and manual control, especially during tool use, which presents additional challenges.

5.2.3. Increased postural-manual coupling while fitting

Weaker postural-manual coupling was expected when using a tool during fitting because this would theoretically reduce the influence of postural movements on hand position, which is especially important when the precision demands are high and the end-effector controllability is low. However, postural-manual coupling unexpectedly increased during tool use. Stronger ML coupling occurred when standing with a normal base of support, while no changes were found across conditions when the support surface extent was reduced. One possible explanation is that greater ML coupling was tolerated because there were more opportunities to adjust postural sway when standing with a normal base of support, which would allow postural corrections to compensate for end-effector variability.

Stronger AP coupling was observed across groups during tool use. The fitting task constraints are primarily in the frontal plane, whereas AP movements of the block are more tolerable. Increases in AP coupling may have reflected the differential importance of ML and AP manual task constraints. Support for this hypothesis is provided by the observations of substantially lower ML coupling during fitting. This suggests that the ability to decouple postural and manual control may be limited because disturbances along the kinematic chain cannot be completely attenuated. As a consequence, postural-manual coupling may be reduced in directions that have the greatest implications for task performance.

5.2.4. Dynamic modulation of postural-manual coupling when transitioning from dynamic to static postural control

Postural-manual coupling varied throughout the time-course of the fitting task. The coupling strength between the CoP and end-effector position in the ML and AP directions was substantially lower while fitting compared to object transport. Weaker postural-manual coupling may be expected when using a tool and engaging in static postural control, such as during fitting. This would reduce the influence of postural movements on hand position, which is especially important when the precision demands are high. However, stronger postural-manual coupling would be expected during dynamic postural control, such as reaching, when the body and hand are transported to a different configuration. As a result, stronger postural-manual coupling was expected when standing and reaching because both the CoM and hand are transported towards the target (Pozzo et al., 2002).

Interactions between postural and manual control are dynamically modulated to maintain task performance. For example, when balancing a stick on the fingertip while standing, the coupling between postural and manual control varies to prevent postural fluctuations from disturbing the hand while still allowing posture to apply corrections when the stick becomes unstable (Balasubramaniam, 2013; Cluff et al., 2011; Cluff et al., 2012). Similar dynamic modifications of postural-manual coupling were observed as people transitioned from transporting the object (dynamic postural control) to holding it in place (static postural control). Coordinated movements of the body and hand/tool occurred during object transport, but postural and manual behaviors were decoupled while fitting, possibly to reduce the interference of postural fluctuations on manual performance (Amado et al., 2016).

5.2.5. Direction-dependent effects of postural-manual coupling

Direction dependent differences in postural-manual coupling are expected because postural variability may have different implications for manual performance depending on the task demands (Balasubramaniam et al., 2000). For example, during object transport, movement was primarily restricted to the AP direction, leading the body and hand to be directed towards the target object and the opening. Conversely, while fitting, there are physical constraints in the frontal plane to adhere to and looser constraints in the AP direction.

During object transport, postural-manual coupling was substantially stronger in the AP direction regardless of whether the task was performed with or without the tool. The same pattern of results was observed during fitting. However, in this case, weaker coupling in the ML direction suggests that postural fluctuations in the frontal plane are decoupled from manual movements to a greater degree than in the AP direction for a different reason. Frontal plane movements of the end-effector are more likely to lead to fitting errors, while there is more tolerance for AP movements of the block. This suggests that the same pattern of direction-dependent effects can lead to different conclusions if the task constraints are not taken into consideration.

5.2.6. Methodological limitations of assessing postural-manual coupling

The main advantage of average mutual information as a measure of coupling is that it is model-free, meaning that it allows the assessment of linear and nonlinear associations between variables without requiring the distributions or relationships between those variables to be established a priori. There are several important limitations of average mutual information. The primary limitation is that the direction of association cannot be estimated—i.e., are the variables positively or negatively correlated. Quantifying positive and negative associations only makes sense when the relationship between variables is linear because the direction of association for nonlinear relationships is not fixed. This makes it difficult to assess how changes in one variable are related to changes in another variable.

Another limitation of average mutual information is that it does not indicate the directionality of the coupling (i.e., what direction the information is flowing), which can be quantified using transfer entropy (Schreiber, 2000). This prevents the assessment of which process might be guiding or directing coordination. This becomes particularly important when there are concurrent changes in postural and manual control and the source of these changes cannot be determined. For example, it could be useful to assess whether changes in postural control driving changes in manual control or vice versa.

One final limitation is that average mutual information assesses the dependence between variables at the same point in time. The dependence may change as a function of time lag, possibly due to delays in information transmission across subsystems. Time-lagged average mutual information can be quantified but it still only measures dependence at one point in time. To circumvent this issue, researchers have turned to detrended cross-correlation analysis (Yuan et al., 2015) to examine changes in coupling across different timescales, which could prove particularly useful for distinguishing coupling due to fast-acting mechanical effects versus slower-acting motor control processes. But this method has not been applied to postural and manual control and was therefore avoided until its strengths and limitations have been assessed.

5.2.7. Conclusions

The degree of coordination between postural and manual control during object transport was unaffected by changes in task context associated with tool use. When standing under normal

conditions, adaptations to postural sway serve to maintain the temporal coupling of postural and manual behaviors during tool use. Perturbing standing posture disrupted postural-manual coordination, especially during tool use. This highlights the importance of postural variability, which was reduced in when standing on a narrow support surface, in in maintaining coordination between postural and focal movements during tool use. Overall, the present findings provide further support for the facilitatory role of postural control for supporting concurrent tool use actions.

5.3. Specific Aim 3

Standing postural stability is achieved by interactions among multiple body segments (Hsu et al., 2007). When standing and reaching, both the lower and upper body ensure postural stability and transport the hand to the target (Kaminski, 2007; Kaminski & Simpkins, 2001), indicating that available degrees of freedom are recruited and exploited in a task-dependent manner (Ricchio, 1993; Ricchio & Stoffregen, 1988). Multi-segment coordination may therefore play an important role in the maintenance of postural stability and suprapostural performance during tool use.

UCM analysis is a popular technique for examining how multiple body segments are coordinated to stabilize task-relevant performance variables has been investigated using UCM analysis (Scholz & Schoner, 1999). UCM analysis has been applied to many different tasks: pointing (Tseng et al., 2003), reach-to-grasp movements (Jacquier-Bret et al., 2009), pistol-shooting (Scholz, Schoner, Latash, 2000), sit-to-stand movements (Scholz & Schoner, 1999), and standing posture (Hsu et al., 2007). This work has recently been extended into the domain of tool use (Valk et al., 2016; van der Steen & Bongers, 2011).

Tools introduce a disturbance to the geometry and dynamics of the arm, which has the potential to affect postural stability and manual control. To date, no studies have examined how multi-joint coordination facilitates postural stability and suprapostural performance during tool use. The purpose of this study was to determine how multi-segment coordination supports postural control and suprapostural task performance under normal and challenging postural conditions with and without tools.

5.3.1. Postural constraints prevent modifications of multi-segment coordination contributing to manual control during tool use

Throughout tool use, multi-segment covariation leading to no changes in the AP and vertical end-effector positions systematically decreased over time when standing with a normal base of support while there were no changes to endpoint variability. These adaptations were not observed when the support surface extent was reduced, providing evidence that increasing the constraints on standing balance attenuates multi-segment adaptations to manual control when using a tool. These findings indicate the importance of having the opportunity to engage in

postural sway and recruit multiple degrees of freedom when learning to accommodate movements to a tool.

The reductions in joint angular covariation during in the AP direction may have occurred because the fitting task demands require controlling the ML and vertical directions. These changes reduced the stability of the endpoint in the AP direction, which suggests that participants were sensitive to the looser task constraints in this direction. By reducing the endpoint stability in directions that had less influence on task performance, participants may have been saving energy or channeling motor variability in other directions to facilitate the maintenance of standing balance or ML and vertical endpoint control.

By contrast, systematic reductions in vertical endpoint variability were observed in the Normal BoS group throughout tool use. These changes lead to increased vertical endpoint stability during tool use, which was entirely driven by adaptations in the Normal BoS group. These results are consistent with previous findings of reductions in both variance components when reaching in novel, velocity-dependent force fields (Yang et al., 2007). However, there were no changes in either variance component in the Reduced BoS group. This further highlights the importance of considering postural control when studying tool use behaviors because reductions in balance interferes with multiple domains of adaptation—postural sway, postural-manual coupling, and multi-segment coordination.

5.3.2. Postural-manual stability is enhanced in task-relevant directions

Previous studies show that joints of the lower and upper body contribute to center of mass stabilization during standing (Hsu et al., 2007). When the postural constraints are increased by having people stand on a reduced base of support, increases in center of mass motion (i.e., V_{ORT} variability) are accompanied by concurrent increases in joint angle variability that leave the stability of the center of mass position unchanged (Hsu et al., 2014). These findings were documented in the present study with increases in V_{UCM} counteracting increases in V_{ORT} to retain similar levels of postural and manual stability during tool use, providing further evidence that multiple body segments are implicated in standing postural control.

When manual task constraints are increased, in this case, constraints associated with wielding a tool, increases joint angular variability contributes to increased endpoint stability in task-relevant directions. These changes may be supported by the invariant of postural stability

across task contexts, specifically in the same task-relevant directions. The AP position of the center of mass was not stabilized while fitting in either group. This suggests that postural variability was tolerated in directions that were less likely to influence task performance. By contrast, increases in the vertical motion of the center of mass while fitting using a tool were offset by increases in joint angular variability, leading to invariant postural stability across conditions. These findings are supportive of the idea that rather than minimizing body movements, the goal of postural control is to permit adaptive modifications to the interactions among body segments to maintain upright stance while meeting concurrent task demands (Bernstein, 1967; Riccio, 1993; Riccio & Stoffregen, 1988) .

5.3.3. Considerations for UCM Analysis in Learning and Adaptation Paradigms

UCM analysis is a powerful analytical tool for examining how the variability of multiple degrees of freedom is structured across repetitions of a task, which provides insights into whether hypothesized performance variables are stabilized. There is, however, an important limitation of UCM analysis with respect to learning and adaptation paradigms. One assumption of UCM analysis is that the mean of the performance variable is stabilized over multiple repetitions of the behavior—i.e. it has reached steady-state. Inherent in this assumption is that performance variables should not exhibit systematic trends over time. For example, if a hypothetical performance variable exhibited a linear drift over trials, then it would be misleading to interpret that the variable was stabilized. By definition, a process that exhibits drift over time is non-stationary and, at least in the short term, cannot be stable.

This was a particularly challenging problem in the context of the present study. Systematic changes to the CoP and CoM displacement occurred throughout all experimental conditions. The current analysis was limited to the fitting portion of the task to avoid this issue. Had the UCM analysis been applied over windows of 20 trials during object transport, the significant and systematic changes to postural displacements would have been erroneously treated as a steady state. The conclusions regarding postural stability might, therefore, have been misinterpreted as evidence that the CoP or CoM position was stabilized over successive trials when the opposite was true.

What are some ways around this problem? Learning paradigms are less susceptible to this steady-state issues. For example, Yang and Scholz (2005) studied changes to joint covariation to

stabilize several task-relevant performance variables during a disk throwing task. Participants performed 150 trials per day over a five-day period—leading to 750 training trials in total. Pre- and post-learning measures were obtained during relatively steady-state windows to quantify how performance variables were stabilized after learning. This approach may be viable in situations where learning or adaptation takes place over hundreds of trials. However, in the present study the postural adaptations appear to reach asymptote—although this was not quantified—within 20-40 trials. This makes it much more challenging to apply UCM analysis with confidence.

One possible methodological adjustment to accommodate non-steady state behavior would be to develop a within-trial UCM analysis (Scholz, Kang, Patterson, & Latash, 2003). UCM analysis examines variability across trials, but there are behaviors that might allow variability to be examined within trials based on the degree of variation among the degrees of freedom. For example, a balance board tuned to continuously disturb upright balance (Cruise et al., 2017) could induce sufficient joint angular variation over extended periods (e.g., 1-2 min) that UCM analysis could be conducted. However, the feasibility of this approach would be limited for many other categories of tasks, including those examined in this dissertation.

5.3.4. Limitations

There are several important limitations of this study. First, the UCM analysis can examine whether single or multiple performance variables are stabilized. For example, in this study, UCM analysis was applied to the AP and vertical CoM position separately, which allows independent inferences to be drawn about the degree to which joint angular variation stabilized a performance variable. This approach is useful when there is expectation of directional differences in the degree of stabilization. In this study, we expected differences because the vertical CoM position is maintained to prevent the lower limb collapse. However, the AP CoM position has more freedom to vary because the fitting task constraints are primarily in the ML and vertical directions. Alternatively, if the research question is concerned with the overall stability of a performance variable that has multiple components, the UCM analysis can be applied to those components in conjunction. For example, if the research question is concerned with whether the two-dimensional, sagittal plane CoM position is stabilized by joint angular variation, then the latter approach is more appropriate. However, it is important to recognize that

any inferences drawn are only applicable at this coarser level. This is because there is no means to decipher whether one performance variable was stabilized more than another or whether the components of a performance variable were differentially stabilized. But, a more coarse grained analysis would have provided information about whether the CoM position *and* hand position are simultaneously stabilized by joint angular variation, which would provide information about the nervous system's ability to control multiple task relevant variables at the same time. The results of this study, in their current form, cannot confirm or deny this hypothesis.

The discussion above highlights a second limitation, namely that the UCM analysis was limited to the sagittal plane. The fitting task requires modulating the block position in the vertical and ML directions with less stringent constraints on AP movement. The UCM analysis was limited to the sagittal plane because joint angle variability primarily occurred in the sagittal plane while performing the fitting task. However, important information regarding postural and manual control in the frontal plane, particularly during the fitting phase, may have been lost by overlooking this dimension of performance. To address this limitation in the future, there are two viable options: 1) add a separate frontal plane model or 2) create a three-dimensional model. Frontal plane models have been used to study foot placement variability during walking (Krishnan, Rosenblatt, Latash, & Grabiner, 2013; Rosenblatt, Hurt, Latash, & Grabiner, 2014; Rosenblatt, Latash, Hurt, & Grabiner, 2015). These models were, however, limited to the lower extremities and would be inappropriate for the fitting task. Frontal plane movements would require a more complex model to characterize ML endpoint or CoM motion and could be inherently difficult to formalize because sagittal plane movement—for example, elbow flexion—could lead to changes in frontal plane endpoint positions. Furthermore, changes to projected segment lengths—especially for the reaching arm—would vary substantially throughout the movement. The model would need to allow segment lengths to vary, which would further complicate the model. A better, but no less challenging, option would be to avoid two-dimensional models and create a full body, three-dimensional model that incorporated all possible joint rotations without allowing segment lengths to vary. This option makes the most sense given the rigid body assumptions of collecting movement kinematics and three-dimensional nature of the movements required to complete the fitting task.

A third limitation follows from the point made above regarding changes to segment lengths when projecting joint centers into the sagittal plane. The UCM analysis was restricted to

the fitting stage of the task. The geometric model included a scapular segment, which is common in studies using UCM analysis to examine standing balance (Hsu et al., 2014; Hsu & Scholz, 2012). Due to significant scapular protraction, there were substantial variations in segment length, indicating out-of-plane rotations between the shoulder joint and C7 during the transport stage. There was also substantial range of motion—sometimes more than 180°—that varied within and across participants. This produced extreme variation in joint angle variability that influenced the UCM analysis, which partitions this variance into the UCM and ORT components. For example, one trial could exhibit 10 deg² of total joint angle variability per degree of freedom while a subsequent trial could exhibit 7500 deg². These variations were not limited to certain participants, which prevented the analysis from proceeding on a subset of participants. As a result, this portion of the analysis was omitted due to the difficulty of interpreting the findings. Similar to above there are two possibilities to address this issue moving forward: 1) find a more appropriate two-dimensional, sagittal plane model or 2) adopt a three-dimensional model.

Finally, there are important limitations on generalizability worth considering. The goal of the study was to identify how the underlying organization of movement variability was adapted to accommodate performing a precision manual task with a tool. The fitting task is by no means the only type of task for which a tool that extends arm length is used. Even if the task remained the same, the specific constraints of the task would likely determine the movement characteristics. For example, the results would likely be sensitive to changes in the reach distance, target size, or tool length. Caution should be taken when extrapolating these findings to different task and environmental contexts. Moreover, the organization of tool use movements is known to change throughout development (Kahrs, Jung, & Lockman, 2012). Therefore, the result that seems most likely to generalize to other situations is that whole-body, multi-segment coordination plays an important role in skillful tool use, particularly when the endpoint needs to be stabilized.

5.3.5. Conclusions

In summary, changes to multi-segment coordination support increases in manual stability during tool use. Importantly, these changes were inhibited by postural interference associated with reducing the support surface extent. Furthermore, adaptations to multi-segment coordination

supported postural stability and endpoint control in task-relevant dimensions while allowing motor variability to accrue in other dimensions. These results provide additional evidence of the importance of postural control, specifically multi-segment coordination, for engaging in tool use actions.

CHAPTER 6 – GENERAL DISCUSSION

Tool use actions have primarily been studied by examining posture and manual control separately. This dissertation is a first attempt at developing an understanding of how postural-manual control supports the integration of tools into goal-directed actions. The goals of the dissertation were to 1) characterize adaptations to postural control over time when performing a manual task with a tool under different levels of postural constraint and how these adaptations relate to manual task performance, 2) postural-manual coupling under different levels of postural constraint during and following an extend bout of tool use, and 3) determine how multi-segment coordination supports postural stability and suprapostural task performance under different levels of postural constraint during and following an extend bout of tool use.

Tool-use-dependent adaptations are not confined to the end-effector. Postural control plays an important role in facilitating changes to manual performance over repeated practice with a tool. Postural adaptations were attenuated when the postural constraints of the task were increased, but reach-related adaptations were consistently observed and supported by changes to multi-segment coordination when postural sway was not tolerable. This suggests that postural variability is crucial for identifying novel behavioral solutions when changing between task contexts while providing a platform for suprapostural performance. Altering the arm geometry and dynamics by engaging in tool use appears to serve as a rate-limiting factor on postural and manual adaptations, which is an area for future research. Interactions between postural and manual control were dynamically modulated when transitioning from object transport to fitting. This suggests that posture and manual control were more coordinated during object transport, but became decoupled while fitting, possibly to reduce the interference of postural fluctuations on manual performance.

These adaptations highlight the flexibility of the neuromuscular system in recruiting and exploiting available degrees of freedom to maintain postural stability and task performance when engaging in novel postural-manual tasks involving tools. Furthermore, this dissertation highlights the importance of considering postural control when studying tool use behaviors because of interactions across in multiple levels of motor behavior—postural control, manual control, postural-manual coupling, and multi-segment coordination.

CHAPTER 7 – FUTURE DIRECTIONS

7.1. Reducing postural interference

Increasing the constraints on standing posture by reducing the width of the base of support interfered with postural adaptations during tool use. When learning to control the tool without postural constraints, adaptations to postural control were strongly associated with concurrent improvements in manual control. These findings are consistent with the main thesis of the dissertation: skillful tool use is built on a foundation of whole-body postural coordination. When the difficulty of maintain standing balance is increased, different strategies may be required to preserve task performance. A possible follow-up study could exploit the phenomenon of stochastic resonance to reduce the influence of more challenging postural constraints (i.e., the reduced base of support) on the rate of adaptation and de-adaptation, as well as task performance.

Noise is inherent in biological systems, including the human neuromuscular system. Recently, there has been a growing interest in augmenting sensorimotor function using subthreshold noise, also known as stochastic resonance (SR). SR originally referred to the enhancement of subthreshold periodic signals in a nonlinear dynamical system due to the presence appropriately scaled noise (Benzi, Sutera, & Vulpiani, 1981). For single unit systems, the optimum magnitude of the noise is signal-dependent (Wiesenfeld, Pierson, Pantazelou, Dames, & Moss, 1994). However, in complex nonlinear systems broadband noise can enhance the detection of subthreshold signals, thereby reducing the effective threshold, without interfering with the ability to detect suprathreshold signals (Collins, Chow, Capela, & Imhoff, 1996; Collins, Chow, & Imhoff, 1995a, 1995b). Both internal and external sources of noise can therefore enhance the bandwidth of sensory function, acting as a “stochastic facilitator” (McDonnell & Abbott, 2009).

SR has been widely documented in natural phenomena, such as climate (Benzi et al., 2002), animal feeding behaviors (Greenwood, Ward, Russell, Neiman, & Moss, 2000; Russell, Wilkens, & Moss, 1999), neural networks (Bulsara, Jacobs, Zhou, Moss, & Kiss, 1991; Douglass, Wilkens, Pantazelou, & Moss, 1993), and somatosensory function in humans (Collins et al., 2003; Dhruv, Niemi, Harry, Lipsitz, & Collins, 2002; Liu et al., 2002). The utility of SR in

standing posture is of both theoretical and practical significance given the prevalence neuromuscular, autoimmune, and metabolic disorders that affect sensory function, balance, and mobility.

Pioneering research demonstrates that subthreshold vibrotactile stimulation of the plantar surface of the feet reduces postural sway in healthy young adults (Priplata et al., 2002), older adults (Costa et al., 2007; Lipsitz et al., 2015; Priplata, Niemi, Harry, Lipsitz, & Collins, 2003), and persons with peripheral and central sensorimotor deficits (Priplata et al., 2006; Zwaferink et al., 2018). Noise-enhanced changes to balance are thought to be mediated by changes to the temporal structure of postural dynamics (Costa et al., 2007; Kelty-Stephen & Dixon, 2013). These findings demonstrate that SR may be exploited for combatting age- and disease-related changes to sensory function that affect balance and mobility. In the context of this dissertation, if the additional postural challenge associated with reducing the base of support interferes with tool use adaptations, vibrotactile stimulation of the foot soles may provide a means of reintegrating postural and manual control during tool use to combat postural interference.

7.2. Manipulating Adaptation and De-Adaptation

Computational motor control theories have identified two independent forms of memory associated with learning new sensorimotor mappings (e.g., adapting to tool use, force fields, or visuomotor rotations): aftereffects, which refers to the persistence of an adapted state during de-adaptation (Yamamoto, Hoffman, & Strick, 2006), and savings, which refers to an increased rate of re-adaptation (Krakauer, Ghez, & Ghilardi, 2005). Previous research has suggested that tool use adaptations, specifically changes to characteristics of the velocity profile following a period of tool use, persist for extended periods of time despite no observations of adaptation during tool use training (Cardinali, Frassinetti, et al., 2009; Cardinali et al., 2012). Movement aftereffects following tool use training reflect resistance to returning to the unperturbed state, i.e. reaching without the tool.

De-adaptation was traditionally assumed to be related to the consolidation of internal models, which become more stable with the passage of time, even in the absence of further practice (Brashers-Krug, Shadmehr, & Bizzi, 1996; Shadmehr, Brandt, & Corkin, 1998; Shadmehr & Holcomb, 1997). This would suggest that more practiced movements, such as unperturbed reaching, should be associated with the faster rates of de-adaptation. P. R. Davidson

and Wolpert (2004) examined reaching adaptations to an initial velocity-dependent force field and the subsequent de-adaptation to a weaker, novel force field or a null field. If de-adaptation is tied to the strength of internal model, the de-adaptation rate should be faster for the null field than the novel field. Faster de-adaptation was found for the novel force field, indicating that the magnitude of the perturbation, more than the familiarity of the de-adapted state, determines the de-adaptation rate.

Tools that extend arm length provide a similar perturbation due to the changes in the forces and moments required to grasp and manipulate the object. The strength of the perturbation is related to the inertial properties of the tool (i.e., mass distribution and geometry). Tools of different lengths are hypothesized to have different effects on motor adaptations. Based on the findings described above, faster rates of adaptation and de-adaptation may be observed for shorter tools due to a reduction in the forces and moments required to hold and manipulate the object. For example, faster adaptations to the straightness or stability of the tool tip may occur for a tool of length $l/4$ versus $l/2$, where l is the length of the dominant arm.

This experiment could be conducted between- or within- participants. A within-participants design could be accommodated by reducing the baseline and tool use training periods based on the results of Study 1. In the first session, participants would perform a baseline No-Tool condition, a Tool condition (either $l/4$ or $l/2$), and washout No-Tool condition. A 30-min break between sessions would be enforced to minimize carryover. In the second session, participants would perform a baseline No-Tool condition, a Tool condition (either $l/4$ or $l/2$), and washout No-Tool condition. Tool length presentation would be counter-balanced across participants. The rate of adaptation and de-adaptation for various movement variables would serve as the primary outcomes.

7.3. Shifting the point of control

Tool use requires the detection of information relating the physical properties of objects to motor abilities (i.e., object affordances) and how objects can be used to interact with the environment (i.e., object-object affordances). People initially, and sometimes ineffectively, rely on visual information to estimate the appropriate grip and lift forces when manipulating novel objects (Baugh, Kao, Johansson, & Flanagan, 2012; Flanagan & Beltzner, 2000). Estimation errors are rapidly compensated as people learn object dynamics, sometimes after a single trial

(Gordon, Westling, Cole, & Johansson, 1993). However, re-adaptation is necessary when lifting the same object from different grasp locations due to differences in the object dynamics, such as the mass distribution relative to the wrist joint (Fu & Santello, 2012, 2014).

Similar adaptations occur when different points on an object need to be controlled while grasping the same location (Heald, Ingram, Flanagan, & Wolpert, 2018; Proud et al., 2019). Tools often have multiple locations that can be used to interact with objects: the face of a hammer is commonly used to drive in nails whereas the claw is used to dislodge them. In some situations, the point of control may change throughout an action. For example, drinking a pint of beer may initially require controlling the nearest edge of the rim as the glass is transported to the mouth and the base when returning it down on the table. This ability to shift the point of control from one position to another is necessary for tool use where the end-effector moves from the body to an object (Arbib et al., 2009). Different parts of the body can serve as the end-effector depending on the task demands—known as motor equivalence (Kelso et al., 1998; Lashley, 1930; Wing, 2000). For example, a person can use their hand, elbow, or another body part switch on a light. Importantly, this indicates that the ability to shift the point of control is not unique to tool use and suggests that the same mechanism(s) may play a role in goal-directed actions performed with and without tools.

Force-field adaptation studies using a velocity-dependent force to perturb reaching show that the neuromuscular system gradually learns to counteract the novel dynamics (Shadmehr & Mussa-Ivaldi, 1994). However, the ability to counter a similar force field acting in the opposite direction is limited, even when visual cues are provided (Gandolfo, Mussa-Ivaldi, & Bizzi, 1996; Howard, Wolpert, & Franklin, 2013). A recent study examined how people adapt reaching movements when separate points of control are associated with different dynamics while maintaining the same grasp location and producing the same movements (Heald et al., 2018). A planar robotic manipulandum integrated with a virtual-reality system was used to link movements of a rectangular virtual object and the hand. The object contained three possible control points: left, right, and center. The left and right points of control were associated with opposing viscous curl fields. One group made straight reaches to move either the left or right point of control to its corresponding target. The targets provided a visual cue about the direction of the curl field. A second group controlled the center point of control while being exposed to the same opposing viscous curl fields. All conditions required the same movement distances and

directions. Reaching adaptations only occurred when separate points of control were associated with different dynamics. This finding is consistent with previous observations that the ability to learn opposing dynamics is limited even when visual cues are provided (Gandolfo et al., 1996; Howard et al., 2013).

In a follow-up experiment, the second group made reaches by controlling the left and right points of control with similar curl field dynamics. As expected, the group exposed to similar curl fields learned to better compensate for the perturbation and showed faster adaptation rates. Like the previous experiment, the group exposed to different curl fields still learned to compensate for the perturbation when the opposing dynamics were associated with different points of control. De-adaptation was studied by separately examining reaches made with each point of control in the null field. Interestingly, distinct de-adaptation processes were observed when they differed between points of control whereas a single de-adaptation process was observed when the points of control were associated with similar dynamics. These findings demonstrate that people are sensitive to locational differences in the dynamics of objects. Furthermore, adaptations to changes in the control dynamics between locations can occur independently. In the study described above, participants were explicitly instructed to control different visible points on the object. More recently, Proud et al. (2019) demonstrated that implicitly specified points of control also facilitate learning to compensate for different dynamics.

One of the limitations of these studies is that there is no direct assessment of whether one location is being controlled relative to another (Proud et al., 2019). The UCM framework can provide insights into what movement variables are stabilized by examining the variability of the degrees of freedom contributing to an action (Scholz & Schoner, 1999). Multiple movement variables may be stabilized depending on the performance context (Hsu et al., 2007; Latash, Scholz, Danion, & Schoner, 2001; Scholz & Schoner, 1999) and the degree of stabilization has been associated with the precision demands of the task (Rosenblatt et al., 2014; Rosenblatt et al., 2015).

Follow-up experiments could examine whether using different locations on the same tool to accomplish the same task leads to stabilization of the trajectory of the effective part of the tool relative to the secondary location. Alternatively, changes to the movement—measured in terms of reach trajectories, postural dynamics, or multi-segment coordination—may reflect adaptations that occur as the point of control is switched from one location to another. Participants could

perform multiple repetitions of a tool use task and subsequently perform the same task using a different location on the tool. Additionally, we could test whether similar adaptation processes—assuming they are observable—occur when shifting the point of control between locations on the body. If the adaptations observed when switching the point of control on a tool mirror those observed when switching the point of control on the body (e.g., from the hand tip to wrist or forearm), then this would provide some initial support that the mechanism(s) contributing to the flexible control of different body parts are involved in the flexible control of tools (Arbib et al., 2009).

APPENDIX A. SCREENING FORM

Inclusion criteria:

Adult between the ages of 18 and 30 years.

Exclusion criteria:

- Do you have normal or corrected-to-normal vision?
Y N
- Do you have normal or corrected-to-normal hearing?
Y N
- Do you have any neurological impairments?
Y N
- Do you have any skeletal impairments?
Y N
- Do you have any muscular impairments?
Y N
- Do you have a history of orthopedic injuries?
Y N

If so, what? _____

- Do you have ideomotor or ideational apraxia?
Y N
 - Are you experiencing any pain?
Y N
-

If the person reports impairments for any exclusion criteria, they are not eligible to participate in the study. Exclude if the person has previous or current orthopedic injuries that could affect balance or prehension.

Is this person eligible to participate?

APPENDIX B. TOOL DESIGN

Anthropometric measures were based on estimates found in (Tilley et al., 2001)(Tilley et al., 2001)(Tilley et al., 2001)(Tilley et al., 2001)Tilley, Drefuss, and Wilcox (2001). Hand width was defined as the horizontal distance between the 2nd and 5th metacarpal heads. To accommodate a variety of hand widths, the handle length on all tools is 10 cm (Table B.1).

Participants will adjust their grasp to align the lateral edge of the palm with the top of the handle.

Arm length was defined as the distance between acromion process and 3rd metacarpophalangeal joint when the elbow is fully extended. Based on the normative arm length measures, tool lengths—excluding the handle—will range from 25–40 cm by 1 cm (Table D.2). Participants will use the tool that that best approximates 50 % of arm length.

Table B.1. Normative hand width measures for men and women.

Percentile	1 %	50 %	99 %
Male	7.87 cm	8.64 cm	10.16 cm
Female	6.35 cm	7.62 cm	8.64 cm

Table B.2. Normative arm length measures for men and women.

	Percentile	1 %	50 %	99 %
Male	Upper Arm	*	27.94 cm	31.24 cm
	Forearm	23.36 cm	25.65 cm	27.43 cm
	Wrist-Metacarpal	10.16 cm	11.68 cm	12.19 cm
	Total Length	*	65.27 cm	70.86 cm
Female	Upper Arm	23.37 cm	26.42 cm	27.94 cm
	Forearm	21.08 cm	23.37 cm	24.64 cm
	Wrist-Metacarpal	9.40 cm	10.67 cm	12.19 cm
	Total Length	53.85 cm	60.46 cm	64.77 cm

* The value reported in Tilley (2001) was misprinted.

Tools were constructed from wooden dowels—3.175 cm in diameter—cut to lengths ranging from 35 cm to 50 cm. Dowel measurements are presented in Table B.3. The bottom 10 cm of each tool was wrapped in black tennis overgrip tape. A neodymium magnet—3.175 cm in diameter and 0.4 cm thick—with a countersunk hole was attached to each tool tip. Each magnet and screw weighs 35 g. To find the CoM of the tool, the wooden dowel was assumed to have constant density. The estimated range of densities is shown in Table B.3. For a cylinder of uniform

density, the CoM can be found by taking the ratio of the moment about the origin—defined as the handle end of the tool—to the total mass of the cylinder, m . Given uniform density, ρ , $m = \int_0^L \rho dx = \rho x|_0^L = \rho L$, where L is the length of the cylinder, and $M_0 = \int_0^L \rho x dx = \frac{\rho x^2}{2} |_0^L = \frac{\rho L^2}{2}$.

The CoM is then defined as $\bar{x} = \frac{M_0}{m} = \frac{\frac{\rho L^2}{2}}{\rho L} = \frac{L}{2}$.

Table B.3. Dowel measurements.

Length (cm)	Volume (cm ³)	Mass (g)	Density (g/cm ³)
10	79.17	45	0.57
35	277.11	144	0.52
36	285.02	155	0.54
37	292.94	170	0.58
38	300.86	183	0.61
39	308.77	196	0.63
40	316.69	199	0.63
41	324.61	200	0.62
42	332.53	185	0.56
43	340.44	188	0.55
44	348.36	195	0.56
45	356.28	188	0.53
46	364.20	177	0.49
47	372.11	185	0.50
48	380.03	208	0.55
49	387.95	211	0.54
50	395.87	227	0.57

With the addition of the overgrip tape and magnet there is a nonuniform density with three discrete sections to consider. Due to the discontinuity of the density function, $\rho(x)$, \bar{x} can be found as the weighted average of the length of each section based on the mass distribution. The three sections to consider are (1) the handle, (2) the tool body, and (3) the magnet.

The length of the first and last sections are $L_1 = 10$ cm and $L_3 = 0.4$ cm. The length of the second section varies with rod length, $L_2 = L - L_1 = L - 10$ cm. Unlike the magnet, the mass of the handle and tool body vary. The handle has a mass $m_1 = \rho_i \pi r^2 10 + m_g$, where ρ_i is the density of the dowel, r is the radius of the cylinder, and m_g is the mass of the handle grip. The tool body

has a mass $m_2 = \rho\pi r^2(L - L_1) = \rho_i\pi r^2 L_2$. Density values, ρ_i , were obtained from Table B.3. The magnet has a mass $m_3 = 35 \text{ g}$.

To solve for the CoM location, the section masses relative to the total mass are used as weighting factors (Eq. B.1). The estimated CoM locations and tool masses by length are presented in Table B.4. The CoM position is approximately constant for tools ranging from 35–50 cm.

$$\bar{x} = \left(\frac{m_1}{\sum m_i}\right)\left(\frac{L_1}{2}\right) + \left(\frac{m_2}{\sum m_i}\right)\left(L_1 + \frac{L_2}{2}\right) + \left(\frac{m_3}{\sum m_i}\right)\left(L_1 + L_2 + \frac{L_3}{2}\right) \quad \text{Eq. (B.1)}$$

Table B.4. Tool mass and CoM location by length.

Tool Length (cm)	CoM Position (cm)	CoM Position (% of length)	Tool Mass (g)
10	7.14	0.69	85
35	20.53	0.58	184
36	20.93	0.58	195
37	21.30	0.57	210
38	21.70	0.57	223
39	22.11	0.56	236
40	22.64	0.56	239
41	23.20	0.56	240
42	23.94	0.56	225
43	24.47	0.56	228
44	24.94	0.56	235
45	25.60	0.56	228
46	26.33	0.57	217
47	26.78	0.56	225
48	27.03	0.56	248
49	27.56	0.56	251
50	27.93	0.55	267

APPENDIX C. APPROVED CONSENT FORM

RESEARCH PARTICIPANT CONSENT FORM

Adaptations to Posture and Movement Associated When Using a Hand-Held Tool

Jeffrey M. Haddad, PhD

Health and Kinesiology

Purdue University

Please take time to review this information carefully. This is a research study. Your participation in this study is voluntary which means that you may choose not to participate at any time without penalty or loss of benefits to which you are otherwise entitled. You may ask questions to the researchers about the study whenever you would like. If you decide to take part in the study, you will be asked to sign this form, be sure you understand what you will do and any possible risks or benefits.

What is the purpose of this study?

Tool use is a common activity in daily life. Even though adult humans are expert tool users, there is little understanding of how movements are adapted to accommodate tools with such ease. We would like to better understand how people adapt their movements when using tools while standing. We first plan to conduct this paradigm in younger adults. The data we obtain will help us develop hypotheses about declines in balance and manual function in atypically developing children, older adults, and persons with neurological impairments. You are being asked to participate in this study because you fit within the age-group of participants we plan to recruit. We expect this project to be completed within 12 months. In this study you perform a precision reaching task with and without a tool. The reaching task consists of acquiring and transporting a block to an opening while standing. We will measure various aspects of your movement (described below) and examine differences in balance and manual function between conditions with and without the tool, as well as over successive trials of tool use. We expect to enroll 50 participants in the study.

What will I do if I choose to be in this study?

Upon entering the lab, an experimenter will first ask you if you have any diagnosed medical issues that influence balance, manual function, vision, or tool use (e.g., ideational or ideomotor apraxia). Your age, height, arm length, foot length, hand dominance, and weight will be obtained. An experimenter will then attach retro-reflective markers to your head, arms, trunk, and legs. These markers, visible by the motion capture system in the laboratory, will record movements of your body segments. Next, the researcher will adjust the experimental setup to your body dimensions. You will be assigned two tools: one with a handle that fits in your palm (No Tool condition) and one that extends from your hand by 50% of your arm's length (Tool condition). You will use these tools to transport a block from a pedestal to a target. The block opening will be positioned 133% of your arm length or tool + arm length. You will then stand on a support surface placed on top of a force plate, which measures body movements.

The experiment will consist of four phases. During the first phase, you will perform the No Tool condition 30 times to familiarize yourself. During the next phase, you will perform the No Tool condition an additional 30 times. During the next phase, you will perform the Tool condition for 90 trials. During the final phase, you will again perform the No Tool condition 30 times. Each trial takes approximately 5-10 s. Thus, you will perform 180 total trials. Two-minutes seated rest will be provided for every 10 trials. All data will be collected in the Biomechanics Lab (LAMB 026).

How long will I be in the study?

You will participate in a single 120-minute session. There will be 15 min of preparation, 15 min of setup, and 75 minutes for the experimental tasks described above. Rest breaks will be provided throughout the session.

What are the possible risks or discomforts?

The risks encountered in this study are no greater than those encountered in daily life. The potential risks are primarily physical in nature. In this study, you will perform reach-to-grasp actions with and without a hand-held tool while standing. The risk for injury associated with wielding the tool is minimal due to its light weight (0.5 kg). The risk of losing balance or falling is no higher than other routine activities of daily living, such as standing and putting dishes away. If you are randomly assigned to the group that must stand on a narrow support surface there is an elevated risk of falling. However, the platform is designed to tip as little as possible, to reduce this risk. There is a risk of skin irritation from the Velcro that will be wrapped around each body segment. There is a small risk that a breach of confidentiality is may occur; however, safeguards are in place to help minimize this risk (see the Confidentiality section below).

Are there any potential benefits?

This research will provide insights into how individuals coordinate balance and manual actions while using tools. The findings from this research may ultimately lead to the creation of assistive devices and rehabilitative paradigms to improve balance and manual function in children, older adults, and individuals with neurological impairments.

Will I receive payment or other incentive?

You will receive 1% extra credit towards your final grade in the HK class you were recruited from. An additional 10 cents will be rewarded per trial based on performance up \$10. If you choose to drop out at any point, your compensation will be pro-rated based on the amount of time you have committed (e.g., 1 h = 0.5 %) but will retain any money earned based on performance.

Will information about me and my participation be kept confidential?

The project's research records may be reviewed by departments at Purdue University responsible for regulatory and research oversight. Your identity will remain strictly confidential. Breach of confidentiality is a risk related to research. Although this risk is a possibility, safeguards are in place. The data from this study will be retained indefinitely as encrypted digital files stored on a password protected digital storage system for future research purposes. Only Dr. Haddad and his research associates will have access to the data.

What are my rights if I take part in this study?

Your participation in this study is voluntary. You may choose not to participate or, if you agree to participate, you can withdraw your participation at any time without penalty or loss of benefits to which you are otherwise entitled. If you choose to withdraw from the study, you will receive compensation proportional to the amount of time you have committed.

Who can I contact if I have questions about the study?

If you have questions, comments or concerns about this research project, you can talk to one of the researchers. Please contact Dr. Jeffrey Haddad by phone (765-496-9489) and/or by email (jmhaddad@purdue.edu).

If you have questions about your rights while taking part in the study or have concerns about the treatment of research participants, please call the Human Research Protection Program at (765) 494-5942, email (irb@purdue.edu) or write to:

Human Research Protection Program - Purdue University
Ernest C. Young Hall, Room 1032
155 S. Grant St.
West Lafayette, IN 47907-2114

Documentation of Informed Consent

I have had the opportunity to read this consent form and have the research study explained. I have had the opportunity to ask questions about the research study, and my questions have been answered. I am prepared to participate in the research study described above. I will be offered a copy of this consent form after I sign it.

APPENDIX D. MODIFIED EDINBURGH HANDEDNESS INVENTORY

Participant ID: _____

Please indicate your preferences in the use of hands in the following activities by putting + in the appropriate column. Where the preference is so strong that you would never try to use the other hand unless absolutely forced to, put ++. If you are indifferent put + in both columns. Some of the activities require both hands. In these cases, the part of the task, or object, for which hand preference refers is indicated in parentheses. Please try to answer all the questions, and only leave a blank if you have no experience with the object or task.

	Task	Left Hand	Right Hand
1	Writing		
2	Throwing		
3	Scissors		
4	Toothbrush		
5	Knife (without fork)		
6	Spoon		
7	Striking match (match)		
	TOTAL		

Laterality Quotient (λ): _____ $\lambda = 100 \left(\frac{\sum_{i=1}^{10} X_{i,R} - \sum_{i=1}^{10} X_{i,L}}{\sum_{i=1}^{10} X_{i,R} + \sum_{i=1}^{10} X_{i,L}} \right)$

Handedness is determined by previously defined cutoffs (Dragovic, 2004; Milenkovic & Dragovic, 2013).

Left: $-100 \leq \lambda \leq 71$ Mixed: $-70 \leq \lambda \leq 70$ Right: $71 \leq \lambda \leq 100$

Preferred Hand: _____

REFERENCES

- Amado, A. C., Palmer, C. J., Hamill, J., & van Emmerik, R. E. (2016). Coupling of postural and manual tasks in expert performers. *Hum Mov Sci*, *46*, 251-260. doi:10.1016/j.humov.2015.12.008
- Andersen, G. J., & Dyre, B. P. (1989). Spatial orientation from optic flow in the central visual field. *Percept Psychophys*, *45*(5), 453-458. doi:10.3758/bf03210719
- Arbib, M. A., Bonaiuto, J. B., Jacobs, S., & Frey, S. H. (2009). Tool use and the distalization of the end-effector. *Psychol Res*, *73*(4), 441-462.
- Assländer, L., & Peterka, R. J. (2014). Sensory reweighting dynamics in human postural control. *J Neurophysiol*, *111*(9), 1852-1864.
- Assländer, L., & Peterka, R. J. (2016). Sensory reweighting dynamics following removal and addition of visual and proprioceptive cues. *J Neurophysiol*, *116*(2), 272-285.
- Atkeson, C. G., & Hollerbach, J. M. (1985). Kinematic features of unrestrained vertical arm movements. *J Neurosci*, *5*(9), 2318-2330.
- Baber, C. (2006). Cognitive aspects of tool use. *Appl Ergon*, *37*(1), 3-15.
- Baird, K. M., Hoffmann, E. R., & Drury, C. G. (2002). The effects of probe length on Fitts' law. *Appl Ergon*, *33*(1), 9-14.
- Balasubramaniam, R. (2013). On the control of unstable objects: The dynamics of human stick balancing. In M. J. Richardson, M. A. Riley, & K. Shockley (Eds.), *Progress in Motor Control: Neural, Computational, and Dynamical Approaches* (pp. 149-168). New York, NY: Springer.
- Balasubramaniam, R., Riley, M. A., & Turvey, M. T. (2000). Specificity of postural sway to the demands of a precision task. *Gait & Posture*, *11*(1), 12-24.
- Bardy, B. G., Marin, L. C., Stoffregen, T. A., & Bootsma, R. J. (1999). Postural coordination modes considered as emergent phenomena. *J Exp Psychol Hum Percept Perform*, *25*(5), 1284.
- Batani, H., Zecevic, A., McIlroy, W. E., & Maki, B. E. (2004). Resolving conflicts in task demands during balance recovery: does holding an object inhibit compensatory grasping? *Exp Brain Res*, *157*, 49-58. doi:10.1007/s00221-003-1815-8
- Bates, E., Carlsonluden, V., & Bretherton, I. (1980). Perceptual aspects of tool using in infancy. *Infant Behavior & Development*, *3*(2), 127-140. doi:Doi 10.1016/S0163-6383(80)80017-8

- Baugh, L. A., Hoe, E., & Flanagan, J. R. (2012). Hand-held tools with complex kinematics are efficiently incorporated into movement planning and online control. *J Neurophysiol*, *108*(7), 1954-1964.
- Baugh, L. A., Kao, M., Johansson, R. S., & Flanagan, J. R. (2012). Material evidence: Interaction of well-learned priors and sensorimotor memory when lifting objects. *J Neurophysiol*, *108*(5), 1262-1269.
- Belenkiy, V. E., Gurfinkel, V. S., & Paltsev, E. I. (1967). On elements of control of voluntary movements. *Biofizica*, *12*, 135-141.
- Benzi, R., Sutera, A., & Vulpiani, A. (1981). The mechanism of stochastic resonance. *J Phys A: Math Gen*, *14*(11), L453.
- Bernstein, N. A. (1967). *The Co-ordination and Regulation of Movements*. Oxford, UK: Pergamon Press.
- Biddiss, E. A., & Chau, T. T. (2007). Upper limb prosthesis use and abandonment: a survey of the last 25 years. *Prosthet Orthot Int*, *31*(3), 236-257.
- Biryukova, E., & Bril, B. (2012). Biomechanical analysis of tool use: A return to Bernstein's tradition. *Zeitschrift für Psychologie*, *220*(1), 53-54.
- Bock, O. (1990). Load compensation in human goal-directed arm movements. *Behav Brain Res*, *41*(3), 167-177.
- Bongers, R. M., Michaels, C. F., & Smitsman, A. W. (2004). Variations of tool and task characteristics reveal that tool-use postures are anticipated. *J Motor Behav*, *36*(3), 305-315.
- Bongers, R. M., Smitsman, A. W., & Michaels, C. F. (2003). Geometries and dynamics of a rod determine how it is used for reaching. *J Motor Behav*, *35*(1), 4-22.
- Bouisset, S., & Zattara, M. (1990). Segmental movement as a perturbation to balance? Facts and concepts. In J. M. Winters & S. L. Y. Woo (Eds.), *Multiple muscle systems* (pp. 498-506). New York, NY: Springer.
- Bouwsema, H., van der Sluis, C. K., & Bongers, R. M. (2010). Movement characteristics of upper extremity prostheses during basic goal-directed tasks. *Clin Biomech (Bristol, Avon)*, *25*(6), 523-529. doi:10.1016/j.clinbiomech.2010.02.011
- Brashers-Krug, T., Shadmehr, R., & Bizzi, E. (1996). Consolidation in human motor memory. *Nature*, *382*(6588), 252-255. doi:10.1038/382252a0
- Breteler, M. D. K., Meulenbroek, R. G. J., & Gielen, S. C. A. M. (1998). Geometric features of workspace and joint-space paths of 3D reaching movements. *Acta Psychologica*, *100*(1-2), 37-53.

- Bulsara, A., Jacobs, E. W., Zhou, T., Moss, F., & Kiss, L. (1991). Stochastic resonance in a single neuron model: theory and analog simulation. *J Theor Biol*, *152*(4), 531-555.
- Cardinali, L., Brozzoli, C., & Farne, A. (2009). Peripersonal space and body schema: two labels for the same concept? *Brain Topogr*, *21*(3-4), 252-260. doi:10.1007/s10548-009-0092-7
- Cardinali, L., Brozzoli, C., Finos, L., Roy, A. C., & Farne, A. (2016). The rules of tool incorporation: Tool morpho-functional & sensori-motor constraints. *Cognition*, *149*, 1-5. doi:10.1016/j.cognition.2016.01.001
- Cardinali, L., Frassinetti, F., Brozzoli, C., Urquizar, C., Roy, A. C., & Farne, A. (2009). Tool-use induces morphological updating of the body schema. *Curr Biol*, *19*(12), R478-479. doi:10.1016/j.cub.2009.05.009
- Cardinali, L., Jacobs, S., Brozzoli, C., Frassinetti, F., Roy, A. C., & Farne, A. (2012). Grab an object with a tool and change your body: tool-use-dependent changes of body representation for action. *Exp Brain Res*, *218*(2), 259-271. doi:10.1007/s00221-012-3028-5
- Carpenter, M. G., Murnaghan, C. D., & Inglis, J. T. (2010). Shifting the balance: evidence of an exploratory role for postural sway. *Neuroscience*, *171*(1), 196-204. doi:10.1016/j.neuroscience.2010.08.030
- Carver, S., Kiemel, T., & Jeka, J. J. (2006). Modeling the dynamics of sensory reweighting. *Biol Cybern*, *95*(2), 123-134. doi:10.1007/s00422-006-0069-5
- Chagdes, J. R., Huber, J. E., Saletta, M., Darling-White, M., Raman, A., Rietdyk, S., . . . Haddad, J. M. (2016). The relationship between intermittent limit cycles and postural instability associated with Parkinson's disease. *J Sport Health Sci*, *5*(1), 14-24.
- Chagdes, J. R., Rietdyk, S., Haddad, J. M., Zelaznik, H. N., Cinelli, M. E., Denomme, L. T., . . . Raman, A. (2016). Limit cycle oscillations in standing human posture. *J Biomech*, *49*(7), 1170-1179. doi:10.1016/j.jbiomech.2016.03.005
- Cisek, P. (1999). Beyond the computer metaphor: Behaviour as interaction. *J Conscious Stud*, *6*(11-12), 125-142.
- Cluff, T., Boulet, J., & Balasubramaniam, R. (2011). Learning a stick-balancing task involves task-specific coupling between posture and hand displacements. *Exp Brain Res*, *213*(1), 15-25.
- Cluff, T., Manos, A., Lee, T. D., & Balasubramaniam, R. (2012). Multijoint error compensation mediates unstable object control. *J Neurophysiol*, *108*(4), 1167-1175. doi:10.1152/jn.00691.2011
- Collins, J. J., Chow, C. C., Capela, A. C., & Imhoff, T. T. (1996). Aperiodic stochastic resonance. *Phys Rev E*, *54*(5), 5575.

- Collins, J. J., Chow, C. C., & Imhoff, T. T. (1995a). Aperiodic stochastic resonance in excitable systems. *Phys Rev E Stat Phys Plasmas Fluids Relat Interdiscip Topics*, 52(4), R3321-R3324.
- Collins, J. J., Chow, C. C., & Imhoff, T. T. (1995b). Stochastic resonance without tuning. *Nature*, 376(6537), 236-268.
- Collins, J. J., Priplata, A. A., Gravelle, D. C., Niemi, J., Harry, J., & Lipsitz, L. A. (2003). Noise-enhanced human sensorimotor function. *IEEE Eng Med Biol Mag*, 22(2), 76-83.
- Conolly, K., & Dalglish, M. (1989). The emergence of a tool-using skill in infancy. *Cogn Sci*, 14, 107-133.
- Costa, M., Priplata, A. A., Lipsitz, L. A., Wu, Z., Huang, N. E., Goldberger, A. L., & Peng, C. K. (2007). Noise and poise: enhancement of postural complexity in the elderly with a stochastic-resonance-based therapy. *Europhys Lett*, 77, 68008.
- Cruise, D. R., Chagdes, J. R., Liddy, J. J., Rietdyk, S., Haddad, J. M., Zelaznik, H. N., & Raman, A. (2017). An active balance board system with real-time control of stiffness and time-delay to assess mechanisms of postural stability. *J Biomech*, 60, 48-56. doi:10.1016/j.jbiomech.2017.06.018
- Cruse, H., & Brüwer, M. (1987). The human arm as a redundant manipulator: The control of path and joint angles. *Biol Cybern*, 57(1-2), 137-144.
- Davidson, J. (2002). A survey of the satisfaction of upper limb amputees with their prostheses, their lifestyles, and their abilities. *J Hand Ther*, 15(1), 62-70.
- Davidson, P. R., & Wolpert, D. M. (2004). Scaling down motor memories: de-adaptation after motor learning. *Neurosci Lett*, 370(2-3), 102-107. doi:10.1016/j.neulet.2004.08.003
- Davis III, R. B., Ounpuu, S., Tyburski, D., & Gage, J. R. (1991). A gait analysis data collection and reduction technique. *Hum Mov Sci*, 10(5), 575-587.
- Deprá, P. P., Amado, A., & van Emmerik, R. E. A. (2019). Postural Control Underlying Head Movements While Tracking Visual Targets. *Motor Control*, 23(3), 365-383. doi:10.1123/mc.2018-0064
- Dhruv, N. T., Niemi, J. B., Harry, J. D., Lipsitz, L. A., & Collins, J. J. (2002). Enhancing tactile sensation in older adults with electrical noise stimulation. *Neuroreport*, 13(5), 597-600. doi:10.1097/00001756-200204160-00012
- Douglass, J. K., Wilkens, L., Pantazelou, E., & Moss, F. (1993). Noise enhancement of information transfer in crayfish mechanoreceptors by stochastic resonance. *Nature*, 365(6444), 337-340. doi:10.1038/365337a0

- Dragovic, M. (2004). Towards an improved measure of the Edinburgh Handedness Inventory: A one-factor congeneric measurement model using confirmatory factor analysis. *Laterality*, 9(4), 411-419.
- Dreyfus, H. (1991). *Being-in-the-world: A commentary on Heidegger's Being and Time, Division I*. Cambridge, MA: The MIT Press.
- Farnè, A., & Làdavas, E. (2000). Dynamic size-change of hand peripersonal space following tool use. *Neuroreport*, 11(8), 1645-1649.
- Fitts, P. M. (1954). The information capacity of the human motor system in controlling the amplitude of movement. *J Exp Psychol*, 47(6), 381-391.
- Flanagan, J. R., & Beltzner, M. A. (2000). Independence of perceptual and sensorimotor predictions in the size-weight illusion. *Nature Neurosci*, 3(7), 737-741.
- Flanagan, J. R., & Rao, A. K. (1995). Trajectory adaptation to a nonlinear visuomotor transformation: evidence of motion planning in visually perceived space. *J Neurophysiol*, 74(5), 2174-2178. doi:10.1152/jn.1995.74.5.2174
- Fu, Q., & Santello, M. (2012). Context-dependent learning interferes with visuomotor transformations for manipulation planning. *J Neurosci*, 32(43), 15086-15092. doi:10.1523/JNEUROSCI.2468-12.2012
- Fu, Q., & Santello, M. (2014). Retention and interference of learned dexterous manipulation: interaction between multiple sensorimotor processes. *J Neurophysiol*, 113(1), 144-155.
- Gage, W. H., Winter, D. A., Frank, J. S., & Adkin, A. L. (2004). Kinematic and kinetic validity of the inverted pendulum model in quiet standing. *Gait & Posture*, 19(2), 124-132. doi:10.1016/S0966-6362(03)00037-7
- Galgon, A. K., Shewokis, P. A., & Tucker, C. A. (2010). Changes in standing postural control during acquisition of a sequential reaching task. *Gait & Posture*, 31(2), 265-271. doi:10.1016/j.gaitpost.2009.11.002
- Gandolfo, F., Mussa-Ivaldi, F. A., & Bizzi, E. (1996). Motor learning by field approximation. *Proc Natl Acad Sci*, 93(9), 3843-3846. doi:10.1073/pnas.93.9.3843
- Gelfand, I. M., & Latash, M. L. (1998). On the problem of adequate language in motor control. *Motor Control*, 2(4), 306-313.
- Gibson, J. J. (1966). *The senses considered as perceptual systems*. Boston, MA: Houghton Mifflin.
- Gibson, J. J. (1979). *The ecological approach to visual perception*. Boston, MA: Houghton Mifflin Company.

- Gordon, A. M., Westling, G., Cole, K. J., & Johansson, R. S. (1993). Memory representations underlying motor commands used during manipulation of common and novel objects. *J Neurophysiol*, *69*(6), 1789-1796.
- Gouzien, A., de Vignemont, F., Touillet, A., Martinet, N., De Graaf, J., Jarrasse, N., & Roby-Brami, A. (2017). Reachability and the sense of embodiment in amputees using prostheses. *Sci Rep*, *7*(1), 4999.
- Greene, P. H. (1972). Problems of organization of motor systems. *Prog Theor Biol*, *2*, 303-338.
- Greenwood, P. E., Ward, L. M., Russell, D. F., Neiman, A., & Moss, F. (2000). Stochastic resonance enhances the electrosensory information available to paddlefish for prey capture. *Phys Rev Lett*, *84*(20), 4773-4776. doi:10.1103/PhysRevLett.84.4773
- Gruber, A. H., Busa, M. A., Gorton Iii, G. E., Van Emmerik, R. E., Masso, P. D., & Hamill, J. (2011). Time-to-contact and multiscale entropy identify differences in postural control in adolescent idiopathic scoliosis. *Gait & Posture*, *34*(1), 13-18. doi:10.1016/j.gaitpost.2011.02.015
- Haddad, J. M., Claxton, L. J., Keen, R., Berthier, N. E., Riccio, G. E., Hamill, J., & Van Emmerik, R. E. A. (2012). Development of the coordination between posture and manual control. *Journal of experimental child psychology*, *111*(2), 286-298. doi:10.1016/j.jecp.2011.08.002
- Haddad, J. M., Gagnon, J. L., Hasson, C. J., Van Emmerik, R. E., & Hamill, J. (2006). Evaluation of time-to-contact measures for assessing postural stability. *J Appl Biomech*, *22*(2), 155-161.
- Haddad, J. M., Rietdyk, S., Claxton, L. J., & Huber, J. E. (2013). Task-dependent postural control throughout the lifespan. *Exerc Sport Sci Rev*, *41*(2), 123-132. doi:10.1097/JES.0b013e3182877cc8
- Haddad, J. M., Ryu, J. H., Seaman, J. M., & Ponto, K. C. (2010). Time-to-contact measures capture modulations in posture based on the precision demands of a manual task. *Gait & Posture*, *32*(4), 592-596. doi:10.1016/j.gaitpost.2010.08.008
- Haddad, J. M., Van Emmerik, R. E., Wheat, J. S., & Hamill, J. (2008). Developmental changes in the dynamical structure of postural sway during a precision fitting task. *Exp Brain Res*, *190*(4), 431-441. doi:10.1007/s00221-008-1483-9
- Haddad, J. M., van Emmerik, R. E., Whittlesey, S. N., & Hamill, J. (2006). Adaptations in interlimb and intralimb coordination to asymmetrical loading in human walking. *Gait & Posture*, *23*(4), 429-434. doi:10.1016/j.gaitpost.2005.05.006
- Hasson, C. J., Van Emmerik, R. E. A., & Caldwell, G. E. (2008). Predicting dynamic postural instability using center of mass time-to-contact information. *J Biomech*, *41*(10), 2121-2129.

- Heald, J. B., Ingram, J. N., Flanagan, J. R., & Wolpert, D. M. (2018). Multiple motor memories are learned to control different points on a tool. *Nat Hum Behav*, 2(4), 300-311. doi:10.1038/s41562-018-0324-5
- Hegele, M., & Heuer, H. (2010). Implicit and explicit components of dual adaptation to visuomotor rotations. *Conscious Cogn*, 19(4), 906-917. doi:10.1016/j.concog.2010.05.005
- Heidegger, M. (1962). *Being and Time*. New York: Harper & Row.
- Heuer, H., & Sülzenbrück, S. (2009). Trajectories in operating a handheld tool. *J Exp Psychol Hum Percept Perform*, 35(2), 375-389. doi:10.1037/0096-1523.35.2.375
- Hof, A. L., Gazendam, M. G., & Sinke, W. E. (2005). The condition for dynamic stability. *J Biomech*, 38(1), 1-8. doi:10.1016/j.jbiomech.2004.03.025
- Hogan, N., & Sternad, D. (2009). Sensitivity of smoothness measures to movement duration, amplitude, and arrests. *J Mot Behav*, 41(6), 529-534. doi:10.3200/35-09-004-RC
- Holmes, N. P., Calvert, G. A., & Spence, C. (2004). Extending or projecting peripersonal space with tools? Multisensory interactions highlight only the distal and proximal ends of tools. *Neurosci Lett*, 372(1-2), 62-67. doi:10.1016/j.neulet.2004.09.024
- Holmes, N. P., & Spence, C. (2004). The body schema and the multisensory representation(s) of peripersonal space. *Cogn Process*, 5(2), 94-105. doi:10.1007/s10339-004-0013-3
- Horak, F. B. (2006). Postural orientation and equilibrium: what do we need to know about neural control of balance to prevent falls? *Age Aging*, 35(S2), ii7-ii11.
- Horak, F. B., & Diener, H. C. (1994). Cerebellar control of postural scaling and central set in stance. *J Neurophysiol*, 72(2), 479-493. doi:10.1152/jn.1994.72.2.479
- Horak, F. B., & Nashner, L. M. (1986). Central programming of postural movements: adaptation to altered support-surface configurations. *J Neurophysiol*, 55(6), 1369-1381. doi:10.1152/jn.1986.55.6.1369
- Horgan, O., & MacLachlan, M. (2004). Psychosocial adjustment to lower-limb amputation: a review. *Disabil Rehabil*, 26(14-15), 837-850. doi:10.1080/09638280410001708869
- Howard, I. S., Wolpert, D. M., & Franklin, D. W. (2013). The effect of contextual cues on the encoding of motor memories. *J Neurophysiol*, 109(10), 2632-2644. doi:10.1152/jn.00773.2012
- Hsu, W. L., Lin, K. H., Yang, R. S., & Cheng, C. H. (2014). Use of motor abundance in old adults in the regulation of a narrow-based stance. *Eur J Appl Physiol*, 114(2), 261-271.
- Hsu, W. L., & Scholz, J. P. (2012). Motor abundance supports multitasking while standing. *Hum Mov Sci*, 31(4), 844-862.

- Hsu, W. L., Scholz, J. P., Schoner, G., Jeka, J. J., & Kiemel, T. (2007). Control and estimation of posture during quiet stance depends on multijoint coordination. *J Neurophysiol*, *97*(4), 3024-3035. doi:10.1152/jn.01142.2006
- Huys, R., Daffertshofer, A., & Beek, P. J. (2003). Learning to juggle: on the assembly of functional subsystems into a task-specific dynamical organization. *Biol Cybern*, *88*(4), 302-318.
- Huys, R., Daffertshofer, A., & Beek, P. J. (2004a). Multiple time scales and multiform dynamics in learning to juggle. *Motor Control*, *8*(2), 188-212. doi:10.1123/mcj.8.2.188
- Huys, R., Daffertshofer, A., & Beek, P. J. (2004b). Multiple time scales and subsystem embedding in the learning of juggling. *Hum Mov Sci*, *23*(3-4), 315-336. doi:10.1016/j.humov.2004.08.009
- Ingram, J. N., & Wolpert, D. M. (2011). Naturalistic approaches to sensorimotor control. In A. M. Green, E. Chapman, J. F. Kalaska, & F. Lepore (Eds.), *Progress in Brain Research: Multisensory Integration, Neuroplasticity, and Neuroprosthetics, Part I* (Vol. 191, pp. 3-29): Elsevier.
- Iriki, A., Tanaka, M., & Iwamura, Y. (1996). Coding of modified body schema during tool use by macaque postcentral neurones. *Neuroreport*, *7*(14), 2325-2330.
- Jacquier-Bret, J., Rezzoug, N., & Gorce, P. (2009). Adaptation of joint flexibility during a reach-to-grasp movement. *Motor Control*, *13*(3), 342-361. doi:10.1123/mcj.13.3.342
- Johnson-Frey, S. H. (2003). What's So Special about Human Tool Use? *Neuron*, *39*(2), 201-204. doi:10.1016/s0896-6273(03)00424-0
- Johnson-Frey, S. H. (2004). The neural bases of complex tool use in humans. *Trends Cogn Sci*, *8*(2), 71-78.
- Kahrs, B. A., Jung, W. P., & Lockman, J. J. (2012). What is the role of infant banging in the development of tool use? *Exp Brain Res*, *218*(2), 315-320.
- Kahrs, B. A., Jung, W. P., & Lockman, J. J. (2013). Motor origins of tool use. *Child Dev*, *84*(3), 810-816.
- Kaminski, T. R. (2007). The coupling between upper and lower extremity synergies during whole body reaching. *Gait & Posture*, *26*(2), 256-262. doi:10.1016/j.gaitpost.2006.09.006
- Kaminski, T. R., Bock, C., & Gentile, A. M. (1995). The coordination between trunk and arm motion during pointing movements. *Experimental Brain Research*, *106*(3), 457-466. doi:10.1007/bf00231068

- Kaminski, T. R., & Simpkins, S. (2001). The effects of stance configuration and target distance on reaching. I. Movement preparation. *Exp Brain Res*, *136*(4), 439-446. doi:10.1007/s002210000604
- Karok, S., & Newport, R. (2010). The continuous updating of grasp in response to dynamic changes in object size, hand size and distractor proximity. *Neuropsychologia*, *48*(13), 3891-3900. doi:10.1016/j.neuropsychologia.2010.10.006
- Kelso, J. A., Fuchs, A., Lancaster, R., Holroyd, T., Cheyne, D., & Weinberg, H. (1998). Dynamic cortical activity in the human brain reveals motor equivalence. *Nature*, *392*(6678), 814-818. doi:10.1038/33922
- Kelty-Stephen, D. G., & Dixon, J. A. (2013). Temporal correlations in postural sway moderate effects of stochastic resonance on postural stability. *Hum Mov Sci*, *32*(1), 91-105. doi:10.1016/j.humov.2012.08.006
- Kirsh, D., & Maglio, P. (1994). On distinguishing epistemic from pragmatic action. *Cogn Sci*, *18*(4), 513-549.
- Krakauer, J. W. (2009). Motor learning and consolidation: the case of visuomotor rotation. In D. Sternad (Ed.), *Progress in Motor Control: A Multidisciplinary Perspective* (pp. 405-421). New York, NY: Springer.
- Krakauer, J. W., Ghez, C., & Ghilardi, M. F. (2005). Adaptation to visuomotor transformations: consolidation, interference, and forgetting. *J Neurosci*, *25*(2), 473-478. doi:10.1523/JNEUROSCI.4218-04.2005
- Krakauer, J. W., & Mazzoni, P. (2011). Human sensorimotor learning: adaptation, skill, and beyond. *Curr Opin Neurobiol*, *21*(4), 636-644. doi:10.1016/j.conb.2011.06.012
- Krishnan, V., Rosenblatt, N. J., Latash, M. L., & Grabiner, M. D. (2013). The effects of age on stabilization of the mediolateral trajectory of the swing foot. *Gait & Posture*, *38*(4), 923-928. doi:10.1016/j.gaitpost.2013.04.023
- Lacquaniti, F., Soechting, J. F., & Terzuolo, C. A. (1982). Some factors pertinent to the organization and control of arm movements. *Brain Research*, *252*(2), 394-397.
- Lashley, K. S. (1930). Basic neural mechanisms in behavior. *Psychol Rev*, *37*(1), 1-24.
- Latash, M. L. (2000). There is no motor redundancy in human movements. There is motor abundance. *Motor Control*, *4*(3), 259-261.
- Latash, M. L. (2012). The bliss (not the problem) of motor abundance (not redundancy). *Exp Brain Res*, *217*(1), 1-5.
- Latash, M. L. (2018). Abundant degrees of freedom are not a problem. *Kinesiol Rev*, *7*(1), 64-72.

- Latash, M. L., Scholz, J. F., Danion, F., & Schoner, G. (2001). Structure of motor variability in marginally redundant multifinger force production tasks. *Exp Brain Res*, *141*(2), 153-165. doi:10.1007/s002210100861
- Latash, M. L., & Zatsiorsky, V. M. (2015). *Biomechanics and motor control: defining central concepts*. London, UK: Academic Press.
- Lee, D. N., & Lishman, J. R. (1975). Visual proprioceptive control of stance. *J Hum Mov Stud*(1), 87-95.
- Liddy, J. J., Arnold, A. J., Cho, H., Romine, N. L., & Haddad, J. M. (2019). The effect of holding an object on postural stability and suprapostural task performance. *J Appl Biomech*, *1*(Ahead of Print), 1-8.
- Lipsitz, L. A., Lough, M., Niemi, J., Travison, T., Howlett, H., & Manor, B. (2015). A shoe insole delivering subsensory vibratory noise improves balance and gait in healthy elderly people. *Arch Phys Med Rehabil*, *96*(3), 432-439. doi:10.1016/j.apmr.2014.10.004
- Liu, W., Lipsitz, L. A., Montero-Odasso, M., Bean, J., Kerrigan, D. C., & Collins, J. J. (2002). Noise-enhanced vibrotactile sensitivity in older adults, patients with stroke, and patients with diabetic neuropathy. *Arch Phys Med Rehabil*, *83*(2), 171-176.
- Lockman, J. J. (2000). A perception–action perspective on tool use development. *Child Dev*, *71*(1), 137-144.
- Loram, I. D., Gollee, H., Lakie, M., & Gawthrop, P. J. (2011). Human control of an inverted pendulum: is continuous control necessary? Is intermittent control effective? Is intermittent control physiological? *J Physiol*, *589*(2), 307-324.
- Loram, I. D., Maganaris, C. N., & Lakie, M. (2005). Human postural sway results from frequent, ballistic bias impulses by soleus and gastrocnemius. *J Physiol*, *564*(Pt 1), 295-311.
- Ma, S., & Feldman, A. G. (1995). Two functionally different synergies during arm reaching movements involving the trunk. *J Neurophysiol*, *73*(5), 2120-2122. doi:10.1152/jn.1995.73.5.2120
- MacKenzie, C. L., Marteniuk, R. G., Dugas, C., Liske, D., & Eickmeier, B. (1987). Three-dimensional movement trajectories in Fitts' task: Implications for control. *Q J Exp Psychol*, *39*(4), 629-647.
- Maravita, A., & Iriki, A. (2004). Tools for the body (schema). *Trends Cogn Sci*, *8*(2), 79-86. doi:10.1016/j.tics.2003.12.008
- Marteniuk, R. G., MacKenzie, C. L., Jeannerod, M., Athenes, S., & Dugas, C. (1987). Constraints on human arm movement trajectories. *Canadian Journal of Psychology*, *41*(3), 365.

- Martin, T. A., Keating, J. G., Goodkin, H. P., Bastian, A. J., & Thach, W. T. (1996). Throwing while looking through prisms: II. Specificity and storage of multiple gaze—throw calibrations. *Brain*, *119*(4), 1199-1211.
- Massion, J. (1992). Movement, posture and equilibrium: interaction and coordination. *Prog Neurobiol*, *38*(1), 35-56.
- Massion, J. (1994). Postural control system. *Curr Opin Neurobiol*, *4*(6), 877-887.
- Massion, J., Alexandrov, A., & Frolov, A. (2004). Why and how are posture and movement coordinated? *Prog Brain Res*, *143*, 13-27.
- McCarty, M. E., Clifton, R. K., & Collard, R. R. (2001). The beginnings of tool use by infants and toddlers. *Infancy*, *2*(2), 233-256.
- McDonnell, M. D., & Abbott, D. (2009). What is stochastic resonance? Definitions, misconceptions, debates, and its relevance to biology. *PLoS Comput Biol*, *5*(5), e1000348.
- Merleau-Ponty, M. (1962). *The phenomenology of perception*. New York: Routledge & Kegan Paul.
- Milenkovic, S., & Dragovic, M. (2013). Modification of the Edinburgh Handedness Inventory: a replication study. *Laterality*, *18*(3), 340-348.
- Miller, L. E., Longo, M. R., & Saygin, A. P. (2014). Tool morphology constrains the effects of tool use on body representations. *J Exp Psychol Hum Percept Perform*, *40*(6), 2143.
- Milton, J. G. (2013). Intermittent motor control: The "drift-and-act" hypothesis. In M. J. Richardson, M. A. Riley, & K. Shockley (Eds.), *Progress in Motor Control: Neural, Computational and Dynamic Approaches* (pp. 169-193). New York, NY: Springer New York.
- Morasso, P. G. (1981). Spatial control of arm movements. *Exp Brain Res*, *42*(2), 223-227. doi:10.1007/bf00236911
- Morasso, P. G., & Schieppati, M. (1999). Can muscle stiffness alone stabilize upright standing? *J Neurophysiol*, *82*(3), 1622-1626.
- Morton, S. M., & Bastian, A. J. (2006). Cerebellar contributions to locomotor adaptations during splitbelt treadmill walking. *J Neurosci*, *26*(36), 9107-9116. doi:10.1523/JNEUROSCI.2622-06.2006
- Nagell, K., Olguin, R. S., & Tomasello, M. (1993). Processes of social learning in the tool use of chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *J Comp Psychol*, *107*(2), 174-186.

- Nashner, L. M., & Mccollum, G. (1985). The organization of human postural movements: A formal basis and experimental synthesis. *Behav Brain Sci*, 8(1), 135-150. Retrieved from [Go to ISI://WOS:A1985ANN3200080](https://doi.org/10.1037/0033-295x.108.1.57)
- Newell, K. M., Liu, Y. T., & Mayer-Kress, G. (2001). Time scales in motor learning and development. *Psychol Rev*, 108(1), 57-82. doi:10.1037/0033-295x.108.1.57
- Newell, K. M., van Emmerik, R. E. A., Lee, D., & Sprague, R. L. (1993). On postural stability and variability. *Gait & Posture*, 1(4), 225-230.
- Oliveira, L. F., Simpson, D. M., & Nadal, J. (1996). Calculation of area of stabilometric signals using principal component analysis. *Physiol Meas*, 17(4), 305-312.
- Patron, J., Stapley, P. J., & Pozzo, T. (2005). Human whole-body reaching in normal gravity and microgravity reveals a strong temporal coordination between postural and focal task components. *Exp Brain Res*, 165(1), 84-96.
- Peterka, R. J. (2002). Sensorimotor integration in human postural control. *J Neurophysiol*, 88(3), 1097-1118. doi:10.1152/jn.2002.88.3.1097
- Piaget, J. (1952). *The origins of intelligence in children*. New York, NY: W. W. Norton.
- Povinelli, D. J. (2000). *Folk physics for apes: The chimpanzee's theory of how the world works*. Oxford, UK: Oxford University Press
- Pozzo, T., Stapley, P. J., & Papaxanthis, C. (2002). Coordination between equilibrium and hand trajectories during whole body pointing movements. *Exp Brain Res*, 144(3), 343-350.
- Prado, J. M., Stoffregen, T. A., & Duarte, M. (2007). Postural sway during dual tasks in young and elderly adults. *Gerontol*, 53(5), 274-281.
- Priplata, A. A., Niemi, J., Salen, M., Harry, J., Lipsitz, L. A., & Collins, J. J. (2002). Noise-enhanced human balance control. *Phys Rev Lett*, 89(23), 238101. doi:10.1103/PhysRevLett.89.238101
- Priplata, A. A., Niemi, J. B., Harry, J. D., Lipsitz, L. A., & Collins, J. J. (2003). Vibrating insoles and balance control in elderly people. *Lancet*, 362(9390), 1123-1124. doi:10.1016/S0140-6736(03)14470-4
- Priplata, A. A., Patriitti, B. L., Niemi, J. B., Hughes, R., Gravelle, D. C., Lipsitz, L. A., . . . Collins, J. J. (2006). Noise-enhanced balance control in patients with diabetes and patients with stroke. *Ann Neurol*, 59(1), 4-12. doi:10.1002/ana.20670
- Proud, K., Heald, J. B., Ingram, J. N., Gallivan, J. P., Wolpert, D. M., & Flanagan, J. R. (2019). Separate motor memories are formed when controlling different implicitly specified locations on a tool. *J Neurophysiol*, 121(4), 1342-1351.

- Rat-Fischer, L., O'Regan, J. K., & Fagard, J. (2012). The emergence of tool use during the second year of life. *Journal of experimental child psychology*, *113*(3), 440-446. doi:10.1016/j.jecp.2012.06.001
- Reed, E. S. (1982). An outline of a theory of action systems. *J Motor Behav*, *14*(2), 98-134.
- Reed, E. S. (1988). Applying the theory of action systems to the study of motor skills. In O. G. Meijer & K. Roth (Eds.), *Complex movement behavior: The motor-action controversy* (Vol. 50, pp. 45-86). Amsterdam: North-Holland.
- Reed, E. S. (1989). Changing theories of postural development. In M. H. Woolacott & A. Shumway-Cook (Eds.), *Development of posture and gait across the lifespan* (pp. 3-24). Columbia, SC: University of South Carolina.
- Riccio, G. E. (1993). Information in Movement Variability about the Qualitative Dynamics of Posture and Orientation. In K. M. Newell & D. M. Corcos (Eds.), *Variability and Motor Control* (pp. 317-358). Champaign, IL: Human Kinetics.
- Riccio, G. E., & Stoffregen, T. A. (1988). Affordances as constraints on the control of stance. *Hum Mov Sci*, *7*(2-4), 265-300.
- Rietdyk, S. (under review). Slips, trips, and falls act to identify and sustain 'failure boundaries'. *Exerc Sport Sci Rev*.
- Riley, M. A., Mitra, S., Stoffregen, T. A., & Turvey, M. T. (1997). Influences of body lean and vision on unperturbed postural sway. *Motor Control*, *1*(3), 229-246.
- Riley, M. A., Stoffregen, T. A., Grocki, M. J., & Turvey, M. T. (1999). Postural stabilization for the control of touching. *Hum Mov Sci*, *18*(6), 795-817.
- Rosenbaum, D. A. (2017). *Knowing hands: The cognitive psychology of manual control*. Cambridge, UK: Cambridge University Press.
- Rosenbaum, D. A., Chapman, K. M., Weigelt, M., Weiss, D. J., & van der Wel, R. (2012). Cognition, action, and object manipulation. *Psychol Bull*, *138*(5), 924-946. doi:10.1037/a0027839
- Rosenblatt, N. J., Hurt, C. P., Latash, M. L., & Grabiner, M. D. (2014). An apparent contradiction: increasing variability to achieve greater precision? *Exp Brain Res*, *232*(2), 403-413. doi:10.1007/s00221-013-3748-1
- Rosenblatt, N. J., Latash, M. L., Hurt, C. P., & Grabiner, M. D. (2015). Challenging gait leads to stronger lower-limb kinematic synergies: The effects of walking within a more narrow pathway. *Neurosci Lett*, *600*, 110-114.
- Russell, D. F., Wilkens, L. A., & Moss, F. (1999). Use of behavioural stochastic resonance by paddle fish for feeding. *Nature*, *402*(6759), 291-294.

- Scholz, J. P., Kang, N., Patterson, D., & Latash, M. L. (2003). Uncontrolled manifold analysis of single trials during multi-finger force production by persons with and without Down syndrome. *Exp Brain Res*, *153*(1), 45-58.
- Scholz, J. P., & Schoner, G. (1999). The uncontrolled manifold concept: identifying control variables for a functional task. *Exp Brain Res*, *126*(3), 289-306.
- Schöner, G. (1991). Dynamic theory of action-perception patterns: the “moving room” paradigm. *Biol Cybern*, *64*(6), 455-462.
- Schreiber, T. (2000). Measuring information transfer. *Phys Rev Lett*, *85*(2), 461-464. doi:10.1103/PhysRevLett.85.461
- Searle, J. R. (1990). Cognitive science and the computer metaphor. In B. Göranzon & M. Florin (Eds.), *Artificial Intelligence, Culture and Language: On Education and Work* (pp. 23-34). Berlin, DE: Springer-Verlag.
- Shadmehr, R., Brandt, J., & Corkin, S. (1998). Time-dependent motor memory processes in amnesic subjects. *J Neurophysiol*, *80*(3), 1590-1597. doi:10.1152/jn.1998.80.3.1590
- Shadmehr, R., & Holcomb, H. H. (1997). Neural correlates of motor memory consolidation. *Science*, *277*(5327), 821-825. doi:10.1126/science.277.5327.821
- Shadmehr, R., & Mussa-Ivaldi, F. A. (1994). Adaptive representation of dynamics during learning of a motor task. *J Neurosci*, *14*(5 Pt 2), 3208-3224.
- Shadmehr, R., Smith, M. A., & Krakauer, J. W. (2010). Error correction, sensory prediction, and adaptation in motor control. *Annu Rev Neurosci*, *33*, 89-108. doi:10.1146/annurev-neuro-060909-153135
- Shumaker, R. W., Walkup, K. R., & Beck, B. B. (2011). *Animal tool behavior: the use and manufacture of tools by animals*. Baltimore, MD: The Johns Hopkins University Press.
- Shumway-Cook, A., Woollacott, M. H., Kerns, K. A., & Baldwin, M. (1997). The effects of two types of cognitive tasks on postural stability in older adults with and without a history of falls. *J Gerontol A Biol Sci Med Sci*, *52*(4), M232-M240.
- Simon-Kuhn, K. L., Haddad, J. M., & Huber, J. E. (2019). Multi-task prioritization during the performance of a postural-manual and communication task. *Exp Brain Res*. doi:10.1007/s00221-019-05473-7
- Slobounov, S. M., Cao, C., Sebastianelli, W., Slobounov, E., & Newell, K. (2008). Residual deficits from concussion as revealed by virtual time-to-contact measures of postural stability. *Clin Neurophysiol*, *119*(2), 281-289.
- Slobounov, S. M., Moss, S. A., Slobounova, E. S., & Newell, K. M. (1998). Aging and time to instability in posture. *J Gerontol A Biol Sci Med Sci*, *53*(1), B71-78.

- Slobounov, S. M., Slobounova, E. S., & Newell, K. M. (1997). Virtual Time-to-Collision and Human Postural Control. *J Mot Behav*, 29(3), 263-281. doi:10.1080/00222899709600841
- Smith, M. A., Ghazizadeh, A., & Shadmehr, R. (2006). Interacting adaptive processes with different timescales underlie short-term motor learning. *PLoS Biol*, 4(6), e179. doi:10.1371/journal.pbio.0040179
- Smitsman, A. W. (1997). The development of tool use: Changing boundaries between organism and environment. In C. Dent-Read & P. Zukow-Goldring (Eds.), *Evolving explanations of development: Ecological approaches to organism-environment systems* (pp. 301-329). Washington, D.C.: American Psychological Association.
- Smitsman, A. W., & Bongers, R. (2003). Tool use and tool making: A developmental action perspective. In J. Valsiner & K. J. Connolly (Eds.), *Handbook of developmental psychology* (pp. 172-193). London, UK: SAGE.
- Soechting, J. F., & Lacquaniti, F. (1981). Invariant characteristics of a pointing movement in man. *J Neurosci*, 1(7), 710-720.
- Stoffregen, T. A., Bardy, B. G., Bonnet, C. T., & Pagulayan, R. J. (2006). Postural stabilization of visually guided eye movements. *Ecol Psychol*, 18(3), 191-222.
- Stoffregen, T. A., Pagulayan, R. J., Bardy, B. G., & Hettinger, L. J. (2000). Modulating postural control to facilitate visual performance. *Hum Mov Sci*, 19(2), 203-220.
- Stoffregen, T. A., & Riccio, G. E. (1988). An ecological theory of orientation and the vestibular system. *Psychol Rev*, 95(1), 3.
- Stoffregen, T. A., Smart, L. J., Bardy, B. G., & Pagulayan, R. J. (1999). Postural stabilization of looking. *J Exp Psychol Hum Percept Perform*, 25(6), 1641-1658.
- Sülzenbrück, S., & Heuer, H. (2010). The trajectory of adaptation to the visuo-motor transformation of virtual and real sliding levers. *Exp Brain Res*, 201(3), 549-560.
- Sülzenbrück, S., & Heuer, H. (2012). Enhanced mechanical transparency during practice impedes open-loop control of a complex tool. *Exp Brain Res*, 218(2), 283-294.
- Sülzenbrück, S., & Heuer, H. (2013). Movement paths in operating hand-held tools: tests of distal-shift hypotheses. *J Neurophysiol*, 109(11), 2680-2690.
- Thelen, E., & Smith, L. B. (1994). A dynamic systems approach to the development of perception and action. In: Cambridge, MA: MIT Press.
- Tilley, A. R., Dreyfuss, H., & Wilcox, S. B. (2001). *The measure of man and woman: Human factors in design* (Revised Edition ed.). New York, New York: Wiley.

- Tseng, Y. W., Scholz, J. P., Schoner, G., & Hotchkiss, L. (2003). Effect of accuracy constraint on joint coordination during pointing movements. *Exp Brain Res*, *149*(3), 276-288. doi:10.1007/s00221-002-1357-5
- Turvey, M. T. (1990). Coordination. *Am Psychol*, *45*(8), 938-953.
- Turvey, M. T., & Shaw, R. E. (1995). Toward an ecological physics and a physical psychology. In R. L. Solso & D. W. Massaro (Eds.), *The science of the mind: 2001 and beyond* (pp. 144-169). New York, NY: Oxford University Press
- Vaesen, K. (2012). The cognitive bases of human tool use. *Behav Brain Sci*, *35*(4), 203-218.
- Valk, T. A., Mouton, L. J., & Bongers, R. M. (2016). Joint-Angle Coordination Patterns Ensure Stabilization of a Body-Plus-Tool System in Point-to-Point Movements with a Rod. *Front Psychol*, *7*, 826. doi:10.3389/fpsyg.2016.00826
- van der Steen, M. M., & Bongers, R. M. (2011). Joint angle variability and co-variation in a reaching with a rod task. *Exp Brain Res*, *208*(3), 411-422. doi:10.1007/s00221-010-2493-y
- Van Emmerik, R. E. A., Remelius, J. G., Johnson, M. B., Chung, L. H., & Kent-Braun, J. A. (2010). Postural control in women with multiple sclerosis: effects of task, vision and symptomatic fatigue. *Gait & Posture*, *32*(4), 608-614. doi:10.1016/j.gaitpost.2010.09.002
- van Emmerik, R. E. A., Rosenstein, M. T., McDermott, W. J., & Hamill, J. (2004). A nonlinear dynamics approach to human movement. *J Appl Biomech*, *20*(4), 396-420.
- van Emmerik, R. E. A., & van Wegen, E. E. H. (2002). On the functional aspects of variability in postural control. *Exerc Sport Sci Rev*, *30*(4), 177-183.
- van Wegen, E. E., van Emmerik, R. E., & Riccio, G. E. (2002). Postural orientation: age-related changes in variability and time-to-boundary. *Hum Mov Sci*, *21*(1), 61-84.
- Verwey, W. B., & Heuer, H. (2007). Nonlinear visuomotor transformations: locus and modularity. *Q J Exp Psychol (Hove)*, *60*(12), 1629-1659. doi:10.1080/17470210601100472
- Vygotsky, L. S. (1978). *Mind in society*: Cambridge, MA: Harvard University Press.
- Wallman, J., & Fuchs, A. F. (1998). Saccadic gain modification: visual error drives motor adaptation. *J Neurophysiol*, *80*(5), 2405-2416. doi:10.1152/jn.1998.80.5.2405
- Wiesenfeld, K., Pierson, D., Pantazelou, E., Dames, C., & Moss, F. (1994). Stochastic resonance on a circle. *Phys Rev Lett*, *72*(14), 2125-2129. doi:10.1103/PhysRevLett.72.2125
- Wing, A. M. (2000). Motor control: Mechanisms of motor equivalence in handwriting. *Curr Biol*, *10*(6), R245-248.

- Winter, D. A. (1980). Overall principle of lower limb support during stance phase of gait. *J Biomech*, 13(11), 923-927.
- Winter, D. A., Patla, A. E., Ishac, M., & Gage, W. H. (2003). Motor mechanisms of balance during quiet standing. *J Electromyogr Kinesiol*, 13(1), 49-56.
- Winter, D. A., Patla, A. E., Prince, F., Ishac, M., & Gielo-Perczak, K. (1998). Stiffness control of balance in quiet standing. *J Neurophysiol*, 80(3), 1211-1221.
- Winter, D. A., Patla, A. E., Rietdyk, S., & Ishac, M. G. (2001). Ankle muscle stiffness in the control of balance during quiet standing. *J Neurophysiol*, 85(6), 2630-2633. doi:10.1152/jn.2001.85.6.2630
- Wolpert, D. M., Ghahramani, Z., & Jordan, M. I. (1995). An internal model for sensorimotor integration. *Science*, 269(5232), 1880-1882.
- Woodworth, R. S. (1899). The accuracy of voluntary movement. *Psychol Rev*, 3(3), 1-119.
- Yamamoto, K., Hoffman, D. S., & Strick, P. L. (2006). Rapid and long-lasting plasticity of input-output mapping. *J Neurophysiol*, 96(5), 2797-2801. doi:10.1152/jn.00209.2006
- Yang, J. F., Scholz, J. P., & Latash, M. L. (2007). The role of kinematic redundancy in adaptation of reaching. *Exp Brain Res*, 176(1), 54-69. doi:10.1007/s00221-006-0602-8
- Yuan, N., Fu, Z., Zhang, H., Piao, L., Xoplaki, E., & Luterbacher, J. (2015). Detrended partial-cross-correlation analysis: a new method for analyzing correlations in complex system. *Sci Rep*, 5(1), 8143. doi:10.1038/srep08143
- Zwaferink, J. B. J., Hijmans, J. M., Schrijver, C. M., Schrijver, L. K., Postema, K., & van Netten, J. J. (2018). Mechanical Noise Improves the Vibration Perception Threshold of the Foot in People With Diabetic Neuropathy. *J Diabetes Sci Technol*, 1932296818804552. doi:10.1177/1932296818804552