Dexterous Manipulation: Sensorimotor Learning and Control

By

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A Dissertation Presented in Partial Fulfillment of the Requirements for the Degree Doctor of Philosophy

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August 2013
Humans' ability to perform fine object and tool manipulation is a defining feature of their sensorimotor repertoire. How the central nervous system builds and maintains internal representations of such skilled hand-object interactions has attracted significant attention over the past three decades. Nevertheless, two major gaps exist: a) how digit positions and forces are coordinated during natural manipulation tasks, and b) what mechanisms underlie the formation and retention of internal representations of dexterous manipulation. This dissertation addresses these two questions through five experiments that are based on novel grip devices and experimental protocols. It was found that high-level representation of manipulation tasks can be learned in an effector-independent fashion. Specifically, when challenged by trial-to-trial variability in finger positions or using digits that were not previously engaged in learning the task, subjects could adjust finger forces to compensate for this variability, thus leading to consistent task performance. The results from a follow-up experiment conducted in a virtual reality environment indicate that haptic feedback is sufficient to implement the above coordination between digit position and forces. However, it was also found that the generalizability of a learned manipulation is limited across tasks. Specifically, when subjects learned to manipulate the same object across different contexts that require different motor output, interference was found at the time of switching contexts. Data from additional studies provide evidence for parallel learning processes, which are characterized by different rates of decay and learning. These experiments have provided important insight into the neural mechanisms underlying learning and control of object
manipulation. The present findings have potential biomedical applications including brain-machine interfaces, rehabilitation of hand function, and prosthetics.
ACKNOWLEDGMENTS

I would like to extend my sincerest gratitude to the following people whose guidance and support helped to make this work possible:

Dr. Marco Santello for his professional guidance, continued assistance, invaluable inspiration, motivation, and suggestions throughout the research work. This thesis would not have been complete without his expert advices and unfailing patience. Thank you for helping me to grow as a scientist and as a person.

The members of my dissertation committee, Dr. Stephen Helms Tillery, Dr. Christopher Buneo, Dr. Panagiotis Artemiadis, and Dr. Veronica Santos for their continuous support, honesty and availability through my graduate career.

Dr. Jennie Si, Dr. Natalia Dounskaia, and Dr. David Frakes at Arizona State University, Dr. Ziaul Hasan at University of Illinois at Chicago, Dr. Wei Zhang at College of Staten Island – City University of New York, Dr. Andrew Gordon at Columbia University for the insightful discussion on several important research projects.

Dr. Venkat Krovi and Dr. Tarunraj Singh, at State University of New York at Buffalo who first guide me into scientific research and helped me to establish a solid background in mechanics, control and robotics.

Dr. Robert Howe at Harvard University who provided me opportunity as a visiting student to work on haptic devices, and as a collaborator in several research projects.

The members of the Neural Control of Movement laboratory and all my other academic peers whose friendship and camaraderie has gotten me through the years.
All my friends who let me enjoy the real world besides academic life. I am very grateful for your friendship and encouragement.

My girlfriend Lei who have given me endless support and for continuously making me happy.

And most importantly, my incredible parents and grandparents whose unconditional love and support have helped guide me through all of life.

This work was partially supported by the Bioengineering Research Partnership Grant R01-NS050265 from the National Institute of Neurological Disorders and Stroke (NINDS) at the National Institutes of Health (NIH), a National Science Foundation (NSF) Collaborative Research Grant BCS-0819547, a NSF Collaborative Research Grant BCS-1153034, and a NSF Collaborative Research Grant IIS-0904504.
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Chapter 1

INTRODUCTION

Object manipulation is an important sensorimotor task through which humans learn about, and interact with, the physical world. Among the many tasks humans can perform with their hands, dexterous manipulation is one of the most sophisticated behaviors. The ability to manipulate objects relies on coordinating multiple degrees of freedom arising from the complex musculoskeletal structure, and the abundant sensory input generated by visual, proprioceptive, and tactile sensors. A large cortical network is involved in storing and processing these high dimensional information that guides hand-object interactions (Davare et al., 2011). During the past few decades, a wide range of neurophysiological approaches has been applied to reveal how the Central Nervous System (CNS) shapes motor commands in response to sensory cues from the environment for controlling manipulation tasks. Researchers have focused on quantifying kinematics and kinetics of the hand, sensory feedback from afferents, hand muscle activity, and/or record or stimulate cortical areas. Among these studies, behavioral experiments play an important role for the inference of neural mechanisms underlying manipulative actions and are often studied in conjunction with electrophysiological recordings.

Dexterous manipulation usually involves positioning the fingers on the object and exerting forces through finger-object contacts such that the net finger force acting on the object can counteract environmental forces. Therefore, researchers have measured finger motions and forces to gain insight about how manipulative actions are planned and executed. Analysis of kinematics has revealed how the hand is shaped during reach-to-
grasp tasks as a function of task goal or object properties (Santello and Soechting, 1998; Santello et al., 1998; Cohen and Rosenbaum, 2004; Lukos et al., 2007). Investigation of finger forces has revealed how the digits distribute forces on objects to satisfy physical constraints and maintain grasp stability (Johansson and Westling, 1984; Jenmalm and Johansson, 1997; Burstedt et al., 1999; Jenmalm et al., 2010). Although these results provided ample evidences about how digit positions or forces are controlled independently, until recently little was known about how these two variables interact with each other during manipulation. This limitation was mostly due to the limitations of previous experimental protocols that either constrained placement of finger tips to fixed small areas (force sensors) to measure force, or could not measure finger forces when allowing subjects to choose finger placement. However, manipulation tasks in daily life do not impose tight constraints on finger positions. Therefore, it is important to understand how kinematic and kinetics are planned and coordinated as a whole.

Another limitation of previous behavioral research on dexterous manipulation is lack of systematic investigation about trial-to-trial learning. Sensorimotor learning and adaptation have been extensively examined in reaching tasks (Wolpert et al., 2011). However, the results may not be directly transferable to manipulation due to two fundamental differences: a) learning of object manipulation is usually a very fast process in which both visual cues and prior knowledge of object properties provide rich information about task dynamics; and b) object manipulation often involves making and breaking contacts, which requires sensing of contact forces and positions, as well as coordination between these two variables. In addition, unlike reaching studies, many of the previous research of finger control have used simple tasks (e.g., grasp and lift an
object) that do not require high precision and are usually not quantifiable. Only few studies investigated the formation and retrieval of sensorimotor memory for dexterous manipulation with precise task goal (Salimi et al., 2000; Quaney and Cole, 2004; Bursztyn and Flanagan, 2008; Ingram et al., 2011). In these dexterous manipulation tasks, it is necessary to form an internal representation of the object dynamics which can be updated with trial-by-trial learning to achieve good and stable performance. Furthermore, an object can be manipulated in different contexts, each requiring different hand actions that, in turn, depend on the object properties and hand-object spatial relations. Therefore, it is important to understand whether learning one manipulation would benefit learning of other manipulations with the same object. Due to lack of data, it remains unclear how learned manipulation is represented in the CNS.

This dissertation focuses on exploring the digit position and force coordination in response to trial-to-trial variability in the execution of learned manipulation, as well as the formation and retention of internal representations of dexterous manipulation. The results and discussion of this work are expected to bridge the gap between classic hand control research and other areas of motor neuroscience.

**Hand Preshaping During Reach-to-grasp**

To interact with an object, the hand has to be transported toward the object and the fingers have to be positioned on the object. It is well known that hand transport is usually characterized by a bell-shaped velocity profile with peak velocity occurring at about 40% of the reach (Jeannerod, 1984). When precise finger placement is required (e.g., when fingers has to be placed on small sensor surfaces for force measurement), the deceleration phase of the hand increases (Marteniuk et al., 1990). During hand transport,
finger joint movement is temporally coupled with hand motion. Specifically, the aperture
of the hand usually increases to a maximum width, which is a function of the object size,
in the middle of reach (Goodale and Jakobson, 1991). More detailed analyses revealed
that the posture of the hand gradually conforms to the contours of the object. There are
several factors that have been shown to alter the posture of the hand during the reach and
where the hand lands on the object. For object transportation tasks, subjects tended to
maximize the end-state comfort by choosing sub-optimal hand locations for initial grasp
(Cohen and Rosenbaum, 2004). The shaping of the hand can be also changed according
to the task goals (Ansuini et al., 2006) and object dynamics (Lukos et al., 2007). Attempts
has been made to classify hand postures for grasping by creating grasp taxonomies
(Cutkosky, 1989; Romero et al., 2010). Most importantly, the multi-degrees of freedom
hand can be modulated with joint coordination patterns based on the geometry and
function of the target object (Santello et al., 1998, 2002). The concept of coordination
among finger joints as synergies for controlling hand movements was later supported by
many experiments on human (Mason et al., 2001; Schettino et al., 2003; Todorov and
Ghahramani, 2004) and non-human primates (Mason et al., 2004; Theverapperuma et al.,
2006). These results all suggest that the CNS plans a broad range of finger spatial
distributions for natural hand-object interactions. Mechanically, as interaction forces are
exerted through contact sites between object and hand, the same force could produce
different net output with different contact locations. Modulation of digit positions
implicitly requires the CNS to select appropriate digit forces to ensure task completion.
Constraining finger positions in force measurement tasks may overlook the complex
sensorimotor transformations associated with goal directed grasping and manipulation behavior.

**DIGIT FORCE PRODUCTION DURING MANIPULATION**

Although most of the digit force control research used devices that constrained finger positions, they provided important insight into how the CNS control forces at contact sites. In these experiments, the task goal was often simply lifting or holding a symmetrical object upward with a two-digit precision grasp. The thumb and index finger have to produce opposing normal force to generate friction that sustains tangential force production for object lifting and holding (Johansson and Westling, 1988a; Johansson and Edin, 1993; Jenmalm and Johansson, 1997). Digit force and force rate have been used to assess the anticipatory control of manipulation. It has been shown that, in adults, the force rate profiles are usually bell-shaped with normal and tangential force increasing in parallel (Johansson and Westling, 1984). These patterns were considered to indicate feedforward control based on anticipation of object properties as peak grip force rates scaled with object weight *before* object mass could be sensed, i.e., before object lift (Flanagan et al., 2009). In contrast, multi-peaked force rate profile was documented for young child indicating a shift from feedback control to feedforward control of simple manipulation associated with growth (Forssberg et al., 1991). In addition, force profile usually demonstrates a coupling between normal and tangential forces, which is a function of surface friction coefficients. Subjects also attend to exert digit forces that are slightly larger than the necessary normal/tangential force ratio, i.e., a “safety margin” (Johansson and Westling, 1984). This is because grasp stability is crucial for many dexterous manipulation tasks. An automatic correction mechanism reinforces stability by
increasing normal force in response to micro slips with a delay of about 70 ms (Johansson and Westling, 1987).

Similar to reach-to-grasp kinematics, digit forces are also modulated as a function of object properties and task goals. Local constraints at contact sites have been shown to drive anticipatory control of finger forces. The normal/tangential force coupling could be anticipated through visual information about surface texture, or adjusted to different friction condition within 100 ms of the initial contact (Johansson and Westling, 1984). Similar vision- or tactile- based modulation of digit force as a function of local shape has been also demonstrated (Jenmalm and Johansson, 1997). Gravity-induced forces can also be anticipated. When subjects lift familiar objects, finger forces are scaled to the weight of the object whereas for unfamiliar objects, subjects infer the weight for size cues by assuming a default density (Gordon et al., 1993).

It should be noted that anticipatory control does not ensure correct motor commands to generate finger forces appropriate for a given task. Mismatch between predicted sensory outcome and actual sensory outcome may occur when interacting unfamiliar objects (e.g. incorrect estimation of density or mass distribution), or familiar object with uncertain dynamics (e.g., container with an opaque lid containing an unknown amount of liquid). In these circumstances, digit forces can be quickly updated after a mismatch is detected within a single trial (see next section). Furthermore, humans are able to establish memory processes that store the newly acquired information for future use. It has been proposed that the CNS could update internal models of manipulation based on prediction errors (Flanagan and Beltzner, 2000; Salimi et al., 2000; Flanagan et al., 2001). Associative processes were also demonstrated to link the
visual cues of object properties with appropriate force scaling within a few trials (Cole and Rotella, 2002; Nowak et al., 2007). These memories can be maintained for at least 24 hours (Gordon et al., 1993; Berner et al., 2007). Moreover, unexpected changes in the weight of an object that is lifted over consecutive trials cause normal and tangential force scaling appropriate to the weight experienced in the preceding lift (Johansson and Westling, 1988b). This ‘bias’ has been termed ‘sensorimotor memory’ and shown to be task-independent (Quaney et al., 2003).

**SENSORY FEEDBACK FOR CONTROL MANIPULATION**

In the previous two sections, I showed that hand shaping and digit forces can be modulated as a function of object properties and/or task. Sensory feedback conveying information about object properties is responsible for driving modulation of hand shaping and digit forces. Vision of the object prior to movement initiation can be used to extract information such as object identity and function (affordances), location and orientation, material, texture, as well as shape (Johansson and Westling, 1988b; Gordon et al., 1993; Jenmalm and Johansson, 1997; Salimi et al., 2003; Cohen and Rosenbaum, 2004; Buckingham et al., 2009). However, elimination of visual feedback after reach onset or making contact with the object does not significantly affect hand shaping (Winges et al., 2003) or force production (Lukos et al., 2013). This indicates that the CNS uses vision in the planning phase to guide manipulation in anticipatory fashion, and later relies on tactile and proprioceptive feedback to compensate for making further adjustments. Vision can also modify anticipatory control for both hand shaping (Fan et al., 2006) and force scaling (Loh et al., 2010) during manipulation execution. In these experiments, object
properties were either changed or became visually available during reach, but subjects were able to adapt to the new visual information relatively quickly (150-200 ms).

The “sensorimotor control point” framework has been proposed to describe how the CNS adjust motor output for finger forces based on tactile information (Johansson and Flanagan, 2009). This theory argues that manipulation tasks consist of a sequence of actions separated by contact events that define task subgoals (e.g., finger positioning, object lifting). These contact events can be characterized by specific afferent neural signals in different sensory modalities. When generating motor commands for manipulation, each action-phase controller also predicts the expected sensory events associated with each subgoal. Therefore, the CNS could generate force corrections if mismatches between predicted and actual feedback are detected. In this framework, feedback provided by tactile afferents is particularly important since they provide information directly through physical contact.

In human glabrous skin, there are four populations of tactile afferents that are functionally critical for providing sensory feedback at contact sites (Johnson, 2001). They can be categorized by their response characteristics and their sensitivity to specific mechanical and are defined as either fast (FA) or slow (SA) adapting, and by their location as either superficial (type I) or deep (type II). SA-I afferents end in Merkel cell neurite complexes. They have small receptive fields and relatively high innervation density in fingertips, thus being sensitive to fine spatial details texture, curvature. In addition, SA-I afferents are also sensitive to the tangential force component in the distal direction. FA-I units terminate in Meissner’s corpuscles. They have the highest density and also have small receptive field. Although FA-I units are not sensitive to fine spatial
details, they respond to transient deformation with very high temporal resolution. This allows FA-I to be extremely useful to detect contact events between hand, object, and environment, as well as micro motions between the hand and an object. FA-I units also respond to tangential force in proximal and radial directions. FA-II units end in Pacinian corpuscle. They have large receptive field and are distributed less densely, therefore having no spatial sensitivity. FA-II units are most sensitive to high-frequency vibrations. SA-II units terminate in Ruffini endings and also have low density and large receptive field. They are sensitive to skin stretch. Together with muscle spindles, they contribute in perceiving motion of grasped object, hand configuration, and finger positions. By integrating tactile information encoded in these channels, the CNS is able to acquire robust knowledge about the local constraint of the contact (e.g., friction, surface shape) and dynamic changes of the hand-object interaction (e.g., contact, collision, slip). In addition to firing rate coding, the tactile feedback can also be encoded with spike timing thus providing fast updates about contact and local force directions (Johansson and Birznieks, 2004).

In addition to tactile and visual feedback, proprioceptive feedback also contributes to monitoring manipulation task progression. Joint receptors provide additional information about the configuration of the hand (Edin, 1990). The muscle spindles and Golgi tendon organs (GTOs) provide information about muscle length changes, which is thought to form the basis for perception of movement and relative positions of the finger and hand. In addition, muscle spindles and GTOs allow the acquisition of information about object weight and compliance by providing force feedback (Jami, 1992; Jones and Lederman, 2006). It has been proposed that the
perception of force (Gandevia, 1996) and positions (Gandevia et al., 2006) may also rely on internal neural correlates of motor commands, i.e., corollary discharge or efferent copy.

The use of tactile feedback in sensorimotor control point theory can be illustrated by a task in which subject repeatedly lifting objects with unpredictable weight. The action stage could be defined as reach, load, lift and hold, which are sequentially separated by subgoals of digit contact, object lift, object height. When subjects try to lift an object that is heavy while the previous lift was light, a short load phase is expected due to the existence of sensorimotor memory. However, the absence of the expected sensory feedback about object lift triggers corrective force response recorded as small incremental changes in force until actual lift onset occurs. In contrast, if the subject plans the manipulation for a heavy object, the earlier response in FA-II afferents triggers abortion of the implemented motor command if the lift onset occurs earlier than predicted (Johansson and Flanagan, 2009). This minimum intervention feature (i.e., make a correction only when an event/disturbance impairs attainment of the task goal) in the sensorimotor control point theory agrees with the prediction of optimal control theory (Todorov and Jordan, 2002) in which continuous feedback corrections is not necessary when no task-related error is detected.

**SENSORIMOTOR LEARNING AND MEMORY**

As mentioned in the previous sections, memory is a significant component in anticipatory control of manipulation. The ability to learn, store, and retrieve knowledge about previously performed manipulation tasks is advantageous for adapting to the ever-changing environment, and serves as the backbone for skillful tool use. However, the
The process of memory formation (learning) and retrieval has received less attention in the grasping literature. Most research has focused on force modulation to object weight to lift an object. When subjects initially misjudged the weight, trial-to-trial learning was usually assessed by the improvement in force generation (peak force rate modulation to object weight) that most closely matched the actual weight. The weakness of this approach is the lack of explicit task goal, which therefore prevents the quantification of ‘performance error’ or ‘task success’. However, both of these variables are fundamentally important in motor learning theories (see below). Nevertheless, there is evidence that the internal representation of force scaling could be updated, maintained, and retrieved given appropriate visual cues (Gordon et al., 1993; Flanagan et al., 2003; Nowak et al., 2007).

In addition to memory associated to a specific task, it has also been demonstrated that task-independent memory could be formed and influence the subsequent manipulation (Quaney et al., 2003). A new experimental protocol using objects with asymmetrical mass distribution (Salimi et al., 2000) has been developed to provide more insights about how manipulation is learned and represented. In this protocol, task performance can be assessed by errors made during lift since subjects are required to lift the object straight and have to produce a torque to counter-balance the object’s asymmetrical mass distribution. It has been shown that learning of this dexterous manipulation task has very limited generalizability: following the object’s physical rotation, subjects have to re-learn digit force distribution to generate a torque appropriate to minimize object tilt (Salimi et al., 2003; Bursztyn and Flanagan, 2008). Despite these observations, it remains unclear how manipulation is represented in the CNS.
In contrast to the lack of evidence for manipulation tasks, sensorimotor learning and memory have been studied extensively in other areas of motor neuroscience such as reaching and oculomotor adaptation (Wolpert et al., 2011). In general, all skilled motor behavior relies on learning both control and prediction which can be considered as two reciprocal procedures: control generates motor commands to produce desired consequences whereas the prediction maps motor command (i.e., efferent copy) into expected sensory consequences (Flanagan et al., 2003). The mechanisms underlying these procedures have been traditionally proposed as inverse and forward internal models, respectively (Haruno et al., 2001). The update of internal models is considered to be driven by the error between sensed and predicted sensory outcome on a trial-by-trial basis. This error is assumed to signal the direction of adjustment for the next trial for error reduction. Error-based learning has been demonstrated in many motor adaptation schemes, including saccade adaptation (Kording et al., 2007), visuomotor adaptation (Krakauer et al., 2005), and force-field adaptation (Thoroughman and Shadmehr, 2000). State-space models are often used to describe the error-based updates by defining the estimation of the task dynamics as states that can be modified by errors with learning rates. The exact structure of the model may vary as it could consist of a single learning rate (Ingram et al., 2011) or multiple rates (Smith et al., 2006), and could include context selectors (Lee and Schweighofer, 2009). These models are able to capture many well-known phenomena including interference and savings. However, it remains an open question whether learning of dexterous manipulation can be explained by these models.

Recent research has also demonstrated other sensorimotor learning processes that do not require a ‘model’. These non-error based learning processes could explain
additional performance improvement after error has been minimized, but were also found to be operating in parallel with error-based learning (Huang et al., 2011). Reinforcement learning uses signals, such as success and failure, which do not provide the gradient of error reduction, therefore being exploratory to some extent. Rewards or penalties are given to a certain action that might have led to the success or failure and eventually lead to optimal solutions (Wolpert et al., 2011). Another learning process has been termed use-dependent learning that describe the ability to change motor system through repetition of movements without outcome information (Classen et al., 1998). There is evidence that use-dependent learning could induce bias to the subsequent sensorimotor tasks (Diedrichsen et al., 2010b; Huang et al., 2011; Verstynen and Sabes, 2011).

Sensorimotor learning and memory can also be evaluated from the perspective of retention and generalization. Generalization tests how a learned task could benefit other related tasks. It has been shown that learning might be context dependent and the ability to generalize to other tasks follows a bell-shaped tuning curve depending on the extent to which the new context is similar to the learned one (Ingram et al., 2010). Retention requires subjects to recall a learned task after a break of various durations. A learned motor task can be retained for at least 24 hours (Brashers-Krug et al., 1996; Nowak et al., 2007). However, learning a secondary task in the opposite direction has been shown to interfere with the retention of the first learned one (Krakauer and Shadmehr, 2006). The protection and retrieval of motor memory remain unclear and require further investigation (Pekny et al., 2011).
NEURAL MECHANISMS UNDERLYING MANIPULATION CONTROL

In addition to behavioral studies, brain stimulation, neurophysiological recordings, functional neural imaging, and clinical population have been used extensively to infer the neural mechanisms underlying control and learning of dexterous manipulation. However, due to the limitation of current techniques (e.g., limited spatial and temporal resolution of brain imaging, anatomical differences between human and non-human primates, etc.), the specific functions of each brain region during manipulation control and learning are still debated. Therefore, our understanding about the complex brain circuitry underlying sensorimotor control and learning for dexterous manipulation remains limited.

The classical model of the neural control of reaching and grasping has defined a ‘ventral’ to occipito-temporal stream that would be responsible for semantic object recognition, and a ‘dorsal’ to occipito-parietal stream that would underlie the control of goal-directed actions (Goodale and Milner, 1992). More recently, this classification was demonstrated by functional magnetic resonance imaging (fMRI) that the lateral occipital cortex (LOC) of the ventral stream exhibited greater activity for object perception task, whereas the anterior intraparietal area (AIP) in the dorsal stream was activated more for the actual grasping task (Cavina-Pratesi et al., 2007). The disassociations between the ventral and dorsal streams can be also observed in patients who have lesions in temporal lobes have semantic dementia but preserve the ability of tool use (Hodges et al., 1999).

The dorsal stream can be further identified as two sub systems for reaching and grasping (Grafton, 2010). The dorsomedial circuits in the intraparietal sulcus (IPS) and dorsal premotor (PMd) area contribute to the reaching component of the hand (Grol et al.,
It has been shown that the medial intraparietal area (MIP) and V6A neurons are tuned to reach direction (Andersen and Buneo, 2002). The dorsolateral circuit in the IPS and the ventral premotor (PMv) area are associated with the grasping aspect (Jeannerod et al., 1995). AIP contains both visual and visuomotor neurons that can be selectively activated by specific grasp type (Murata et al., 2000). Neurons in area F5, the rostral part of PMv in macaque monkey, have also been found to be activated by different grasps for different object shapes (Murata et al., 1997; Umilta et al., 2007). In fact, AIP has long been known as the key area for object grasping as it receives projections from a large portion of grasping network and projects to the motor cortex for generating motor commands. Hand shaping and force control were affected by repeated transcranial magnetic stimulation (rTMS) that generates virtual lesion in AIP (Tunik et al., 2005; Davare et al., 2008). AIP also exhibited increased activity when grasp precision increased (Begliomini et al., 2007). Recent evidence showed that interactions exist between the reach and grasp subsystem. Grasp-specific neural activity has been found in the ‘dorsal’ subsystem, such as V6A (Fattori et al., 2010) and PMd (Stark et al., 2007). This could be due to the control of extrinsic muscles crossing the wrist as they would be functionally involved in both reaching and grasping (Davare et al., 2011).

Although ventral and dorsal streams have distinct functions, there is growing consensus that they are functionally coupled for the control of grasping and manipulation. While the dorsomedial visuomotor stream (V6A and PMd) is insensitive to viewing conditions (monocular vs. binocular, i.e., whether stereoscopic depth cue about object angle is available), the AIP-PMv pathway appears to be coupled with LOC to process pictorial depth information (Verhagen et al., 2008). AIP also receives inputs from
the lower bank of the superior temporal sulcus in the areas TEa/TEm and the middle temporal gyrus (Borra et al., 2008). In addition, human diffusion tensor imaging (DTI) has shown strong connections between posterior middle temporal gyrus and IPL when tool use was involved (Ramayya et al., 2010). These results indicate the important role of object identity information in manipulation planning and execution. The interaction between ventral and dorsal streams may also involve memory. Using single-pulse TMS to AIP delivered at movement onset with or without delay between the object presentation and movement onset both disrupted grasp planning. In contrast, TMS on LOC only disrupted grasp kinematics in delayed condition (Cohen et al., 2009). This suggested that ventral stream may maintain grasp related object information when dorsal stream cannot monitor the task in real time.

The primary motor cortex (M1) is necessary for fine control of fingers as it sends connection to finger muscles directly through corticospinal tract (Muir and Lemon, 1983). The output of M1 could be organized with convergence or divergence allowing digits to act synergistically or individually. This has been demonstrated by the spatial overlap in the cortical fields activated by finger movements (Schieber and Hibbard, 1993), as well as the contraction of same muscle elicited by stimulation of different sites within M1 hand area (Donoghue et al., 1992). PMv was found to influence M1 in a grasp-specific fashion both in humans (Davare et al., 2008) and non-human primates (Shimazu et al., 2004). The grasp aperture can be adjusted by PMv as soon as 75 ms after the object changed (Buch et al., 2010). Furthermore, PMv-M1 interactions were found to be driven by information provided by AIP (Davare et al., 2010). M1 has also been proposed to be a candidate area for some learning processes. For example, the direction of thumb
movement elicited by TMS could be biased by repeated execution of thumb abduction (Classen et al., 1998), suggesting use-dependent learning in M1. It has also been shown that rTMS to M1 could inhibit the ability to scale grip force based on the immediately preceding lift, or sensorimotor memory (Chouinard et al., 2005; Nowak et al., 2005).

Subcortical areas are also extensively involved in sensorimotor control and learning. The basal ganglia (BG) have been shown to be crucial for online grasp force scaling (Prodoehl et al., 2009). Patients with degeneration of the basal ganglia (e.g., Parkinson’s disease) exhibit abnormal digit force regulation (Fellows et al., 1998; Rearick et al., 2002). BG could be also facilitating reward-driven learning as the ventral tegmental area has dopaminergic projections to M1 (Wolpert et al., 2011). Another important area is the cerebellum. It has been shown that patients with cerebellar lesions were impaired in performing fast adaptation tasks (Tseng et al., 2007; Rabe et al., 2009). Cerebellum has also been proposed to be involved in forming and updating internal models by monitoring errors (Wolpert et al., 1998; Kawato et al., 2003).

**Rationale for Studies**

As evident from the numerous studies discussed above, studies of grasping have provided substantial amount of knowledge on the behavioral and neural aspects of sensorimotor control and learning of dexterous manipulation such as hand shaping to object properties, force production, and role of sensory feedback and memory. However, our understanding of how the CNS learns and controls dexterous manipulation is far from complete. The overall aim of this dissertation was to provide further insight into sensorimotor learning and control of object manipulation, with the focus on investigation on a) how the digit position and force are coordinated in response to trial-to-trial
variability in the control of manipulation, and b) how dexterous manipulations are
learned, stored, and retrieved. These aims were addressed by five experiments, starting
with emphasis on the coordination of fingers and gradually moving into higher level
representation of the manipulation tasks (Fig. 1.1). Specifically:

The aim of experiment #1 was to investigate how subjects systematically adjust
their digit positions and forces in two-digit precision grasp when object center of mass
was altered, as well as the mutual dependency of the digit positions and forces.

The aim of experiment #2 was to study the planning and control of digit forces
when predictable or unpredictable change occurred at digit positions.

The aim of experiment #3 was to extend the result of the first experiment by
studying the coordination of digit positions and forces when subjects were asked to alter
the grasp configuration (i.e., change of degrees of freedom). This experiment was also
designed to investigate how learned manipulation was represented.

The aim of experiment #4 was to study the effect of visual geometric cues on
learning and retrieval of manipulation tasks as well as the interactions between the
learning of different contexts.

The aim of experiment #5 was to identify the temporal characteristics of the
interference and retention in the paradigm of switching between multiple contexts of
manipulation. In addition, the purpose of this study was to bridge the gap between the
motor learning of manipulation and reaching.
Figure 1.1 Rationale of the studies

The arrangement of the experiments 1-5 with respect to the two main research themes.
OVERVIEW OF EXPERIMENTS

Natural object manipulation requires anticipatory control of digit positions and forces. Most existing work examined only the digit position or the digit force. The first experiment was the first study that investigated digit position and forces together in the learning and control of manipulation tasks (Fu et al., 2010). We asked human subjects to grasp and lift an inverted T-shaped object using precision grip at constrained or self-chosen locations. The task requirement was to minimize object roll during lift. When digit position was not constrained, subjects could have implemented many equally valid digit position-force coordination patterns. However, choice of digit placement might also have resulted in large trial-to-trial variability of digit position, hence challenging the extent to which the Central Nervous System could have relied on sensorimotor memories for anticipatory control of digit forces. We hypothesized that subjects would modulate (1) digit placement for optimal force distribution and (2) digit forces as a function of variable digit positions. While all subjects learned to minimize object roll within the first three trials, the unconstrained device was associated with significantly smaller grip forces but larger variability of digit positions. Importantly, however, digit load force modulation compensated for position variability, thus ensuring consistent object roll minimization on each trial. This indicates that subjects learned object manipulation by integrating sensorimotor memories with sensory feedback about digit positions. These results are discussed in the context of motor equivalence and sensorimotor integration of grasp kinematics and kinetics.

An important open question that arose from the first study was whether the coordination between digit positions and forces was accomplished in a feed-forward or
feedback fashion. The second experiment addressed this question by using a virtual reality environment to induced predictable or unpredictable changes to the relative positions of the digits. We hypothesized that feed forward planning is always implemented, but can be later adjusted when feedback is acquired after making contacts. This was tested using a virtual reality (VR) environment consisted of two haptic devices and a monitor. Subjects’ thumb and index finger were attached to the haptic devices and interaction forces between the digits and the virtual object were simulated. Subjects were initially trained to perform two-digit unconstrained torque production task (90 Nmm) using virtual boxes with either large or small widths (72 mm or 42 mm, L or S). Subjects had to learn to use small and large forces for L and S width respectively, because the two widths would elicit significantly different horizontal digit relative positions. After learning, subjects were tested with random sequence of L and S with (Test A) or without (Test B) visual information about the actual width. The visual cues allowed subject to plan the manipulation forces prior to making contact with the box in Test A. In contrast, for Test B subjects had to make corrections to their motor plan after contact if the actual width did not coincided with the box width they had planned for. We found that subjects were able to eventually to produce the task torque regardless of whether visual information about box width was available. A close examination of the time course of the forces revealed that force development was delayed in all cases for Test B condition. Subjects made appropriate adjustment to digit forces that match the current box width (therefore the digit relative positions) until 250-300 ms after initial contact. This result supports our hypothesis that position dependent modulation of finger forces can be
explained by combining pre-contact feed-forward anticipation and post-contact feedback control.

As an extension of the first study, the third experiment was designed to determine whether manipulation learned with a set of digits can be transferred to grips involving a different number of digits, and possible mechanisms underlying such transfer (Fu et al., 2011). The goal of the task was to exert a torque and vertical forces on a visually symmetrical object at object lift onset to balance the external torque caused by asymmetrical mass distribution. Subjects learned this manipulation through consecutive practice using one grip type (two or three digits), after which they performed the same task but with another grip type, e.g., after adding or removing one digit, respectively. Subjects were able to switch grip type without compromising the behavioral outcome, i.e., the direction, timing, and magnitude of the torque exerted on the object was unchanged, despite the use of significantly different digit force-position coordination patterns in the two grip types. Our results support the transfer of learning for anticipatory control of manipulation and indicate that the Central Nervous System forms an internal model of the manipulation task independent of the effectors that are used to learn it. We propose that sensory information about the new digit placement - resulting from adding or removing a digit immediately after the switch in grip type - plays an important role in the accurate modulation of new digit force distributions. We discuss our results in relation to studies of manipulation reporting lack of learning transfer and propose a theoretical framework that accounts for failure or success of motor learning generalization.
The third study, together with other findings from our lab brought up an interesting question about the limitation of the ability to transfer learned manipulation. The fourth study examined how the central nervous system transforms visual information of object properties into motor commands for manipulation, as well as what limited the transfer of learned manipulation (Fu and Santello, 2012). We designed novel apparatus and protocols in which subjects had to learn manipulations in two different contexts. The first task involved manipulating a U-shaped object that can afford two actions by grasping different parts of the same object. The second task involved manipulating two L-shaped objects that were posed at different orientations. In both experiments, subjects learned the manipulation over consecutive trials in one context before switching to a different context. For both objects and tasks, the visual geometric cues were effective in eliciting anticipatory control with little error at the beginning of learning of the first context. However, subjects failed to use the visual information to the same extent when switching to the second context as sensorimotor memory built through eight consecutive repetitions in the first context exerted a strong interference on subjects’ ability to use visual cues again when the context changed. A follow-up experiment where subjects were exposed to a pseudo random sequence of context switches with the U-shaped object revealed that the interference caused by the preceding context persisted even when subjects switched context after only one trial. Our results suggest that learning generalization of dexterous manipulation is fundamentally limited by context-specific learning of motor actions and competition between vision-based motor planning and sensorimotor memory.
Lastly, we asked the final question about how the central nervous system builds and maintains internal representations of such skilled hand-object interactions. It remains unclear whether the inability to generalize a learned manipulation can be explained by current theoretical frameworks of sensorimotor learning of reaching movements. We performed a series of experiments in which dexterous manipulation performed in different contexts had to be learned and recalled. Subjects interacted with an L-shaped object that had to be dynamically balanced during lifting. Correct execution of this task required subjects to produce a torque on the vertical handle at object lift onset to compensate for the asymmetrical object mass distribution. The direction of the compensatory torque depended on the context, i.e., orientation of the object, which could be changed by the subject by rotating the object 180 degrees about a vertical axis. Subjects learned the action by reducing the torque error within the first block of eight consecutive trials performed in the same context. However, despite the rich contextual cues provided by object geometry, subjects made large errors in anticipating the torque when switching to the second unlearned context immediately after the first one (anterograde interference). Furthermore, anticipatory torque error also occurred when they were asked to recall the first learned action after learning the second one through another block of eight consecutive lifts (retrograde interference). According to classic sensorimotor learning theories, anterograde and retrograde interferences are caused by multiple learning rates of error-driven updates of internal models. However, our results suggest an alternative mechanism underlying interference and retention. Specifically, we identified a practice-induced context-independent sensorimotor memory characterized by a 10 minutes half-life. This memory could inhibit the establishment and retrieval of long
lasting (up to two weeks), context-dependent internal models, thus producing interference on both learning transfer and retrieval.
Chapter 2

ANTICIPATORY PLANNING AND CONTROL OF GRASP POSITIONS AND FORCES FOR DEXTEROUS MANIPULATION

INTRODUCTION

Dexterous object manipulation is learned through the formation and retrieval of sensorimotor memories generated by previous hand-object interactions (Johansson and Westling, 1984, 1988a), thus allowing the modulation of digit forces in an anticipatory fashion, i.e., before the object is lifted (Gordon et al., 1993; Burstedt et al., 1999; Salimi et al., 2000). Anticipating, rather than reacting to, the effect of a given object property, e.g., slip or tilt, leads to a more efficient grasp control than reflex-driven corrective force responses (Johansson and Westling, 1984, 1988b).

Object manipulation is achieved by generating net forces and torques that are appropriate for a desired behavioral outcome, e.g., a compensatory torque at the onset of the manipulation to prevent roll when lifting an object with an asymmetrical center of mass (Salimi et al., 2000). It should be emphasized that net forces and torques can be modulated not only by changing the neural drive to hand muscles, but also by applying digit forces at different locations on the object (Lukos et al., 2007). Therefore, the coordination between digit forces and positions is critical for successful manipulation. However, no previous studies have investigated how subjects learn to control both variables through consecutive manipulations. Specifically, most previous research has focused on how subjects learn digit force modulation by grasping an object at fixed locations often constrained by the position of force sensors. Conversely, studies that examined the modulation of digit placement as a function of task or object properties
have not measured the concurrent modulation of individual digit forces (Cohen and Rosenbaum, 2004; Friedman and Flash, 2007; Lukos et al., 2007, 2008; Ciocarlie and Allen, 2009). Therefore, it is unknown how the removal of digit placement constraints on an object affects digit force control.

It should be emphasized that allowing subjects the choice of digit placement enables them to explore a wider range of relations between digit forces and positions, which has been speculated to lead to a more optimal digit force distribution (Lukos et al., 2007). At the same time, the removal of digit placement constraints might result in significant trial-to-trial variability of digit position. Consequently, reliance on sensorimotor memories of digit forces from previous trials for anticipatory grasp control might not be sufficient to attain a consistent performance. This is because the points of force application in the current trial might be very different from those used in previous trials, thus requiring a digit force distribution that has not been previously experienced.

To determine the extent to which choice of digit placement affects anticipatory force control, we asked subjects to grasp an object with and without digit placement constraints while minimizing object roll during lift. The grip devices were designed to quantify trial-to-trial learning and execution of the anticipatory control of both digit positions and forces. We hypothesized that subjects (1) would learn to modulate digit positions to optimize the distribution of digit forces and (2) would modulate digit forces to compensate for trial-to-trial variability of digit position to attain a consistent grasp performance.
MATERIALS AND METHODS

Subjects

Twenty-four right-handed subjects (12 females and 12 males, ages 20-26) with normal or corrected-to-normal vision took part in the experiments. The subjects had no history of musculoskeletal or neurological disorders. All subjects were naïve to the experimental purpose of the study and gave informed consent to participate in the experiment. The experimental procedures were approved by the Institutional Review Board at Arizona State University and were in accordance with the Declaration of Helsinki.

Experimental apparatus

We asked subjects to reach, grasp, lift, and replace one of two custom-made inverted T-shaped grip devices consisting of a vertical block attached to a horizontal base (Fig. 2.1A, D) using the thumb and index finger of their right hand. The only difference between the two devices was the dimension of the graspable surfaces. Specifically, the graspable surfaces of one of the grip devices consisted of two long parallel PVC bars (length and width: 140 mm and 22 mm, respectively; c, Fig. 2.1A, B). For the second grip device, the graspable surfaces consisted of two collinear circular plates (diameter: 22 mm; c, Fig. 2.1C, D), similar to those of grip devices used by previous studies of two-digit grasping (Salimi et al., 2000, 2003; Bursztyn and Flanagan, 2008). Therefore, one grip device allowed subjects to choose digit placement anywhere along the vertical graspable bars (unconstrained device, Fig. 2.1A) whereas the other constrained digit placement at fixed locations on the object (constrained device, Fig. 2.1D). For both grip devices, the horizontal distance between the two graspable surfaces was 60.7 mm. Each
**Figure 2.1.** Experimental setup.

**A-D.** Two custom-built grip devices used for the study. The ‘unconstrained device’ allowed subjects to choose digit placement on two long graspable surfaces (A, c), whereas the ‘constrained device’ could only be grasped on two small graspable surface (D, c). For both grip devices, the graspable surfaces were mounted on force/torque sensors (B, C, d,) mounted on either side of a central block (e). The force/torque sensors measured the x-, y-, and z-components of forces and torques applied by the thumb and index finger. A magnetic tracker (a) was mounted on the top of each grip device to measure its position and orientation. Two panels (b) were mounted on the front and back of each grip device to block the sensors from view. A light mass (50 g; C, f) was added to the constrained device for the purpose of matching the weight of both devices. Units of the dimensions of the grip device components are in mm. A mass (400 g) was added to the left, center or right slots at the bottom of the device (L, C and R, respectively; A, D). The dimensions of the slot prevented motion of the mass during object movement. Object rolls towards the thumb and finger sides were defined as negative and positive angles, respectively, relative to the vertical (0°) in the gravitational frame of reference. **E,** The position of the subject’s hand relative to the object before reach onset (top view; figure is not to scale). **F,** The difference (error) between the computed and actual center of pressure of loads of different magnitudes applied perpendicular to the graspable surface (c) mounted on the thumb and index finger sensors of the unconstrained device. The center of pressure of each load was computed using the force and torque outputs of each sensor (see text for more details).
A graspable surface was mounted on a force/torque transducer (d, Fig. 2.1B, C; see below for details). The location of the sensors relative to the graspable surfaces were blocked from view by two panels (b, Fig. 2.1A, D) to prevent visual cues that might have biased choice of digit placement in the unconstrained group.

The center of mass (CM) of the object could be changed across blocks of trials by adding a mass (400 g) in one of three slots at the base of the object (Fig. 2.1A, D). The external torques resulting from the added mass with respect to the CM of the unloaded grip device were −255 N·mm, 0 N·mm, and +255 N·mm when the mass was added at the left, center, or right slot, respectively. Note that throughout the text the definitions of “left” and “right” CM locations refer to the mass added on the thumb and index finger side of the grip device, respectively. For both grip devices, the total mass of the object (grip device plus added mass) was 0.796 Kg. The difference between the weights of the graspable surfaces of the two grip devices was eliminated by placing a 50 g mass in the middle of the object (f, Fig. 2.1C).

Experimental task

Subjects were assigned to one of two groups (n = 12 for each group): the unconstrained group used the apparatus with long graspable surfaces, whereas the constrained group used the apparatus with small circular graspable surfaces. Both subject groups were given the same task instructions.

The apparatus was placed on the table at a distance of 30 cm from the hand start position and aligned with the subjects’ right shoulder, the object’s and subject’s frontal planes being parallel to each other (Fig. 2.1E). The subject sat on a height-adjustable chair with the wrist resting on a table, the forearm pronated, the arm oriented in the
parasagittal plane passing through the shoulder, and the right hand in the designated start position. Subjects started the reach movement after a verbal signal from the experimenter. We instructed subjects (1) to reach, grasp, lift and replace the object at a natural speed, (2) to grasp the object only with the thumb and index fingertips on the graspable surfaces, (3) to lift the object vertically to a comfortable height of 15-20 cm above the table while trying to maintain its vertical alignment, i.e., to minimize object roll, (4) hold it for approximately 1 second, and (5) replace it on the table. Subjects were aware of that they could grasp anywhere on the graspable surfaces while avoiding the edges. As the object was located at chest height, subjects had full view of the object and their hand, as well as where they grasped the object.

We also asked subjects to extend the middle, ring and little fingers during the grasp to prevent these fingers from exerting force on either the object or the index finger. Before starting data collection, the experimenter demonstrated the task, after which subjects performed three practice trials. For both the demonstration and the practice trials, the mass was added to the center slot of the grip device. The practice trials were used to allow subjects to become familiarized with object weight and friction. During data collection, one of the experimenters visually verified that subjects complied with all of the above instructions on each trial.

After practice trials, subjects performed three blocks of ten consecutive trials per CM location for a total of 30 experimental trials. Although subjects could not anticipate CM location at the beginning of each block of trials (i.e., trial 1), they were informed that CM location would remain the same for the entire block of trials. Changes of object CM across blocks of trials were performed out of view to prevent subjects from
anticipating object CM location. The consecutive presentation of a given object CM location was used to allow subjects to gain information (implicit learning) about the magnitude and direction of the external torque caused by the added mass. This, in turn, allowed us to quantify the time course of trial-to-trial learning of anticipatory control of digit forces and position. The order of CM blocks of trials was counterbalanced across subjects. On average, the time between each trial and blocks of trials was 10 seconds and 1 minute, respectively.

Data recording

Forces and torques exerted by the thumb and index finger were recorded by two 6-axis force/torques sensors (ATI Nano-17 SI-50-0.5, ATI Industrial Automation, Garner, NC; force range: 50, 50 and 70 N for x-, y- and z-axes, respectively; force resolution: 0.012 N; torque range: 500 N·mm; torque resolution: 0.063 N·mm; d, Fig. 2.1B, C). A magnetic tracker (Fastrack, Polhemus, Colchester, VT) was fixed on the top of the vertical block (a, Fig. 2.1A, D) to record the position and orientation of the object. Force and torque data were recorded through two analog to digital converter boards (PCI-6220 DAQ, National Instruments, Austin, TX; sampling rate: 1 kHz) whereas position data was recorded through a serial port (sampling rate: 120 Hz). Collection of force and position data was synchronized using custom software (LabView, National Instruments, Austin, TX).

Data Processing

After data collection, position data were re-sampled at the same sampling rate of the force data after which both data were run though a fifth order Butterworth low-pass filter (cut-off frequency: 30 Hz). For data processing and analysis, we wrote custom
software in MATLAB (Mathworks, Natick, MA) to compute the following variables (see Fig. 2.2 for example trials from both subject groups):

1. **grip force** and **load force** were defined as the normal and tangential components of each digit force exerted at the digit center of pressure (see below) with respect to the graspable surfaces;

2. **digit center of pressure (CoP)** was defined as the vertical coordinates of the center of pressure of the contact between the finger pad and the graspable surface (c, Figure 1A and D) relative to the origin of the sensor frame of reference corresponding to its center. Digit CoP was calculated from the force and torque components measured by the force/torque sensor relative to its frame of reference. Calibration of each sensor with its graspable surface revealed that x- and y-coordinates of each digit center of pressure could be computed with an accuracy of ±1.2 mm (Fig. 2.1F) above a threshold of 0.75 N in normal force. Positive and negative CoP values denote CoP above and below the center of the sensor, respectively (note that the center of the sensor corresponds to the center of the graspable surfaces; c, Fig. 2.1B, C);

3. **object roll** was defined as the angle between the gravity vector and the vertical axis of the object within the frontal plane of the object. Positive and negative values denote clockwise and counterclockwise rolls, i.e., towards the index finger and thumb side, respectively (Fig. 2.1A);

4. **performance variables.** We used digit force and CoP data to compute the following performance variables: (a) the average of the digit grip forces ($F_{GF}$), (b) the difference between thumb and index finger load forces ($d_{LF}$), and (c) the vertical distance between thumb and index finger CoP ($d_v$). These three variables are important to produce
the *compensatory torque* for minimizing object roll, i.e., balancing the external torque caused by the added mass. Specifically, load force distribution $d_{LF}$ acts on the width between two graspable surfaces resulting in a load force torque, whereas $F_{GF}$ acts on digit placement $d_{y}$ producing a normal force torque. The compensatory torque results from the sum of load force torque and normal force torque (see Appendix A for more details).

The aforementioned variables were computed at the following time points:

1. *digit early contact* was defined as the time at which the grip force of both digits crossed a threshold of 0.75 N and remained above it for 300 ms ($c$; Fig. 2.2). This criterion ensured accurate estimation of digit CoPs at early contact, hence the initial positioning of the digits;

2. *object lift onset* was defined as the time at which the vertical position of the grip device crossed a threshold of 0.5 mm and remained above it for 400 ms ($a$, Fig. 2.2). This is the time before subjects could perceive and react to the external torque. Since the present study was designed to examine anticipatory control of grasping, most of the following analyses focused on the time of object lift onset;

3. *peak object roll* was defined as the maximum initial object roll occurring within ~250 ms after object lift onset ($b$, Fig. 2.2). Peak object roll results from erroneous anticipatory control of fingertip forces and/or contact positions before corrective responses to counter object roll can be made at reaction time latencies (see Lukos et al., 2007 for more details).
The experimental variables analyzed in our study are shown for each time epoch from digit contact to object hold for one representative trial performed with the unconstrained and constrained grip device (left and right column, respectively). Data are from two representative subjects. From top to bottom, traces are object vertical position, object roll, thumb and index finger center of pressure (CoP), grip and load forces. Time epochs and variables shown are object lift onset (a), peak object roll (b), early digit contact (c), and vertical distance between thumb and index finger CoPs at object lift onset (d). The vertical coordinate of digit CoP is defined as positive and negative when it is above or below, respectively, the center (y = 0) of the sensor. Data are from the fifth object lift with the mass added to the left of the object. Peak object roll was minimized to a similar extent by both subjects. However, note that at object lift onset the subject grasped the unconstrained grip device by placing the thumb higher than the index finger and exerted similar load forces with both digits. Even though the subject in the constrained group placed the thumb slightly higher than the index finger, he used a much larger load force with the thumb than the index finger.
Statistical analysis

We performed linear regression analysis to quantify the functional role of compensatory torque modulation at object lift onset and peak object roll during the lift. To quantify the time course of learning the relations between digit CoPs, and forces, we performed repeated measures ANOVA with “CM Location” (left, center, and right) and “Trial” (from trial 1 through 10) as within-subject factors, and “Group” (data from the unconstrained vs. constrained device) as between-subject factors on digit CoPs, forces and compensatory torque. Note that for the analyses of anticipatory control of digit CoPs and forces, we focused on these variables measured at object lift onset. Comparisons of interest exhibiting statistically significant differences ($p < 0.05$) were further analyzed using post hoc tests with Bonferroni corrections.

We found that subjects approached a stable level of performance (object roll minimization) within the first three trials, after which no further improvement occurred. To quantify anticipatory control of digit forces and positions after learning had occurred, we performed a second set of analyses that focused on trials 4 through 10. ANOVA and post hoc tests were performed on digit position and forces to assess the effects of “CM location” and “Group” across the last seven trials within each CM condition. The effects of these two factors were also tested on the variability (standard deviations of means computed over the last seven trials) of compensatory torque, digit position and forces. For these analyses, we used a logarithmic transformation to normalize the standard deviations.

We also examined the correlation between digit CoP vertical distance ($d_y$), digit grip force ($F_{GF}$), and digit load force difference ($d_{LF}$) over the last seven trials of each
Figure 2.3. Time course of object roll and compensatory torque.

Top to bottom rows show the time course of object roll (solid line), compensatory torque (dotted line) and external torque (dashed horizontal line) from right, center and left CM conditions, respectively, for one representative subject (subject #6). Left to right columns show data from trials 1, 2, and 5 obtained from the unconstrained grip device (Fig. 2.1A). To facilitate visual comparison between the external and compensatory torques, both torques are plotted with the same sign even though their signs are opposite. Object lift onset and peak object roll are denoted by the first and second dashed vertical lines, respectively.
CM trial block. Before computing Pearson’s correlation coefficients ($r$), we normalized each of these three variables for each subject by removing the mean of the last seven trials from the value of each trial and dividing the result by the standard deviation of the mean. Comparisons between pairs of correlation coefficients were performed on Fisher’s $z$-transformed coefficients.

**RESULTS**

*Compensatory torque and peak object roll*

Figure 2.3 shows the time course of object roll and compensatory torque (solid and dotted lines, respectively) from one representative subject grasping and lifting the unconstrained device for each object CM location. For successful object roll minimization to occur, subjects have to learn to match the external torque with a compensatory torque of equal magnitude and opposite sign *before* the object is lifted (note that, for graphical purposes, in Fig. 2.3 the external torque is plotted with the same sign as the compensatory torque). Therefore, subjects have to anticipate, rather than react to, the external torque. Such anticipation could not occur on trial 1 since CM location is unknown to the subject, as shown by the little or no compensatory torque exerted on the object prior to lift onset for any of the three CM object location (Fig. 2.3, left column). As a result, for the right and left CM conditions (Fig. 2.3, top and bottom rows, respectively) the object undergoes a large roll ($\pm 15^\circ$). For the center CM condition (Fig. 2.3, middle row), the added mass does not create an external torque on the object, and therefore only a small object roll ($< 5^\circ$) during object lift occurs.

However, subjects learned to compensate for asymmetric mass distribution and object roll following a single trial (trials 2 and 5, middle and right columns, respectively;
Fig. 2.3). This was accomplished by generating a compensatory torque in the direction opposite to that caused by the added mass (right and left CM) starting at ~400 ms before object lift onset. Consequently, a significant reduction in peak object roll (within ±3°) is observed in these trials relative to trial 1.

The compensatory torque produced at object lift onset was a good predictor of the grasp performance, i.e., peak object roll, for both subject groups and all CM conditions. This was confirmed by a strong linear correlation between compensatory torque and peak object roll with an r-value of 0.89 (p < 0.001; data pooled across all trials, subjects, CM locations and grip devices). Therefore, we used compensatory torque as a measure of learning anticipatory grasp control for object roll minimization throughout the rest of the manuscript.

**Learning of compensatory torque**

Compensatory torque generation (i.e. roll minimization) was learned equally well within the first three trials by both subject groups (Fig. 2.4A and B; no significant interaction Group × Trial). Therefore, here we describe data from the *unconstrained* group only. On trial 1, subjects exerted little or no compensatory torque (mean ± SE: −26.6 ±16.9 N·mm, −14.1 ±33.8 N·mm, and 22.5 ±17.5 N·mm for left, center and right CM, respectively). This large between-subject variability in the compensatory torques on the first trial reflect idiosyncratic preferences in how each subject chose digit force and CoPs distributions in response to the unpredictability of object CM. Note also that, unlike the compensatory torques developed after trial 1, the direction and magnitude of these torques are not correctly scaled to the external torque.
Figure 2.4. Anticipatory control of compensatory torque as a function of trial.

A, B. The performance curves of compensatory torque at lift onset for each object CM location as a function of trial averaged across all subjects (± S.E.) for the unconstrained and constrained group, respectively. Dashed horizontal lines denote the external torque caused by the added mass (note that the external and compensatory torques are plotted using the same convention used for Fig. 2.3). Asterisks indicate significant differences ($p < 0.05$) between trials.
However, on trial 2 and 3 the compensatory torque gradually approached the external torque and settled at a mean value of $-188.3 \, (±13.9) \, \text{N} \cdot \text{mm}$ and $189.7 \, (±17.0) \, \text{N} \cdot \text{mm}$ (right and left CM, respectively) from trial 4 through 10, i.e., $\sim30\%$ smaller than the external torque (Fig. 2.4A, horizontal dashed lines). The compensatory torque at lift onset for the center CM condition changed little after trial 1, reaching a mean value of $11.3 \, (±13.1) \, \text{N} \cdot \text{mm}$. The learning curves of compensatory torque of both groups were consistent with the learning curve of peak object roll reported by previous literature (e.g., Salimi et al., 2000).

Despite the fact that subjects’ performances were different for center vs. left and right CM locations (significant CM $\times$ Trial interaction: $F_{(18,396)} = 38.67, p < 0.001$), post hoc comparisons performed between neighboring trials (1 vs. 2, 2 vs. 3, etc.) revealed that subjects learned to generate anticipatory compensatory torque to minimize object roll early in the trial sequence (Fig. 2.4), the only significant difference in compensatory torque occurring between trial 1 and trial 2 ($p < 0.05$ for both right and left CM in both groups).

Although subjects learned to generate compensatory torque equally well, the underlying compensatory mechanisms differed between two subject groups. Figure 2 shows data from the fifth lift by a representative subject from each group. The subject in the unconstrained group placed the thumb CoP higher than the index finger CoP, thus exhibiting a greater vertical separation of the digit CoPs ($d_y$) at object lift onset than the subject from the constrained group. In contrast, the subject from the constrained group exerted a larger load force with the thumb than the index finger, thus revealing a much larger load force asymmetry ($d_{LF}$) than the subject from the unconstrained group. Digit
Figure 2.5. Learning of digit placement.

A, B. The vertical distance between thumb and index finger CoPs ($d_y$) as a function of trial at object lift onset and early contact, respectively. Data shown in top and bottom rows are from the unconstrained and constrained subject groups, respectively. All data are averages of all subjects (± S.E.).
placement distribution ($d_y$), digit load force asymmetry ($d_{LF}$), and digit grip force ($F_{GF}$) contribute to the magnitude and direction of the compensatory torque (see Appendix A). Therefore, below we present the analyses of each of these three variables.

**Learning of digit positions**

The centers of pressure (CoP) of thumb and index finger at object lift onset were modulated as a function of trial and object CM location. Figure 5A shows $d_y$ averaged across all subjects as a function of trial for each CM location and subject group. On the first trial, subjects tended to position the digits collinear to each other regardless of CM location. After trial 1, when lifting the object during the center CM condition, thumb and index finger CoP tended to remain collinear across all subsequent trials in both groups. In contrast, left and right CM locations elicited opposite patterns of digit CoP modulation. Specifically, the thumb CoP tended to be positioned progressively higher and lower relative to the index CoP for the left and right CM locations, respectively, and for both subject groups (significant CM × Trial interaction: $F_{(18,396)} = 18.34, p < 0.001$; no Group × Trial interaction, $p > 0.05$). Similar to the above results on compensatory torque, post hoc comparisons performed between neighboring trials revealed that the only significant change in $d_y$ occurred between trial 1 and 2 but only for right and left CM in both groups ($p < 0.05$).

In addition to measuring the digit CoP vertical distance at object lift onset, we also examined the digit CoP vertical distance at early contact (see Methods). The separation of the thumb and index finger occurs at initial contact, suggesting that the hand has been rotated during reach in the direction opposite to the anticipated torque (unconstrained group, Fig. 2.2; Fig. 2.5B). Furthermore, the digits do not seem to move
vertically on the contact plates after initial contact. Statistical analysis of digit CoP at early contact revealed a very similar pattern to that described above for digit CoP vertical distance at object lift onset (Fig. 2.5B), i.e., a significantly different CoP distributions as a function of object CM location as a function of practice (significant CM × Trial interaction: $F_{(18,396)} = 6.62, p < 0.001$). Post hoc comparisons between neighboring trials revealed that the only significant change in $d_y$ at early contact occurred between trial 1 and 2 for the right CM conditions in the *unconstrained* group ($p < 0.05$). For the left CM, there was a significant effect of trial within the left CM condition in the *unconstrained* group ($p < 0.05$) but no significant difference between adjacent trials. However, the center CM condition in the *unconstrained* group and all CM conditions in the *constrained* group did not elicit a significant modulation of $d_y$ at early contact ($p > 0.05$). Note that the digit CoPs at early contact are more variable than those at lift onset (Fig. 2.5A and B), suggesting that some further repositioning occurs in both subject groups as grip and load forces are applied prior to lift.

**Learning of digit forces**

In both subject groups, grip forces ($F_{GF}$) tended to increase as a function of trial for left and right CM conditions and decrease for center CM (Fig. 2.6A; significant CM × Trial interaction, $F_{(18,396)} = 4.09, p < 0.001$; no Group × Trial interaction, $p > 0.05$). However, post hoc analyses showed that these trends were significant only for the left CM condition in both groups ($F_{(9,99)} = 9.08, p < 0.001$ and $F_{(9,99)} = 2.82, p < 0.005$ for *unconstrained* and *constrained* groups, respectively).
Figure 2.6. Learning of digit forces.

A, B. Averaged thumb and index finger grip forces ($F_{GF}$), and the difference between thumb and index finger load forces ($d_{LF}$), respectively, at object lift onset as a function of trial and object CM location for the unconstrained and constrained subject group (left and right columns, respectively). All data are averages of all subjects (±S.E.).
Subjects also used different patterns of load force distribution across CM locations (Fig. 2.6B). When lifting the object in the center CM condition, thumb and index finger load forces remained symmetrical across all trials in both subject groups. In contrast, the difference between thumb and index finger load forces ($d_{LF}$) tended to be modulated as a function of trial early in the trial sequence to then remain relatively constant for lateral CM conditions (left and right) for both subject groups. On the first trial, subjects tended to use nearly symmetrical load forces for both CM and subject groups. After trial 1, load forces applied by the thumb and index finger were applied asymmetrically to counteract the CM asymmetries. Specifically, the thumb load force tended to be progressively larger and smaller relative to the index load force for the left and right CM conditions, respectively, in both subject groups (significant CM × Trial interaction: $F_{(18,396)} = 11.12, p < 0.001$; no Group × Trial interaction, $p > 0.05$). However, post hoc comparisons between neighboring trials revealed that only the constrained group modulated $d_{LF}$ significantly from trial 1 to 2 for both CM conditions (both $p < 0.05$).

*Digit placement and forces during stable performance*

All subjects attained a stable level of performance within the first 3 trials (Fig. 2.4). Therefore, trial 3 was used as the cut-off after which (trial 4 through 10) we defined subjects’ performance as stable, i.e., the trial after which further practice did not lead to statistically significant improvements in compensatory torque at object lift onset and object roll minimization. Therefore, the following analyses focused on both magnitude and variability of digit forces and CoP during the last seven trials of each block.
Figure 2.7. Digit placement and forces across trial 4 to 10.

A-C, The vertical distance between thumb and index finger CoPs ($d_y$), the average grip force ($F_{GF}$), and digit load force difference ($d_{LF}$), respectively for left (L), center (C) and right (R) CM locations for each subject group and averaged across the last seven trials of each CM block. Data are means of all subjects (±S.E.).
The two groups showed significant differences in overall strategy with 
*constrained* trials focusing almost entirely on grasp kinetics (force application), and 
*unconstrained* trials relying primarily on kinematics (hand placement on the object). 
Furthermore, subjects from the *constrained* group used higher grip force than subjects 
from the *unconstrained* group. While the amplitude of force application and digit 
alignment differed between groups, the overall direction and resultant forces (net 
compensatory torque) applied by the two groups were similar.

Although the *constrained* group also showed digit position modulation to object 
CM, this modulation was significantly smaller than that exhibited by the *unconstrained* 
group in left and right CM conditions (Fig. 2.7A, Table 2.1. 3-way ANOVA on factors 
Group, CM, and Trial; CM × Group interaction: \( F_{(2,44)} = 15.94, p < 0.001 \); post hoc tests 
on Group effects within right CM: \( p < 0.05 \); non-significant Group effects within left 
CM). Another important observation is that subjects exhibited a larger modulation of \( d_y \) 
for right than left CM, but only in the *unconstrained* group (post-hoc tests on CM effects: 
\( p < 0.05 \)).

The *constrained* group used larger grip force than the *unconstrained* group 
across trial 4 to 10 (Fig. 2.7B, Table 2.1. 3-way ANOVA on factors Group, CM, and 
Trial; main effect of CM: \( F_{(2,44)} = 5.53, p < 0.01 \); main effect of Group: \( F_{(1,22)} = 9.47, p < 
0.001 \)). Post hoc tests also revealed that subjects used significantly larger grip force only 
for left and right CM conditions (\( p < 0.05 \)).

As expected, the *constrained* group showed larger asymmetry of digit load 
forces than the *constrained* group in left and right CM conditions (Fig. 2.7C, Table 1.2; 
significant CM × Group interaction: \( F_{(2,44)} = 9.24, p < 0.001 \); post-hoc tests on Group 
...
effects within left and right CM: both \( p < 0.05 \). Similar to the differences between the two CM conditions in the extent of digit CoP modulation, subjects exhibited a larger modulation of \( d_{LF} \) for left than right CM (post-hoc tests on CM effects within the *unconstrained* group: \( p < 0.05 \); non-significant CM effects within *constrained* group).

**Production of compensatory torques: covariation of digit CoPs and digit forces under different CoP variability**

The above analysis revealed that digit forces and positions at object lift onset were controlled differently depending on whether or not the grip device constrained digit placement. Surprisingly, however, subjects from the *unconstrained* and *constrained* groups learned to generate compensatory torques with similar consistency (Fig. 2.4A, B, Table 1.2.). This was confirmed by a lack of a significant Group effect on the standard deviation of \( T_{com} \) of the mean compensatory torque averaged from trial 4 to 10 (\( p > 0.05 \)). This result is remarkable particularly when considering that the variability of digit placement at object lift onset of the *unconstrained* group was much larger than the *constrained* group (Fig. 2.5A). With regard to standard deviation of individual digit CoP, we found only a significant main effect of Group (\( F_{(1,22)} = 60.96, p < 0.001 \)). The standard deviation of \( d_y \) was significantly different across subject groups and CM (\( F_{(1,22)} = 26.64 \) and \( F_{(1,22)} = 10.34 \), respectively; both \( p < 0.001 \)).

In contrast, there was no significant difference between the two groups with regard to the standard deviation of either digit load forces or grip forces (\( p > 0.05 \)). Recall that the two grip devices share the same mechanics. \( T_{com} \) is the net result of \( d_y \), \( F_{GF} \), and \( d_{LF} \). Therefore, the large variability in digit placement in the *unconstrained*
**Table 2.1** Summary of performance variables across trial 4 to 10.

<table>
<thead>
<tr>
<th>Center of Mass Condition</th>
<th>$d_y$ (mm)</th>
<th>$d_{LF}$ (N)</th>
<th>$F_{GF}$ (N)</th>
<th>$T_{com}$ (Nmm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unconstrained</td>
<td>7.1 ±1.7</td>
<td>16.6 ±1.3</td>
<td>2.3 ±0.7</td>
<td>189.7 ±17.0</td>
</tr>
<tr>
<td>Constrained</td>
<td>4.2 ±0.6</td>
<td>20.7 ±1.2</td>
<td>3.9 ±0.7</td>
<td>201.6 ±16.2</td>
</tr>
<tr>
<td>Unconstrained</td>
<td>0.7 ±0.5</td>
<td>14.6 ±1.1</td>
<td>−0.4 ±0.4</td>
<td>11.3 ±13.1</td>
</tr>
<tr>
<td>Constrained</td>
<td>−1.1 ±0.9</td>
<td>17.1 ±0.9</td>
<td>0.5 ±0.4</td>
<td>−7.8 ±12.3</td>
</tr>
<tr>
<td>Unconstrained</td>
<td>−11.8 ±1.8</td>
<td>14.6 ±1.2</td>
<td>−1.1 ±0.7</td>
<td>−188.3 ±13.9</td>
</tr>
<tr>
<td>Constrained</td>
<td>−2.6 ±0.7</td>
<td>20.0 ±0.6</td>
<td>−3.4 ±0.6</td>
<td>−172.1 ±18.9</td>
</tr>
</tbody>
</table>

Data are mean values (±S.E.) of distance between digit center of pressure ($d_y$), difference between digit load forces ($d_{LF}$), average grip force ($F_{GF}$), and compensatory torque ($T_{com}$) averaged across trial 4 to 10 for each center of mass condition and subject group.
group was effectively compensated by digit force modulation such that trial-to-trial variability of $T_{com}$ was similar to the \textit{constrained} group.

The significantly different variability in digit placement between the \textit{unconstrained} and \textit{constrained} subject groups raised the question of how subjects modulated, on a trial-to-trial basis, digit forces as a function of position. We addressed this question by performing linear regression analyses on data normalized to zero mean and unit standard deviation (see Methods). Most importantly, we observed significant negative correlations between $d_y$ and $d_{LF}$ in both the \textit{unconstrained} group ($r = -0.615$, $p < 0.001$) and \textit{constrained} group ($r = -0.263$, $p < 0.001$). Furthermore, the correlation coefficient of the \textit{unconstrained} group was significantly larger than that of the \textit{constrained} group ($p < 0.001$). We also found that center CM was different from left and right CM conditions, therefore we tested the correlation between $d_y$ and $d_{LF}$ on center and lateral CMs separately.

For the center CM condition, both subject groups showed negative correlations between $d_y$ and $d_{LF}$ (Fig. 2.8C and D). This correlation was significantly larger in the \textit{unconstrained} than in the \textit{constrained} group ($p < 0.05$). For left and right CM conditions, the \textit{constrained} group did not exhibit a significant correlation anymore (Fig. 2.8B). In contrast, negative correlations were still found for the \textit{unconstrained} group (Fig. 2.8A). Lastly, the strength of the correlation between $d_y$ and $d_{LF}$ was significantly larger in the \textit{unconstrained} than in the \textit{constrained} group ($p < 0.05$). We found no significant correlation between $d_y$ and $F_{GF}$ (Fig. 2.8E and F) or between $d_{LF}$ and $F_{GF}$ in either subject group.
Figure 2.8. Relations between digit centers of pressure, grip force, and load force.

A, B, $d_y$ vs. digit load force difference ($d_{LF}$) from the left and right CM conditions for unconstrained and constrained subject group, respectively. C, D, $d_y$ vs. $d_{LF}$ from the center CM condition for the unconstrained and constrained subject group, respectively. E, F, digit CoP vertical distance ($d_y$) vs. grip force for the unconstrained and constrained subject group, respectively. Data are from trials 4 through 10 from each subject and CM condition and are shown in normalized form (see text for more details). The Pearson’s $r$-value and corresponding $p$-value are shown in each panel (n.s. = not significant, $p > 0.05$).
**DISCUSSION**

Our task required lifting an object while minimizing roll caused by an external torque due to asymmetric mass distribution. Consistent with previous studies of implicit learning of grasping within blocked trials, subjects learned to minimize object roll within the first three trials by changing digit placement (Lukos et al., 2007, 2008) and/or altering force distribution applied by the fingers (Salimi et al, 2000). The compensatory torque generated by the subjects developed from object contact through lift onset, its magnitude approaching that of the external torque (Fig. 2.3). Despite considerable trial-to-trial variability of digit positions, subjects learned to minimize the variability of the compensatory torque by modulating digit forces as a function of the digit positions. Interestingly, removal of digit placement constraints did not affect the rate of learning of the compensatory torque even though subjects implemented different relations between digit positions and forces when grasping the two grip devices (Fig. 2.5 and 2.6). These results are discussed in relation to the neural mechanisms underlying the sensorimotor integration of grasp kinematics and kinetics.

*Functional significance of anticipatory modulation of digit placement and forces for object manipulation*

In order to compensate for the torque generated by asymmetric mass distribution in the test objects, subjects could have altered the applied grip force, load force and/or hand position on the object. A major finding of this study was the inverse relation between the load forces applied by the thumb and index finger, and the vertical spacing between the two fingers.
We found that removal of the digit placement constraints during the stable performance phase (trials 4-10) resulted in (a) a larger digit spacing of the thumb and index finger (Fig. 2.5A), (b) a more symmetrical sharing of load forces between these fingers (Fig. 2.6B), and (c) smaller grip forces (Fig. 2.6A) in the *unconstrained* group than in the *constrained* group. These results suggest that subjects spontaneously chose to alter digit spacing and hand placement on the object, and reduced the magnitude of grip forces and load force asymmetry. These data support our hypothesis that modulation of digit placement on objects contributes to optimal distribution of digit forces. This strategy might be associated with a smaller energy cost while avoiding implementation of largely asymmetric digit load forces, as well as prevent damage to the hand or object from excessive force. This behavior is reminiscent of force optimization implemented by humans exerting grip forces slightly above the minimum necessary to attain stable grasping (safety margin; Johansson and Westling, 1984). Our findings suggest that subjects are able to optimize forces also through an anticipatory adjustment in grasp posture.

The fact that the two CM conditions elicited different digit positions and force patterns in the unconstrained group suggests that factors other than force minimization may play a role in grasp planning. The asymmetric biomechanical capabilities of the two digits might also be important, thereby allowing the thumb to exert a larger load force than the index finger (Salimi et al. 2000, 2003), and reducing the need for wide digit spacing in trials with the left CM.
Variability in digit placement and covariation with load forces

As predicted, a significantly larger variability in digit position was found when digit placement constraints were removed. Subjects might have been unable to store an accurate memory representation of the digit positions without visual cues provided by force sensors. Conversely, errors in reproducing a desired fingertip position might have resulted from errors in sensorimotor transformations (Soechting and Flanders, 1989). Psychophysical evidence, however, indicates that subjects have an accurate sense of fingertip position when matching object size by modulating finger span (Chieffi and Gentilucci, 1993; Santello and Soechting, 1997). Alternatively, subjects might have not tried to reproduce the same digit placement on each trial due to their ability to use a force compensation strategy (see below).

It should be emphasized that similar trial-to-trial variability of compensatory torque was found in the constrained and unconstrained groups. This implies that subjects learned to compensate for digit placement variability through force modulation. These findings indicate that planning and execution of digit forces at object lift onset incorporated digit placement on a trial-to-trial basis. This is the first direct evidence that anticipatory force modulation on a given trial depends not only on sensorimotor memories of digit forces and positions from previous trials, but also on the actual position of each fingertip that requires afferent signals. Such position-dependent force modulation was not necessary to the same extent when the position variability was constrained by the grip device.
Neural mechanisms underlying the concurrent modulation of digit placement and forces

The attainment of a stable compensatory torque despite trial-to-trial variability in digit placement and forces suggests the existence of a higher order motor plan that specifies the task goal independent of the different ways in which it can be reached, i.e., motor equivalence (Lashley, 1930; Cole and Abbs, 1986; Kelso et al., 1998). It has been suggested that kinematic parameters are stored independently from the effectors used to perform a given task, the neural correlates residing in secondary and tertiary cortical areas including premotor dorsal cortex and middle intraparietal area (Rijntjes et al., 1999). However, to the best of our knowledge, no study has addressed how kinematics and kinetics are coordinated to attain motor equivalence in grasping. Here we propose a theoretical framework that accounts for our findings of digit position-dependent force modulation.

(a) Planning of digit positions and forces before contact. Planning of digit positions and forces is thought to involve anterior intraparietal area (AIP), as indicated by the larger variability of digit placement and disruption of force coordination caused by transcranial magnetic stimulation (TMS) of AIP ~250 ms and ~150 ms, respectively, before contact in grasp-to-lift tasks (Davare et al., 2007). In our experiment, the unconstrained group could have planned digit positions based on digit placement used in previous trials as well as past experience (manipulating objects with similar properties). For the constrained group, physical landmarks determined the position of the digits by providing visual cues for digit position planning. Although monitoring of digit placement is likely driven by visual feedback, further work is needed to determine its role for contact point modulation.
With regard to digit force planning, previous grasp research constraining digit placement suggests that subjects quickly learn to program digit forces as indicated by a stereotypical force development shortly after contact (Forssberg et al., 1991; Gordon et al., 1993). We speculate that some degree of digit force planning occurs also when digit placement is not constrained. However, our data suggest that such force planning might require a higher degree of online monitoring and corrections to compensate for the large variability of digit placement.

(b) Sensing of digit placement from contact to object lift onset. Tactile afferents accurately encode information of contact timing, force direction, contact sites on the fingertip, and frictional condition in a very rapid fashion (Birznieks et al., 2001; Johansson and Birznieks, 2004). The extent to which tactile input contributes to sensing of the distance between digit centers of pressure is unknown. Nevertheless, this information is likely to be derived from integrating tactile input with visual and proprioceptive inputs.

(c) Digit-position dependent modulation of digit load forces. For the unconstrained group, the vertical distance between digit centers of pressure at early contact closely resembled that found at object lift onset (Fig. 2.2, “c” and “d”, respectively; Fig. 2.5A and B). This indicates that despite the fact that small changes in digit CoPs occur as forces are being exerted, the relative position of the fingertips at object lift onset was already defined shortly after contact. Following contact, a comparison is made between expected (desired) vs. actual feedback of digit placement. A mismatch would trigger a change in the planned digit forces and possibly update sensorimotor memories.
It has been suggested that force upgrades driven by discrepancies between expected vs. actual feedback involve primary motor cortex, inferior parietal cortex and cerebellum (Jenmalm et al., 2006). Johansson and colleagues have proposed a model for digit force control based on comparing expected vs. actual sensory consequences of the motor plan (Johansson and Flanagan, 2009) at behaviorally crucial epochs of the task, i.e., ‘sensorimotor control points’. These comparisons may trigger corrective modulation of digit forces if a mismatch between planned and actual forces is sensed. Our findings extend this model by introducing several new elements: (1) sensing of digit position, (2) integration of sensed digit position with planning of digit forces, and (3) comparison between the expected sensory consequences associated with the desired vs. sensed compensatory torque to correct digit force distributions at object lift onset.

The present results might lead to the improvement of computational models of how object manipulation is learned and controlled by introducing a new, yet crucial component in the study of grasping: digit placement and force coordination. We propose that the sensorimotor processes revealed here might account for our fundamental ability to manipulate objects despite variable digit positions in everyday grasping and tool use.
Chapter 3

COORDINATION BETWEEN FINGER FORCES AND POSITIONS: ANTICIPATION AND FEEDBACK CONTROL

INTRODUCTION

Dexterous manipulation is a motor task that involves physical interactions between digits and objects through contact sites. In the past three decades, most studies have been focusing on how the central nervous system (CNS) control digit forces using constrained precision grasps. It has been shown that the digit forces can be planned before actual contact based on visual information about the object properties and/or sensorimotor memory built through preceding trials. For instance, vision of the object prior to movement initiation can be used to extract information such as object identity and weight (Gordon et al., 1993), location and orientation, material (Buckingham et al., 2009), texture (Johansson and Westling, 1984), as well as local shape (Jenmalm and Johansson, 1997), all of which could influence the scaling of digit forces. If the visual perception is congruent with the actual object properties, the digit forces could be developed in a feed-forward fashion, usually featuring a ‘bell-shaped’ force rate profile (Johansson and Westling, 1984). When the visual information is not accurate or even unavailable before contact, the CNS compensates for the mismatch by changing the force scaling after receiving information from somatosensory afferents. This mechanism has been nicely described in a sensorimotor control point framework, which proposed that the CNS compares the actual sensory input with the expected sensory event (Johansson and Flanagan, 2009). The common sensory events are usually transient mechanical events, such as digit contact, grasp stability, and object lift onset. To enable fast response to the
mismatches, the framework also proposed spike timing as the means to encode such events in addition to classic rate coding.

In our recent studies using manipulation tasks that did not constrain the digit placement, we have shown that subjects could also scale their digit forces to variable digit relative positions (Fu et al., 2010, 2011). The variability in digit relative positions could be attributed to natural end-point variability caused by the noise during reach, and/or active digit planning to achieve optimality. The first one requires the CNS to adjusts the digit forces if mismatch occurred between the actual digit positions and planned digit position, whereas the second indicates the CNS could have planned the digit positions and forces together as a unit before contact. However, these studies had no power to distinguish the two, thus preventing us to further understand the capability of the CNS to perform dexterous manipulation. In the present study, we address this question by using a virtual reality (VR) setup that could induce predictable and unpredictable change of digit positions, both require significant adjustment to digit force scaling. We hypothesized that a) subjects could plan digit forces correctly based on visual information about the digit positions available before contact, and b) if subjects could not predict the digit positions due to lack of vision, they plan the digit forces based on the sensorimotor memory built from preceding trial and make adjustment quickly after contact if the mismatch between actual and expected digit positions are detected.

**Materials and Methods**

*Subjects*

Twelve healthy right-handed subjects (18–34 years of age, 7 females) participated in this study. All participants were naive to the purpose of the study and gave
their informed written consent according to the Declaration of Helsinki. The protocols were approved by the Office of Research Integrity and Assurance, Arizona State University.

Apparatus

Two haptic devices (Phantom premium 1.5, Geomagic Inc.) were attached to the thumb and index finger (Fig. 3.1A) through custom-made interfaces that were designed to fit the shape of the finger pad and fixed to the finger tips through Velcro strips wrapped on the nail side. Each interface was connected to the arm of the haptic device through a tri-axis gimbal joint, allowing each digit to move and rotate in three dimensions each. The three-dimensional (3D) positions of the tips of the thumb and index finger were recorded through internal encoders for the computation of the forces that are applied to the fingers. The rendering of the virtual environment was achieved using CHAI3d library (Conti et al., 2005). The two fingertips were modeled as two spheres of 9-mm radius whose centers corresponded to the endpoints of the two devices, i.e., the center of the real fingertips. The contact between the fingertips and virtual objects in the virtual reality (VR) environment are based on a stick-slide contact point model which could generate compelling haptic properties such as shape, stiffness, and friction (Conti et al., 2005). The stiffness of the graspable surface was set at 0.5 N/mm.

Subjects were asked to perform a series of tasks in the VR (see below for details), and their digits were always constrained within a virtual plane parallel to the subjects’ frontal plane. All manipulation tasks were located in this plane. Constraint forces were applied to the finger tips when they moved outside of the plane to ensure that subjects remained within the vertical plane. These constraint forces were provided by a
**Figure 3.1.** Experimental apparatus and protocol.

**A,** the arrangement of the haptic devices and monitor. **B,** the virtual environment. a, b, c, and d represent the thumb avatar, index finger avatar, the cursor, and the target. **C,** the mechanics of the manipulation task in which two fingers produce forces $F_T$ and $F_I$ on the virtual box. $F_{TE}$ and $F_{IE}$ are the decomposed effective finger forces that generate the torque to accomplish the task. **D,** the arrangement of the experimental trial blocks.
bi-directional virtual spring-damper (spring constant, K = 0.25 N/mm; damping constant, C = 0.01 Ns/mm). Before the experiment started, subjects were instructed to avoid moving forward or backward during all tasks to avoid feeling the constraint force provided by the virtual wall. All VR tasks involved grasping and manipulating a virtual box which, in turn, controlled a cursor (‘c’, Fig. 3.1B) that was moved laterally to catch a downward moving target ball (‘d’, Fig. 3.1B). Clockwise and counter-clockwise rotations of the box moved the cursor to the right or left, respectively. Note that the box could be translated but the translations were not mapped to the cursor, and therefore had no effects on its lateral motion. The box width (‘w’, Fig. 3.1B) could be changed according to the task conditions. Despite the variable width of the virtual box, resistive external forces and torque were applied to the box according to the same equation:

\[
\begin{bmatrix}
    f_x \\
    f_y \\
    \tau
\end{bmatrix} =
\begin{bmatrix}
    0.1 & 0 & 0 \\
    0 & 0.1 & 0 \\
    0 & 0 & 20
\end{bmatrix}
\begin{bmatrix}
    x_B \\
    y_B \\
    \theta_B
\end{bmatrix} +
\begin{bmatrix}
    0.01 & 0 & 0 \\
    0 & 0.01 & 0 \\
    0 & 0 & 1
\end{bmatrix}
\begin{bmatrix}
    \dot{x}_B \\
    \dot{y}_B \\
    \dot{\theta}_B
\end{bmatrix}
\]

Equation 3.1

The vector \((x_B, y_B, \theta_B)^T\) denotes the position and orientation of the virtual box, and the vector \((f_x, f_y, \tau)^T\) denotes the resistive forces and torques generated on the box. The entries of the vector \((f_x, f_y, \tau)^T\) were computed as a spring-damper system connected to the center of the box with the equilibrium point at \((x_B, y_B, \theta_B)^T = (0,0,0)^T\). These resistive forces required subjects to produce a torque to rotate the box, hence to move the cursor. The box had its own inertia but this was very small and negligible compared to the resistive forces.

There were three possible target ball drop locations: left, center, and right (L, C, and R respectively), which required subjects to exert a torque (\(T_{\text{task}}\) of 90 Nmm, 0, or –
90 Nmm, respectively. The precision requirements were ±10 Nmm (±11% of $T_{task}$). Note that, although torque was zero for the center target, subjects still needed to grasp the box and maintain the cursor at zero position waiting for the ball to drop. There were also three possible box widths: small, medium, and large ($w = 48$ mm, 60 mm, or 72 mm, respectively).

Subjects were asked to learn to use large and small box to control the cursor to catch the ball dropping to the left or right of the start position of the box. Since the magnitude of the torque required for catching the ball was always the same, subjects needed to use larger forces to manipulate the small box and smaller forces for the large box. This can be illustrated in Fig. 3.1C. Let the thumb and finger contact location be $P_T$ and $P_I$, and the position of the center of the box be $O$. The moment arm of the thumb and index finger forces ($F_T$ and $F_I$, respectively) can be written as the distance between the finger positions and object center: $d_T = P_T - O$, and $d_I = P_I - O$. We define the effective finger forces $F_{TE}$ and $F_{IE}$ as the finger force components projected to the vectors perpendicular to the corresponding moment arms (clockwise direction is positive; Fig. 3.1C). These effective finger forces act on the moment arm contributing to the generation of cursor control torque ($T_{con}$) as described in the following equation:

$$T_{con} = F_{TE}d_T + F_{IE}d_I$$  \hspace{1cm} \text{Equation 3.2}

The digit forces and positions, as well as the box position, were recorded from the haptic device at 500 Hz.

To initiate a trial, subjects were asked to first move their digits into start positions. The start positions were denoted by two spheres (12 mm radius) located at with a horizontal distance of 90 mm apart. When both digits reached the start position, the box
was rendered between the two digits and the target ball started to drop from the top of the screen. The target ball always moved downward at a constant velocity of 12mm/s and reached the horizontal line (Fig. 3.1B) at which the cursor moves in 1.5 second. Therefore, subjects had to grasp the box and move the cursor to the desired location within 1.5 second in order to catch the ball. Successful catches were rewarded by an auditory cue, and the target ball stopped moving vertically but moved laterally with the cursor until subjects released the box. A score system was designed to motivate and engage subjects based on the absolute errors they made ($|T_{err}| = |T_{task} - T_{con}|$).

Specifically, successful catches ($|T_{err}| < 10$ Nmm) gave subjects 10 points, success on consecutive trials were awarded with bonus points, whereas barely missing the target ($|T_{err}| < 20$ Nmm) gave 5 points and no points were given for $|T_{err}| > 20$ Nmm. After each trial, subjects were asked to release the box. The box disappeared after it was released and not shown again until the beginning of the following trial.

**Experimental procedure**

*Practice sessions.* Subjects were first introduced to the tasks by asking them to freely explore the VR to familiarize with the experimental setup. A second practice session was designed to teach subjects the basic rules of the tasks. Subjects were presented with the medium width box and R and L targets randomly interspersed with full visual feedback of both cursor and box. These features were used until subjects were able to successfully perform 10 consecutive catches. The first and second practice sessions lasted approximately 3 minutes each. Subjects were given a 2-minute rest before starting the training session.
Training session. The training session consisted of 8 blocks of 20 trials (Fig. 3.1D). Subjects used same box width (either large or small) within each block and switched to the other box width after completing each block. Subjects were counter-balanced to start with either L or S box width. Visual feedback of the cursor position was removed during each trial and subjects were given visual feedback of the cursor position only at the end of the trial to let them see where the cursor ended at. Visual feedback of the box width and digit tip locations was always available during each trial. The target positions were always in the center for the first 3 trials, and then switched pseudo randomly between R and L (Fig. 3.1D). We used the center target location as a ‘washout’ task and subjects were not required to learn this condition. The rationale for this approach was that washout trials have been shown to reduce interference and improve learning in novel dual contexts (Krakauer et al., 2005). The last two blocks (Block 7 and 8) were used to determine baseline performance. A 2- minute rest was given after the training session.

Test session. The first test session (Test A) consisted of 4 blocks of 20 trials. The target ball location was the same (L or R) within each block but was alternated across blocks. Subjects were counter-balanced to start with either L or R target. Visual condition was the same as the previous training session. The box width was always medium for the first 3 trials but then switched pseudo randomly between large and small across trials (Fig. 3.1D). The sequence of box widths was designed to present subjects with four instances of each of the following trial pairs within each block: Large-Small, Large-Large, Small-Small, and Small-Large (LS, LL, SS, and SL, respectively). The goal of this session was to test whether subjects could use visual information about the box
width, which indirectly provides information about the relative digit positions, to plan the required manipulative actions. A 2-minute rest was given after subjects finished this test session.

The second test session (Test B) consisted of 4 blocks of 20 trials. They were similar to the first test session except that visual feedback of the box was removed throughout the entire duration of each trial and visual feedback of the digit tips was removed from beginning to end of the trial. This session was designed to test whether subjects could use only haptic information about box width to modulate digit forces as a function of box width requiring different digit forces.

It should be emphasized that, in Test A, subjects were able to plan the manipulation forces prior to making contact with the box because of the visual width cue. In contrast, in Test B, although subjects could have planned their finger forces, they had to make corrections to their motor plan after contact since the actual width may not have coincided with the box width they had planned for.

Data analysis

The recorded digit forces and positions were filtered using low-pass butterworth filter with a cutoff frequency of 30 Hz. We assessed learning of the manipulation task by computing the mean absolute $T_{con}$ error, $|T_{task} - T_{con}|$, that each subject made within each training block (excluding the first three ‘wash out’ trials). We also computed the within-block $T_{con}$ variability as the standard deviation of $|T_{con}|$ within each block (excluding the first three trials) for each subject. Absolute values were used because the direction of the $T_{task}$ varies within the training session and subjects always produced $T_{con}$ in the correct direction.
Figure 3.2. Single trial performance and experimental variables.

**A** and **B**, time courses of the experimental variables for thumb and index finger: magnitude of finger forces $F_T$ and $F_I$, magnitude of the effective finger forces $F_{TE}$ and $F_{IE}$, as well as the distance between the finger position and object center $d_T$ and $d_I$. **C**, the time courses of the control torque and the object rotation.
Because of the constant magnitude of $T_{\text{task}}$, we evaluated subjects’ ability to respond to different box widths by computing the total effective force, $F_{\text{eff}}$ (Eq. 3.3). It should be pointed out that subjects were not constrained on their finger vertical placement on the box, therefore their digit vertical positions are variable. However, the digit vertical positions have a much smaller influence on the moment arm length $d_T$ and $d_I$, because the moment arm is mainly determined by the width of the box $w$. Therefore we could approximate the compensatory torque production equation as:

$$T_{\text{con}} \approx F_{\text{TE}}d + F_{\text{IE}}d$$

Equation 3.3

where $d$ is the average moment arm length $d = (d_T + d_I)/2$. In turn, $F_{\text{eff}}$ can be expressed as $F_{\text{eff}} = |F_{\text{TE}} + F_{\text{IE}}|$. In principle, to control the cursor for successful ball catching, the subjects should produce a large $F_{\text{eff}}$ for the small box width (i.e., shorter moment arm) and a small $F_{\text{eff}}$ for the large box width (i.e., longer moment arm). Although $F_{\text{eff}}$ is an approximation of the forces subjects used to accomplish task goal, it nicely capture subjects’ ability to respond to the change in digit relative positions in a similar fashion as how averaged grip force has been used in the literature to capture subject’s ability to respond to the object weight (Jenmalm et al., 2006), shape (Jenmalm and Johansson, 1997), and texture (Cole et al., 1999).

It has been shown that, without sensory feedback available for anticipating object properties, the central nervous system (CNS) tends to use the sensorimotor memory of the manipulation forces acquired during the previous trial (Jenmalm and Johansson, 1997; Cole et al., 1999; Loh et al., 2010). Therefore, the test trials can be separated into four categories according to the box size used in the current and preceding trial for the analysis of $F_{\text{eff}}$ in response to the box widths. We performed multiple
repeated-measure three-way analysis of variance (ANOVA) using experimental conditions (A versus B), preceding box size, and current trial box size, as within-subject factors. We computed the mean $F_{eff}$ using the last two blocks in Test A and Test B (i.e., eight trials for each trial pairs for each subject). We performed additional ANOVAs using $F_{eff}$ measured at the end of each trial (i.e., when the target ball arrived at the horizontal line along which the cursor moves), as well as multiple time points ranging from 50 to 300 ms after initial finger contact with the box. The initial finger contact was determined as the time when one of the fingers first made contact with the box. Post-hoc paired t-test were performed when appropriate using Bonferroni corrections.

**RESULTS**

*Learning of the manipulation tasks*

Subjects started the training blocks with small errors as they started training after a practice session in which they performed the task with complete visual information of the box and cursor position. Therefore, subjects had already implicit knowledge about how to successfully perform the task. Nevertheless, subjects still needed to learn to perform the task with two box widths (large and small) they had not interacted with during the practice sessions. Subjects’ performance significantly improved across eight training blocks (Fig. 3.3). Specifically, the within-block mean $|T_{err}|$ decreased from $22.41 \pm 2.15$ Nmm (mean ± SE) in Block 1 to $16.19 \pm 1.71$ Nmm in Block 8 ($F_{(7,77)} = 4.325$, $p < 0.001$; Fig. 3.3A). In addition, the within-block torque variability decreased from $28.84 \pm 2.88$ Nmm in Block 1 to $19.33 \pm 2.19$ Nmm in Block 8 ($F_{(7,77)} = 3.630$, $p = 0.002$; Fig. 3.3B ). We also found that, after an initial improvement in performance after the first two blocks, performance reached a plateau. Planned
Figure 3.3. Learning curve across eight training blocks.

_A_, reduction of within-block mean torque error. _B_, reduction of within block torque variability.
contrasts between each block and the average of the following training blocks revealed significant differences only between the first block and the other seven for both mean torque error \( (F_{(1,11)} = 10.23 , \ p = 0.008) \) and torque variability \( (F_{(1,11)} = 10.06 , \ p = 0.009) \). At the end of the training, subjects were able to perform the task by using significantly different effective force \( (F_{\text{eff}}) \) in response to the large and small box widths. This was quantified by computing mean \( F_{\text{eff}} \) from the last two training blocks (Block 7 and 8, one with large box width and the other with small box width). Subjects used significantly different \( F_{\text{eff}} \), \( 2.22 \pm 0.04 \text{ N} \) and \( 1.77 \pm 0.04 \text{ N} \) for the small and large box, respectively (2-tailed paired t-test, \( t = 8.95, \ p < 0.001 \)).

*Finger forces were controlled equally well with or without vision of the box*

We examined whether subjects could adjust their forces to the actual box width. We found that subjects performed similarly in Test A and Test B, despite the fact that subjects could anticipate digit forces in Test A but not in Test B. This was confirmed by three-way ANOVA showing no effect of experimental condition (Fig. 3.4; \( p > 0.05 \)). Interestingly, we found a statistically significant main effect of both current and preceding box width \( (F_{(1,11)} = 38.80, \ p < 0.001 \) and \( F_{(1,11)} = 13.57, \ p = 0.004 \), respectively). These findings suggest that subjects were able to modulate digit forces to the current box width, but they were also affected by the box width experienced in the previous trial. Furthermore, the effect of previous box width was small compared to the effect of current box width. We used paired t-test to examine the effective forces subjects used in Test A and B with respect to those used in the last two blocks of training. No statistical difference was found between the training S trials and test S trials regardless of the preceding box size in the tests (same for L trials). This result indicates that, although
Figure 3.4. Effective force at the end of target ball drop.

The gray bars represent the total effective force subjects used in the last two blocks of training. The black and white bars represent test with and without vision of the box, respectively. L and S represent the box width. For box width pair LL, LS, SL, and SS, the first one of the pair is the box width used in the preceding trial whereas the second one is the box width used in the current trial.
the preceding box size may slightly bias the forces in the current trial, the resulting force production was similar to those in the training and did not impair the task performance.

*Differential development of the effective force*

The above results indicate that subjects responded to the box width in the same fashion regardless of whether they had visual box width cues to predict the digit forces necessary to generate the required torque. This raises the question of how subjects could adjust their digit forces if the actual box width did not match what they expected. To address this question, we examined the $F_{\text{eff}}$ at 100, 300, 400, 500, and 600 ms after initial digit-object contact (Fig. 3.5). We found no significant effect of vision condition or box widths at 100 ms, but significant differences start to emerge after 100 ms post-contact and were found for all post-contact times with the exception of 600 ms. At 600 ms after contact, the magnitude of $F_{\text{eff}}$ was close to that exerted at the end of trials showing similar box size dependent force differentiation (effect of current box width: $F_{(1,11)} = 28.73$, $p < 0.001$; effect of previous box width: $F_{(1,11)} = 17.14$, $p = 0.002$).

At 300 ms after initial contact, subjects produced significantly larger $F_{\text{eff}}$ in Test A than Test B condition ($F_{(1,11)} = 26.96$, $p < 0.001$). There was also significant interaction between preceding and current box width ($F_{(1,11)} = 7.63$, $p = 0.019$). Post-hoc comparisons revealed that, within each experimental condition, there were no difference between LL and LS, but SL and SS were significantly different ($p < 0.05$).

At 400 ms after initial contact, a significant three-way interaction was found ($F_{(1,11)} = 5.52$, $p = 0.039$). Post-hoc comparisons revealed no difference between Test A and Test B for LL. However, subjects still produced significantly less $F_{\text{eff}}$ in the other three cases. Furthermore, subjects produced significantly different forces across SL and
Figure 3.5. Effective force at different time points.

The blue and red lines represent test with and without vision of the box, respectively. L and S represent the box width. For box width pair LL, LS, SL, and SS, the first one of the pair is the box width used in the preceding trial whereas the second one is the box width used in the current trial.
SS regardless of whether they could see the box width. Forces produced in LL and LS were still not different in Test B condition.

At 500 ms after initial contact, a significant three-way interaction was still found \((F_{(1,11)} = 10.81, p = 0.007)\). Post-hoc comparisons revealed similar results as those described for 400 ms. Subjects produced significantly different digit forces across SL and SS regardless of visual feedback of box width. Forces used in LL and LS were still not significantly different in the Test B condition. Comparison between Test A and Test B revealed that subjects produced similar force magnitudes for all cases except LS in which Test B was characterized by smaller force.

These comparisons at different time point during the development of digit forces clearly suggest that, without visual geometric cue about the box width, subjects delayed their force production. To further quantify the delay time, we compared the force rate profiles from LL, LS, SL, and SS in Test A and B using cross correlation. For each subject and each trial pair case, we took the ensemble average of the effective force traces and effective force rate traces \((n = 8\) for each test). An example of such traces is shown in Fig. 3.6A. The ensemble averages of the force rates represent the force development through time for each case. When unbiased cross correlation was computed between ensemble averages from Test A and B for each trial pair case, the time shift at which the highest correlation was found would indicate the delay between the force production of the two tests. Specifically, the cross correlation was calculated using the 100 – 600 ms interval of the ensemble averages since we have shown that the magnitude of the effective forces were not different between the two tests. We found that for LL, LS, SL, and SS, the force development was delayed \(113.17 \pm 13.71\) ms, \(173.77 \pm 15.14\) ms,
Figure 3.6. Delay of the force development in Test B.

**A**, ensemble average of the effective forces and the ensemble average of the effective force rates from LS case of subject LZ. **B**, the delay time between the force rates form Test B and Test A (mean±SE). **C**, the ensemble average of the effective force rates of all subjects.
121.83 ± 17.55 ms, and 147.67 ± 15.13 ms (Fig. 3.6B). Two-way repeated-measures ANOVA using current trial width (2 levels) and width change (2-level, widths in current and previous trial are same or different) revealed that the small width caused significantly more delay in Test B ($F_{(1,11)} = 8.68$, $p = 0.013$) than the big width, but there was no effect of width change ($F_{(1,11)} = 2.35$, $p = 0.154$). These delays could be further demonstrated by taking the ensemble average of the force rate traces from all subjects (Fig. 6C). This clearly confirmed the results from cross correlation as a delay of 100-200 ms can be observed in all trial pair cases between Test A (blue) and Test B (red).

Lastly, we qualitatively examined how subjects responded to each trial pair cases within each test. This is because there is no accurate way to determine when two force traces starting to diverge. Furthermore, we used the ensemble average of all subjects for the visual examination as the individual force rate profile can be quite noisy. For Test A, the width of the box can be seen before the contact, thus allowing anticipation of the digit forces appropriate for the digit horizontal separations. This is shown by the early divergence (~100 ms) of the force rate profiles depending on the box width in the current trial regardless the width used in the previous trial (Fig. 3.7A). Specifically, if the current box width is small, subjects tended to use a force rate profile with higher peak. In contrast, for Test B, the divergence of the force rates was found to be much later (~300 ms) for all cases (Fig. 3.7B). Specifically, we found that subjects seem to use a ‘default’ rate to develop force and make appropriate adjustments according the actual object width they are experiencing. This is consistent with the overall delay between Test A and Test B and suggests that subjects did not follow the force they used in the last trial when they cannot predict the upcoming box width.
Figure 3.7. Time of divergence between force rates in different trial pairs.

**A**, comparison of the ensemble average of the effective force rates of all subjects between different trial pair cases in Test A. **B**, comparison of the ensemble average of the effective force rates of all subjects between different trial pair cases in Test B.
**DISCUSSION**

We used a virtual reality setup to investigate human’s ability to compensate for predictable and unpredictable change in the digit position induced by the change of object width. It was shown that after learning the novel manipulation task using different box width, subjects could successfully control their finger forces to accomplish the manipulation goal when trial-to-trial changes of box width occurred, regardless of whether they had information about object width before contact. However, our hypothesis of a hybrid anticipatory and feedback control when subjects could not predict the width change was only partially supported. Specifically, while subjects did make force corrections after contact by using haptic feedback of the actual digit relative positions, subjects did not make anticipation according to the previous trial but rather adopted a ‘default’ initial force strategy. Therefore, subjects always had to check the actual digit positions (i.e., box width) after contact to select the correct digit forces, causing a delay in the force development ~150 ms comparing to the test when subjects could predict the object width before contact.

*Anticipatory digit force scaling*

It has been shown that the central nervous system could anticipate the digit forces according to the visual information about the object properties. The anticipatory control was demonstrated using tasks that require to lifting or transporting an object with often small and constrained grasp surface. These tasks have no explicit task goals and the only requirement was to maintain grasp stability (i.e., no local finger slip at contact sites) which was achieved by keeping the grip force larger than a certain magnitude (i.e., safety margin) to sustain frictional load forces. Subjects could scale the grip force appropriately
to the load forces induced by different object weight (Johansson and Westling, 1984) or different local surface shape (Jenmalm and Johansson, 1997), to different friction coefficients (Cole et al., 1999), or even to the movement induced perturbations (Flanagan and Tresilian, 1994). However, when the properties of the upcoming object/task were unpredictable (often due to block of vision), the CNS tended to scale the digit forces according to the object properties experienced in the previous trial. It was believed that the CNS could store ‘sensorimotor’ memory about manipulation with only one or few trials. Recently, the ability to use sensorimotor memory to scale finger forces was also found in tasks which did not constrain the digit placement and had a more explicit task level constraint. When object had to be lifted and balanced, it was shown that subjects could scale the digit forces, as well as choose digit placement, to produce the correct task torque using visual geometric cues about object weight distribution (Salimi et al., 2003; Fu and Santello, 2012). Furthermore, if object weight distribution (therefore the task torque) cannot be predicted, sensorimotor memory of the previous object weight distribution was used to guide the digit force and position control (Lukos et al., 2013).

In our novel VR task, subjects need to scale the digit forces precisely to match the actual box width to attain the control torque for moving the cursor. We found that when subjects had full vision about the box from the beginning of the trial, appropriate force scaling to the box width could be implemented as soon as 100 ms after initial contact (Fig. 3.7A). However, there were differences between our VR task and real object manipulation tasks. First, the force development in our experiment always had one initial impact force with a peak of ~0.3 N during the first 50 ms, or sometimes two impact force peak during the first 100 ms if two digits landed on the object with small delay (Fig.
3.6A). This was caused by lack of deceleration prior to digit contact and the motion of digits was actually mechanically stopped by the simulated object surface. These initial impact forces were not found, at least not to this extent, when subjects made contact with real object using their finger pads (Säfström and Edin, 2008). This could be due to the fact that there was no ‘reaching’ phase in our design and subject simply has to close their digits towards the object. In addition, as our simulation could not render truly ‘rigid’ object surfaces, the transient mechanical response of the contact might be too weak for the mechanoreceptors to sense. The initial impact force could be a strategy subjects used to magnify the contact event. It has been demonstrated that subjects could predict the time of contact and release the digit force plan at the expected contact time (Säfström and Edin, 2008). For our study, we speculated subjects release their digit forces at the predicted time of the end of initial impact when the width of the box could be visually predicted.

Another important difference we found in our study was that, when the object width cannot be predicted, subjects did not use the ‘sensorimotor memory’ of the force in the previous trial (Fig. 3.7B). This could be explained by the fact that our task had very high precision requirement. Specifically, subjects would miss the target if they have an error more than 10%. Given the actual digit forces were less than 4N, the range error they can make in the force was quite small. Since subjects had 1.5 second to accomplish the task goal and there was a score system to motivate subjects, they may have chosen a more conservative default strategy for the initial development of the digit forces. It should be point out that this initial force strategy was still increasing forces, but in a rate smaller than the rates for both small and large box size (Fig. 3.6C).
Contact event and digit force corrections

Despite the aforementioned difference in the anticipatory control of our task and real manipulation tasks, we have demonstrated that CNS has the ability to use somatosensory information about the actual digit relative positions to adjust their digit forces after contact. It has been shown that if the prediction of anticipatory control matches the actual object property, the feedforward force development would not be adjusted. In contrast, if mismatch occurs, the feedback mechanism responds and force development would be changed. It has been proposed that the signal of the initial contact is powerful enough to detect many local features of the contact sites, such as friction and shape, thus leading to observable force rate changes as early as 100 ms in normal population (Jenmalm and Johansson, 1997; Cole et al., 1999). For our study, we found similar feedback mechanisms. Specifically, subjects delayed their force production regardless of whether the current and preceding trial had the same box width. With the first 100 ms mechanical contact response excluded, subjects still had a delay around 100-200 ms to elicit observable differentiation in force development in all cases. This indicates that, when the object width was unpredictable, subjects always did a check on the actual digit positions to scale the digit force to the box width. This check should occur during the initial contact events. Specifically, there could be two sources of information. First, the box width could be sensed by the timing of the contact. As the subjects’ digits always started at the same location, it took longer to make contact with the small box than the large one. Second, the box width could be also determined by the horizontal distance between the two digits during the contact events. This could be sensed by integrating the tactile and proprioceptive signals (Santello and Soechting, 1997). It has to
be pointed out that we cannot determine whether subjects re-computed the digit forces based on the sensed the digit position or they simply recalled the digit forces they have learned in the training session.

Conclusions

In the present study, we have shown that subjects could scale their digit forces to the horizontal digit placement using both visually based anticipatory control (Test A) and somatosensory based feedback control (Test B) in a manipulation task that require very high precision. Although discrepancies exist between this VR task and traditional tasks with real objects, we argue that the CNS could have used similar mechanisms to control digit forces in unconstrained real object manipulation tasks (Fu et al., 2010, 2011). The actual digit placement was always monitored and if mismatch occurs between the predicted and the actual digit placement subjects would adjust the digit force accordingly.
Chapter 4

TRANSFER OF LEARNED MANIPULATION FOLLOWING CHANGES IN DEGREES OF FREEDOM

INTRODUCTION

Neural control of object manipulation is a topic of considerable interest. One paradigm that has been found useful for such studies involves lifting an object whose weight distribution is asymmetric, thus requiring the digits to exert not only a net vertical force but also a torque in order to prevent rolling of the object (Goodwin et al., 1998; Salimi et al., 2000, 2003; Lukos et al., 2007, 2008). Presented with this task, subjects learn to modulate digit forces as a function of digit placement to exert a compensatory torque in an anticipatory fashion, i.e., before lifting the object (Fu et al. 2010). To further understand the sensorimotor mechanisms underlying learning of manipulation, Zhang et al. (2010) examined subjects’ ability to transfer learned digit force-position relations following an object rotation. Learning did not transfer readily as subjects failed to mentally rotate the learned action, i.e., the direction of compensatory torque, in response to the new object center of mass location. Learning of compensatory torque also did not transfer from one hand to another (Bursztyn and Flanagan, 2008). These results suggest that learning of manipulative actions had occurred in a hand-, rather than object-, frame of reference. However, the factors that constrain the extent to which learned digit forces and positions can be transferred are not well understood. The present study was designed to determine whether manipulation learned with a set of digits can be transferred to grips involving a different number of digits.
The ability to perform the same behavioral task using different sensorimotor elements is a manifestation of ‘motor equivalence’ – a phenomenon remarked upon in the early history of motor control (Lashley, 1930; Bernstein, 1967) – but studied only sporadically. The problem of motor equivalence can be defined as follows: are the neural representations of actions specific to, and constrained by, the effectors (e.g., muscles, limbs) used to learn a given action, hence performable only with the same effectors, or are they independent from ‘how’ they were learned? Changing the number of fingers that participate in the lifting task allows us to address this question. An important characteristic of our experimental protocol is that transfer of the compensatory torque across grip types can be implemented through an infinite number of new relations between the control variables: grip force, difference in the lift force between the two sides, and vertical distance between contact points on the two sides. We hypothesized that subjects will be able to transfer the compensatory torque on the first trial following a change in the number of fingers although the combinations of digit forces and positions do not remain the same as those learned before the change in grip type.

**MATERIALS AND METHODS**

*Subjects*

Ten right-handed volunteers (4 males and 6 females, mean age and standard deviation: 21.4 ± 2.2 yr) participated in this study. Subjects had no previous history of orthopedic, neurological trauma, or pathology of the upper limbs and were naïve to the purpose of the study. Subjects gave their informed consent according to the declaration of Helsinki and the protocols were approved by the Office of Research Integrity and Assurance at Arizona State University.
Figure 4.1. Experimental setup and procedures.

A. Front and side views of the grip device used to measure forces and centers of pressure on the grasp surfaces for the thumb and finger sides (units are in mm). Object position and orientation were tracked through a motion capture system and active markers (denoted as small spheres, a) placed on the top and on the extremities of the bottom box of the grip device. Active markers were also placed on the nails of the thumb, index, and middle fingers. A mass (400 g) was inserted either in the left or right compartment (L and R, respectively) in the bottom box of the device to change the center of mass of the object (L_CM and R_CM condition, respectively). The convention for defining the direction of object roll (negative and positive towards the thumb or finger side, respectively) is also shown. The configuration of the grip device consisted of a central block (c) and two bars (grip surfaces; b), each mounted on a force/torque sensor (d). B. The top view of the experimental procedures. Subjects reached to the grip device located at 30 cm from the start position. Infrared cameras (e) were placed around the workspace to track hand and object kinematics. C, D. The trial sequences associated with switching from two to three digits (2d→3d) and vice versa (3d→2d), respectively. Subjects were tested on experimental session #2 two weeks after experimental session #1. All subjects started each experimental session with the left center of mass (L_CM) using each grip type, followed by an equal number of trials with a different grip type and the right CM (R_CM).
**Apparatus**

We used a custom-made grip device to measure digit forces and their points of application (Fig. 4.1A; see Fu et al. 2010 for details). Briefly, two six-component force/torque (F/T) transducers (Nano-17, ATI Industrial Automation, Garner, NC; nominal force resolution: 0.012 N; nominal torque resolution 0.63 N cm; ‘d’, Fig. 4.1A) mounted collinear to each other on the grip device recorded forces and torques exerted by the thumb on one side and finger(s) on the other. The grip surfaces consisted of two parallel PVC plates (‘b’, Fig. 4.1A) each mounted vertically on a F/T transducer and were covered with 100-grit sandpaper (static friction coefficients: 1.4 to 1.5). The distance between the two grip surfaces (grip width) was 6.07 cm.

A plexiglass box attached underneath the grip apparatus was used to change the mass distribution to the left or right of the grip device midline by inserting a mass (400 g) into one of three compartments (Fig. 4.1A). The total mass of the grip device and load was 790 g. When the load was placed in the left or right compartment (L and R, Fig. 4.1A), it introduced a torque on the zy plane of −255 N•mm and +255 N•mm, respectively. View of the added mass location was blocked by a lid to prevent visual identification of the object CM.

We recorded hand and object kinematics using an active marker 3D motion capture system (PhaseSpace, Inc., San Leandro, CA; frame rate: 480 Hz, spatial accuracy ~1 mm, spatial resolution 0.1 mm.) with eight cameras (‘e’, Fig 1B). Subjects were outfitted with light-weight visible red emitting diode (RED) active markers (5 mm in diameter) on the fingernails of thumb, index, and middle fingers. Markers were also placed on the lateral extremities of the object and on its top to track its position and
orientation during the lift (‘a’, Fig. 4.1A). Prior to data collection, we verified that placement of the RED markers did not prevent motion of the digits and/or the wrist by asking subjects to fully flex and extend all digits as well as to grasp the object prior to the start of the experiment. Force and torque data were acquired by 12-bit A/D converter boards (PCI-6225, National Instrument, Austin, TX, USA; sampling frequency: 1 kHz). Data acquisition was performed through LabView (version 8.0, National Instrument, Austin, TX, USA).

Experimental procedures

Subjects were asked to sit facing the grip device (Fig. 4.1B) with the elbow flexed at ~70°-90° in the parasagittal plane, to align their right shoulder with the midpoint of the grip device, and to place their hand (palm facing downward) on a support located 30 cm from the grip device. After a verbal signal from the experimenter, subjects reached from this start location, grasped the grip surfaces with the tip of either the thumb and index finger or thumb, index, and middle fingers of the right hand, lifted the grip device at a natural speed to a height of ~10 cm, held it for ~1 s, and replaced it to its start location. We asked subjects to extend the non-involved fingers throughout the task to ensure that only the tip of the thumb and index finger (or thumb, index, and middle fingers) contacted the grip surfaces. Compliance was visually verified on each trial by one of the experimenters. At the beginning of each block of trials we instructed subjects to minimize object roll during the lift. The experimenter gave no instructions about where to grasp the object, thus leaving subjects the choice of digit placement anywhere along the grip surface (‘b’, Fig. 4.1A) to comply with the requirement of minimizing object roll.
Each subject performed the task under two experimental conditions: (1) two-digit grasping (thumb and index finger; 2d) and (2) three-digit grasping (thumb, index, and middle fingers; 3d). On the first experimental session, subjects performed 10 2d trials followed by 10 3d trials (2d→3d) on the L_CM condition (Fig. 4.1C). The between-trial interval within a block of 10 trials was ~ 10 s. After a short break (~ 20 s), subjects performed the 2d→3d experimental condition on the R_CM condition. Each subject was tested again two weeks later but on a trial sequence opposite to that experienced on his/her first experimental session, i.e., 3d→2d on the L_CM condition followed by 3d→2d on the R_CM condition (Fig. 4.1D). This design was motivated by the need to examine whether learning transfer of the compensatory torque following a switch from 2d to 3d is equivalent to switching from 3d to 2d. The break between the two experimental sessions was used to minimize potential positive or negative learning transfer effects from one sequence to the next. The effectiveness of the two-weeks break in preventing positive or negative learning transfer was confirmed statistically.

Prior to the experiment, we asked subjects to lift the object once with each hand configuration (2d and 3d) with the load placed in the center compartment (C, Fig. 4.1A) to familiarize with the task, texture, and weight of the grip device. Thereafter and at the beginning of each block of trials, we informed subjects that (a) the load could be placed either in the left or right compartment of the plexiglass box (left and right center of mass: L_CM; and R_CM, respectively), (b) it would remain the same for a block of 10 consecutive trials, and (c) told them the number of digits to be used for the upcoming block of trials. After the subject performed 10 consecutive trials with a given grip type for the L_CM condition, we informed the subject to perform another block of 10 consecutive trials but
with a different number of digits. We emphasized that the goal of the task remained the same, that is, to minimize object roll during the lift. After the subject performed a total of 20 trials (10 with each grip type), subjects were informed that the object CM would be changed, and that they will be asked to perform two more blocks of 10 trials each for each grip type. Before subjects started the $R_{CM}$ block of trials, we repeated the same instructions given for the $L_{CM}$ block of trials. Throughout the experiment, we blocked the view of placement of the mass in the left or right compartment of the object to prevent subjects from anticipating the new CM location on the first object lift.

Data processing

Force and position data were temporally aligned offline and analyses were performed using MATLAB. We analyzed the following variables (Fig. 4.2; see Fu et al. 2010 for details): (1) Object lift onset: the time at which the vertical position of the grip device crossed and remained above a threshold for 200 ms; (2) Object roll: the angle between the gravitational vector and the vertical axis of the grip device, and peak roll is the peak of object roll shortly (~150 ms) after object lift onset; (3) Digit forces: force perpendicular (grip force, GF) and parallel (load force, LF) to the grip surface; (4) Digit center of pressure (CoP): the vertical coordinate of the point of resultant digit force application, calculated for each digit using the force and torque output of each sensor (positive and negative values CoP denoted higher and lower CoPs relative to the center of transducer, respectively). Note that GF, LF, and CoP recorded on the finger side of the grip device are the resultant net forces and net center of pressure of both index and middle finger when subjects performed the task using the 3d grip. To quantify the
modulation of individual digit position, we recorded \textit{fingertip marker position} defined as the \textit{vertical position} of the marker on the nail of the thumb, index, and middle fingers.

We used digit forces and CoP to compute the following performance variables: (a) the average of the digit grip forces ($F_{GF}$), (b) the difference between load forces exerted on the thumb and finger side of the grip device ($d_{LF}$), and (c) the vertical distance between the CoP on the thumb and finger side of the grip device ($d_{y}$). These three variables are important to produce the \textit{compensatory torque} ($T_{com}$) for minimizing object roll, i.e., balancing the external torque caused by the added mass (see Fu et al. 2010 for details).

To further understand how digit placement changed following a change in grip type, we also computed the vertical distance between thumb and index finger markers ($d_{tip}$). Note that all of these performance variables were computed at object lift onset.

\textit{Learning and learning transfer of compensatory torque}

Our previous work has shown that subjects learn to generate $T_{com}$ in an anticipatory fashion (i.e., at object lift onset) within the first three consecutive object lifts (Zhang et al. 2010; Fu et al. 2010). Here we quantified again the trial-to-trial learning of $T_{com}$ with a given grip type, 2$d$ or 3$d$, as an intermediate step to test subjects’ ability to generate the same $T_{com}$ after changing grip type to 3$d$ or 2$d$, respectively. For learning transfer to be defined \textit{positive}, $T_{com}$ generated prior to the grip type switch had to be statistically indistinguishable from $T_{com}$ generated on the first trial (trial 11) following the switch. For our study, a positive learning transfer of $T_{com}$ would be evidence for motor equivalence, as the same global variable is generated in an effector-independent fashion, e.g., regardless of the number of digits used to lift the object. Conversely, statistically significant differences in $T_{com}$ pre- vs. post-switch in grip type would suggest failure of
learning transfer, that could result from three different phenomena: (a) same $T_{com}$ on trial 1 and 11, indicating a ‘reset’ of subjects’ learned behavior to the same state associated with the very first trial with the same object CM (no transfer); significantly (b) larger or (c) smaller $T_{com}$ on trial 11 than on trial 10, indicating an anterograde effect of the learned $T_{com}$ with a given grip type on $T_{com}$ with a different grip type. A larger than necessary $T_{com}$ may result in an overcompensation of the external torque, hence generating a roll in the opposite direction to that caused by the added mass, whereas a smaller than necessary $T_{com}$ would be insufficient to prevent object roll to the same extent attained up to the switch to a different grip type. Both of these instances can be defined as partial transfer, as they maintain some features of the learned behavior that, at the same time, are functionally better than the initial state associated with trial 1.

Although on a trial-to-trial basis subjects could theoretically use different relations between $d_y$, $d_{LF}$, and $F_{GF}$ to generate a given $T_{com}$, after the first few lifts each subject tends to use the same relation consistently when performing consecutive object lifts (Fu et al. 2010). Here we address the question of how subjects transfer the learned relation following a change in grip type. For example, a positive transfer of $T_{com}$ on trial 11 might occur through the adoption of the same relation between its three components used before the grip type switch or, alternatively, by changing the relation such that, for example, subjects choose to exert different $d_{LF}$ through different $d_y$. This example shows that, to fully understand learning transfer of $T_{com}$, it is necessary to examine how the individual $T_{com}$ components were transferred across grip types.
The experimental variables analyzed in our study are shown from digit contact to object hold for one representative subject and three trials for the 2d→3d condition: trials 1 and 10, two-digit grip, left center of mass; trial 11, three-digit grip, left center of mass. From top to bottom, traces are compensatory torque and object roll (dashed and solid lines, respectively), object vertical position, digit grip forces (GF), digit load forces (LF), digit center of pressure (CoP), and vertical position of the marker on the tip of the thumb, index, and middle fingers. The arrows (top row) indicate the target torque that subjects should exert at object lift onset to counteract the external torque and peak object roll occurring during object lift. Vertical solid and dashed lines denote object lift onset and the change in grip type, respectively. The vertical coordinate of digit CoP is defined as positive or negative when it is above or below, respectively, the center ($y = 0$) of the force/torque sensor. Note that digit CoP, GF, and LF on the finger side of the grip device are generated by the index finger on trial 1 and 10, and by the index and middle fingers on trial 11. The time course of the vertical marker position of thumb and index fingertip are shown for trials 1 to 10, whereas trajectories of thumb, index, and middle fingertip markers are shown for trial 11.

*Figure 4.2. Experimental variables.*
Statistical analysis

To quantify learning through consecutive object lifts, we performed analysis of variance (ANOVA) with repeated measures within the pre-switch blocks of ten trials for each CM location on $T_{com}$ using Trial (10 levels) as the within-subject factor. The goal of these analyses was to test whether learning of $T_{com}$ had occurred when using a given grip type on a block of consecutive trials before switching to a different grip type. Our previous work (Fu et al. 2010; Zhang et al. 2010) revealed that subjects learn to generate consistent $T_{com}$ after the third trial. We verified this in the present study by performing ANOVA with repeated measures for each CM location with within-subject factors of Trial (4 through 10 of the trial block before the switch in grip type; Fig. 4.3). Lack of significant main effect of Trial would indicate that subjects generated a stable $T_{com}$ throughout the last 7 trials of the pre-switch block. Transfer of $T_{com}$ and modulation of its components ($F_G$, $d_L$, and $d_y$) was quantified using ANOVA with repeated measures in two ways: (1) as the immediate transfer and modulation, quantified by comparing the last trial prior to the switch in grip type vs. the first trial following the switch; and (2) as long term transfer and modulation, quantified by the average difference between pre- vs. post-switch trials. Sphericity assumptions were tested for all analyses (Greenhouse-Geiser) and the results were corrected when appropriate. All tests were performed at the $P \leq 0.05$ significance level.

Results

We describe the results in three sections: (1) learning and learning transfer of compensatory torque ($T_{com}$); (2) immediate modulation of $T_{com}$ components on the trial
following the switch in grip type; and (3) long-term adaptation of $T_{com}$ components throughout consecutive trials following the switch in grip type.

Learning and learning transfer of compensatory torque

Figure 2 shows the time course of $T_{com}$ (top row, dashed line) and its components on the first and last trial performed using a two-digit grip, and data from the first trial performed with a three-digit grip by a representative subject. On trial 1, the subject does not know the CM location (left CM), and therefore no $T_{com}$ is generated at object lift onset (vertical solid line). As a result, the object rolls towards the thumb ~ 20° during the lift due to the external torque caused by the added mass before a corrective response can be initiated. By trial 10, however, this subject generated $T_{com}$ of magnitude and direction appropriate to minimize object roll during the lift. The appropriate $T_{com}$ was generated through a concurrent modulation of digit load forces and center of pressure. Specifically, at object lift onset this subject positioned the thumb higher than the index finger (positive $d_t$), exerted a larger thumb load force (positive $d_{LF}$) and a slightly larger grip force ($F_{GF}$) relative to trial 1. Consistent with previous observations (Zhang et al. 2010; Fu et al. 2010), $T_{com}$ averaged across all subjects changed significantly as a function of consecutive practice in the pre-switch block (significant main effect of Trial; 2$d$, L$_{CM}$: $F_{(1, 9)} = 17.31$; 2$d$, R$_{CM}$: $F_{(1, 9)} = 26.85$; 3$d$, L$_{CM}$: $F_{(1, 9)} = 12.04$; 3$d$, R$_{CM}$: $F_{(1, 9)} = 25.12$; all $p < 0.001$; Fig. 4.3). On average, all subjects learned to anticipate the $T_{com}$ necessary to minimize object roll within the first 3 trials regardless of grip type and CM location (trials 1-3, Fig. 4.3), after which $T_{com}$ did not change any further on subsequent trials (all tests on trials 4 to 10: $p > 0.05$).
Remarkably, following a change in grip type (trial 11), the subject in Figure 2 maintained the ability to generate a similar $T_{\text{com}}$ to that generated on trial 10, hence equally appropriate in minimizing object roll. However, on trial 11 this subject used a different relation between $d_y$, $d_{LF}$, and $F_{GF}$ from that used on trial 10. Specifically, forcing subject to add the middle finger resulted in the application of a slightly larger grip force, less asymmetrical sharing of load forces, and positioning of the index finger to a higher position. Furthermore, the index finger was positioned lower than the thumb in trial 10 but higher than thumb in trial 11, and the middle finger was positioned lower than the thumb. The major normal force contribution on finger side is shifted from index finger to the middle finger as indicated by lowering of net center pressure closer to middle finger position. Note that these changes all occur since early contact suggesting anticipatory planning for new grip type.

We performed ANOVA for each CM location with within-subject factor of Grip type (2 levels; 2d and 3d) to examine the immediate effect of changing grip type on $T_{\text{com}}$. When subjects changed grip type, on the very first trial (trial 11, Fig. 4.3) they were able to generate $T_{\text{com}}$ whose magnitude was statistically indistinguishable from that generated on the pre-switch trial (trial 10, Fig. 4.3) for all but one experimental condition ($3d \rightarrow 2d$, $L_{CM}$; Table 4.1). However, no significant differences were found when comparing peak object roll on trial 10 vs. 11 on any of the four experimental conditions. This indicates that the statistically significant difference for the $3d \rightarrow 2d$ $L_{CM}$ condition did not have significant behavioral consequences on the manipulation, thus suggesting that anticipatory control of $T_{\text{com}}$ in the pre- and post-switch trials was equally appropriate to attain the task goal.
Figure 4.3. Learning curves of compensatory torque: pre- and post-grip type switch.

**A, B,** The compensatory torque ($T_{com}$) for 2-digit grip trials followed by 3-digit grip trials for left and right CM conditions ($L_{CM}$ and $R_{CM}$), respectively. **C, D,** $T_{com}$ data from grip type presented in the reverse order (3-digit grip followed by 2-digit grip) for $L_{CM}$ and $R_{CM}$, respectively. Trials within the dashed box (11 to 20) indicate the grip type subjects switched to after learning $T_{com}$ during consecutive object lifts (trials 1 to 10) with a different grip type. Data are averages of all subjects (vertical bars denote standard errors).
To further quantify the extent to which $T_{com}$ was transferred from one grip type to another, we examined average differences between 7 trials pre- vs. post-switch in grip type by ANOVA with repeated measures for each CM location with within-subject factors of Trial (7 levels; 7 pre- and 7 post-switch) and Grip type (2 levels, pre- and post-switch). We found no significant main effect of Trial, Grip type, or interaction ($p > 0.05$ for each experimental condition). This suggests that no further learning of $T_{com}$ occurred before and after the switch in grip type, the average $T_{com}$ being statistically similar for the two grip types. As expected from the results on $T_{com}$, we found no significant main effect of Trial, Grip type, or interaction on peak object roll ($p > 0.05$ for each experimental condition). Therefore, the significant difference in $T_{com}$ pre- vs. post-switch trial in $3d\rightarrow2d$ $L_{CM}$ condition could have been caused by CM- and hand posture-specific control strategies. With regard to digit position modulation, two-digit grip with the left CM may challenges the modulation of $d_y$, hence $T_{com}$, differently than a three-digit grip. For the left CM condition, subjects can adopt a larger $d_y$ when grasping the object with three than two digits because, in the former case, the middle finger can be positioned lower than index finger, thus further shifting the net CoP on the finger side of the object. However, for the right CM condition, two-digit grip allows subjects to use a larger $d_y$ than three-digit grip because the net CoP on the finger side will always be higher when force is exerted only with the index finger than when force is exerted by both index and middle fingers. With regard to force modulation, index and middle fingers share the load in three-digit grip while index has to sustain by itself most of the load in two-digit grip. Because of the above differences in digit position and force modulation, two-digit
Table 4.1 Statistical results on immediate transfer of action and adaptation of compensatory torque components (trial 10 vs 11)

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<th>$2d \rightarrow 3d \ L_{CM}$</th>
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<td>F=7.45</td>
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<td>$d_{LF}$</td>
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</table>

Each row shows statistical results of simple effects of switching grip type ($2d$: 2 digit grip; $3d$: 3 digit grip) in two CM conditions ($L_{CM}$ and $R_{CM}$) on a single variable, compared between trial 10 (pre-switch trial) and 11 (post-switch trial). The degrees of freedom for all comparisons are (1,9). $T_{com}$ is the compensatory torque; $d_y$ is the vertical difference between the net centers of pressure of thumb and finger side of the grip device; $d_{LF}$ is the difference between the load forces of thumb and finger side of the grip device; $F_{GF}$ is the average grip force; $d_{tip}$ is the vertical difference between the marker of thumb and of index. *n.s.* indicates non-significance
grip for left CM requires subjects to use only the index finger to sustain a relatively larger load than three-digit grip. This might have caused the significant change in $T_{com}$ for the 3d→2d L_CM condition. Nevertheless, and most importantly, the overall task performance (minimizing object roll) was not degraded by switching grip type.

Immediate adaptation of compensatory torque components following a change in grip type

The above positive learning transfer of $T_{com}$ to a different grip type implies that subjects were able to coordinate, in an anticipatory fashion, the three $T_{com}$ components: $d_y$, $d_{LF}$, $F_{GF}$. However, these three components can be coordinated in an infinite number of ways. Therefore, to determine the solutions chosen by subjects to generate the same $T_{com}$ after changing grip type, we analyzed each $T_{com}$ component separately. The analyses below addressed the question of whether subjects chose the same or different compensatory torque components immediately following a change in the number of fingers participating to the grasp using ANOVA for each CM location with within-subject factor of Grip type (2 levels; 2d and 3d).

Digit center of pressure. Subjects used significantly different vertical separations between digit center of pressure ($d_y$) after switching grip type on all but one experimental condition (3d→2d, R_CM; Fig. 4.4D; Table 4.1). For the left CM location, subjects significantly increased $d_y$ when adding middle finger to the grip (Fig. 4.4C) and decreased $d_y$ when removing one finger from the grip (Fig. 4.4D), whereas an opposite pattern was found for the right CM location. However, the change in the net center of pressure on the finger side when adding or removing a finger could have been due to (a) a change in force distribution while keeping the original distance between thumb and
Figure 4.4. Learning transfer of digit center of pressure and position from pre- to post-grip type switch trials (immediate transfer).

A, B, The thumb, index, and middle fingertip position defined by the vertical marker position. To visualize the relative position of the fingertips, the thumb marker position (square) is connected by a line to the index and middle finger marker positions (open and filled circles, respectively). Fingertip marker positions are plotted relative to thumb marker position. Bottom panels show the vertical distance between thumb and finger side center of pressure ($d_y$). “Pre” and “post” denote data from the trial before and after the switch in grip type, respectively (A, C: switch from two to three digits; B, D: switch from three to two digits). For all panels, $L_{CM}$ and $R_{CM}$ denote left and right center of mass, respectively. Asterisks denote a statistically significant difference ($p < 0.05$) between pre- and post-switch trials. Data are averages of all subjects (± S.E.).
index finger the same or (b) to a change in the index finger position relative to thumb position and force distribution. To distinguish between these two possibilities, we tracked the thumb, index, and middle fingertip position through a motion capture system. We found that the distance between thumb and index finger marker \(d_{\text{tip}}\) was significantly modulated such that the index finger was positioned higher (Fig. 4.4A) when adding the middle finger and lower when removing the middle finger (Fig. 4.4B). Therefore, subjects used significantly different digit placement distribution when changing grip type (Table 4.1).

**Digit grip force.** We found no significant main effect of Grip type \((p > 0.05\) for each experimental condition), indicating that subjects exerted similar net grip forces regardless of the number of digits used for the grasp (Table 4.1). However, while grip force is provided by index finger only in 2d grip on finger side, the middle finger may contribute the substantially in 3d grip for left CM condition,

**Digit load force.** Subjects used significantly different load force sharing (thumb minus finger load force; \(d_{LF}\)) after switching grip type on only one experimental condition \((2d \rightarrow 3d, L_{\text{CM}};\) Table 4.1).

In summary, the immediate effects of changing grip type were mostly found on grasp kinematics, as the overall force coordination was little affected by adding or removing the middle finger. This indicates that, since subjects generated similar \(T_{\text{com}}\) on pre- vs. post-switch in grip type, significant changes in digit placement were actively compensated by re-distribution of digit forces. Although we cannot explicitly measure individual grip forces of index and middle finger, the redistribution of grip force can be inferred from the location of the net CoP and fingertip positions. The fact that net CoP
was located about half-way between index and middle fingers indicates an approximately even sharing of grip forces.

*Long term adaptation of compensatory torque components following a change in grip type*

The above analysis quantified subjects’ *immediate* ability to generate the same $T_{com}$ on the trial before and after the switch in grip type. However, a complementary question is whether learning transfer effects might have gone beyond the very first trial performed with a different grip type. The analyses below were performed to quantify the extent to which $T_{com}$ learned with a given grip type had long-term effects on the trial-to-trial adaptation of digit forces and positions when performing object lifts using a different grip type through ANOVA with repeated measures for each CM location with within-subject factors of *Trial* (7 levels; 7 pre- and 7 post-switch) and *Grip type* (2 levels, pre- and post-switch).

*Digit center of pressure.* After the immediate adaptation (i.e., trial 11) following a change in grip type, there were no further significant modulation of $d_y$ (neither significant Trial effect nor Trial $\times$ Grip interaction, $p > 0.05$). Specifically, the new digit placement was maintained for all experimental conditions (significant Grip effect for three conditions and non-significant Grip effect for one condition, $3d \rightarrow 2d$, $R_{CM}$; Fig. 4.5 and Table 4.2; this significant effect is consistent with the statistical significance of immediate adaptation). With regard to the relative fingertip positions, $d_{tip}$ was significantly modulated in a similar fashion to that observed in the immediate adaptation in all conditions (significant Grip type effect only; Table 4.2).
Table 4.2 Statistical results on long-term transfer of action and adaptation of compensatory torque components (trials 4–10 vs 11–17).

<table>
<thead>
<tr>
<th></th>
<th>$2d \rightarrow 3d$ L_CM</th>
<th>$2d \rightarrow 3d$ R_CM</th>
<th>$3d \rightarrow 2d$ L_CM</th>
<th>$3d \rightarrow 2d$ R_CM</th>
</tr>
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<tbody>
<tr>
<td>$T_{com}$</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>Peak Roll</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>$d_y$</td>
<td>F=41.84, $p &lt; 0.001$</td>
<td>F=9.33, $p=0.014$</td>
<td>F=20.98, $p=0.001$</td>
<td>n.s.</td>
</tr>
<tr>
<td>$d_{LF}$</td>
<td>F=22.07, $p=0.001$</td>
<td>F=5.72, $p=0.041$</td>
<td>F=10.03, $p=0.011$</td>
<td>n.s.</td>
</tr>
<tr>
<td>$F_{GF}$</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>$d_{tip}$</td>
<td>F=15.43, $p=0.003$</td>
<td>F=17.36, $p=0.002$</td>
<td>F=81.66, $p &lt; 0.001$</td>
<td>F=75.74, $p &lt; 0.001$</td>
</tr>
</tbody>
</table>

Each row shows statistical results of simple effects of switching grip type ($2d$: 2 digit grip; $3d$: 3 digit grip) in two CM conditions (L_CM and R_CM) on a single variable, compared between trial 4-10 (pre-switch trials) and 11-17 (post-switch trials). The degrees of freedom for all comparisons are (1,9). $T_{com}$ is the compensatory torque; $d_y$ is the vertical difference between the net centers of pressure of thumb and finger side of the grip device; $d_{LF}$ is the difference between the load forces of thumb and finger side of the grip device; $F_{GF}$ is the average grip force; $d_{tip}$ is the vertical difference between the marker of thumb and of index. n.s. indicates non-significance.
**Digit load forces.** Unlike the above-described immediate adaptation in the digit load force difference ($d_{LF}$), three out of four experimental conditions showed long term modulation of $d_{LF}$ throughout the first post-switch trials in response to the modulation of $d_y$ (significant Grip effect; Table 4.2). $d_{LF}$ remained unchanged only in $3d \rightarrow 2d$, $R_{CM}$ condition (Table 4.2) in which also $d_y$ was not modulated significantly. However, there were neither significant Trial effect nor Trial $\times$ Grip type interaction (Fig. 4.5) on $d_{LF}$. In general, subjects tend to use larger load force difference in $2d$ grip than $3d$ grip.

**Digit grip force.** In the trials following the switch in grip type subjects exerted similar grip forces to those exerted before the switch (Fig. 4.5E,F), as indicated by the lack of significant main effects of Grip type, Trial, or interaction ($p > 0.05$ for each experimental condition; Table 4.2).

To summarize, while similar $T_{com}$ was generated over consecutive trials following a switch in grip type, subjects adopted different strategies in digit kinematics and forces. All three conditions that showed significant change of $d_y$ were compensated by significant change of load force coordination, whereas the $3d \rightarrow 2d$, $R_{CM}$ condition did not show any significant change except finger tip position.

**DISCUSSION**

After learning to lift an object with asymmetrical mass distribution using one grip type, subjects were able to immediately transfer the learned compensatory torque despite the addition or removal of one finger, thus preserving the ability to minimize object roll. These results suggest that the manipulation learned through consecutive practice resulted in a high-level neural representation independent from low-level constraints, i.e., the specific effectors used to learn the
Figure 4.5. Learning curves of digit center of pressure and forces: pre- and post-grip type switch (long-term adaptation).

From top to bottom, data shown are the vertical distance (difference) between thumb center of pressure and the center of pressure on the finger side of the grip device ($d_y$), the difference between thumb load force and load force on the finger side of the grip device ($d_{LF}$), and grip force ($F_{GF}$), respectively. For three digit grips (3$d$), the center of pressure and forces exerted on the finger side of the device result from forces exerted by the index and middle fingers. Data on the left and right column are from the left and right center of mass conditions (L_{CM} and R_{CM}, respectively). Each plot shows data from two-digit grip trials followed by three-digit grip trials (squares) and trials performed in the reverse order (circles). Data are averages of all subjects ($\pm$ S.E.).
manipulation. We discuss our results in relation to neural representations of manipulation tasks and the factors that limit their generalization.

*Motor equivalence in anticipatory control of manipulation*

The ability of the sensorimotor system to perform the same task using degrees of freedom that had not been engaged while learning the task has been referred to as motor equivalence (Lashley, 1930; Cole and Abbs, 1986; Rijntjes et al., 1999; Wing, 2000). Further examples of motor equivalence in anticipatory control of grasping are provided by across-hand transfer task which showed that object weight information, acquired by hefting object in left hand, can be used to scale digit forces when using the right hand to lift the same object (Chang et al., 2008). The present findings are evidence of within-hand motor equivalence that use different fingers as different degrees of freedom. Of particular relevance to present study are the observations that subjects can change multi-digit force coordination patterns after removing or adding one finger to the grip *during object hold* with no disruption to the task or its mechanical requirements (Santello and Soechting, 2000; Budgeon et al., 2008). These studies showed that motor output can be re-organized within-hand *while performing the task* with online sensing of the desired manipulation goal. The present findings extend these observations to anticipatory learning transfer. It appears that learned sensorimotor representation of a manipulation task can be used as a ‘reference’ to which incoming sensory inputs can be compared for generating behaviorally equivalent outputs through *different* degrees of freedom, e.g., using of different fingers. This is an important finding as it provides novel insight into high-level action representation of manipulation and the flexibility with which it can be executed.
Control mechanisms

We had proposed a control mechanism that integrates online feedback of digit placement with sensorimotor memories of the manipulation task for compensating the variance in digit placement through digit force modulation to achieve stable behavioral performance (Fu et al., 2010). This compensation is implemented according to a high-level representation of the learned manipulation task before object lift onset. However, in that study force compensation for trial-to-trial variability of digit placement was implemented on the digits that had already experienced the manipulation task (e.g., same degrees of freedom). It is remarkable that this compensation could occur even when adding or removing a digit significantly changes the sensory feedback (activation of cutaneous receptors, proprioceptors, etc.) relative to that associated with the manipulation learned before the switch in grip type. Within this framework, the force compensation for trial-to-trial variability in digit placement described by Fu et al. (2010) appears to be a special case of the general phenomenon revealed by the present study. The proposed concept of decomposing high level representation into different degrees of freedom (digit positions and forces) is similar to the virtual finger hypothesis (Iberall et al., 1986; Baud-Bovy and Soechting, 2001) which argues that prehension is planned first using virtual fingers in opposition space, and then mapped into individual fingers. However, if the position of the virtual finger were to be identified with the location of the CoP, our results do not support an invariant virtual finger in different grips. The manipulation task could have been directly mapped into individual digits without necessarily involving virtual fingers.
Cortical networks required for within-hand transfer of learning in manipulation

Within-hand transfer of dexterous manipulation requires three neural processes: (a) generation of high-level representation (i.e., net force/torque applied on the object) derived from the integration of feedback sensed through arbitrary sensory elements (i.e., digit contact distribution and forces), (b) storage, update, and retrieval of the high-level representation of the task, and (c) effective decomposition into arbitrary degrees of freedom.

Posterior parietal cortex (PPC) receives sensory signals from different sensory modalities as well as efferent copies from motor cortex (Andersen et al., 1997). Brain imaging studies indicate that PPC is involved in the coordination of fingertip forces (Ehrsson et al., 2003; Jenmalm et al., 2006) and sensorimotor transformations (Jeannerod et al., 1995; Avillac et al., 2005). In our task, building a given high-level representation of manipulation means integrating sensory feedback of digit forces and positions from an arbitrary set of digits. We propose that this area is involved in transforming digit-specific force vectors and relative positions into a neural representation of the net torque exerted on the object.

Neural representation of the net force/torque necessary for manipulation (in our task, the compensatory torque to prevent object roll during the lift) needs to be accurately stored and retrieved. Rijntjes and colleagues (1999) showed that end-effector independent functional representations of signing movements performed with fingers and toes appear to be stored in, and retrieved from, the same cortical network involving secondary sensorimotor cortices, i.e., the anterior part of ventral premotor and dorsal cortices, supplementary motor area, middle and ventral intraparietal areas in the intraparietal...
sulcus, thalamus, and cerebellar hemispheres. Therefore, this network could be involved in storing a neural representation of the ‘goal’ of the task (i.e., compensatory torque), as opposed to effector-specific areas (e.g., primary sensorimotor cortex) that are selectively involved when using muscles involved with different grip types.

We propose that the decomposition of the high-level representation into neural commands to degrees of freedom (e.g., muscles of the thumb, index, and middle finger) occurs at the planning stage and is further refined through somatosensory feedback from contact to object lift onset. Prior to contact, planning of digit forces and positions engages a frontal-parietal circuit comprised of anterior intraparietal sulcus and ventral premotor cortex (Davare et al., 2007; Olivier et al., 2007). After contact, we speculate that the same cortical networks are involved for digit position sensing and are used to modulate forces if unexpected deviations from desired contact positions are detected (Fu et al. 2010). Jenmalm and colleagues (2006) have shown that supramarginal gyrus may monitor the mismatch between predicted and actual sensory input and update sensorimotor memories in a lifting task, whereas corrections to erroneously programmed lifting force involved supplementary motor area and cerebellum. It is likely that monitoring the compensatory torque in our task may engage the same neural circuitry but further studies are needed to test this model.

The proposed circuitry underlying learning of object manipulation (Fu et al. 2010) and the above-described neural networks underlying motor equivalence are likely to significantly overlap. Such overlap is mostly determined by the fact that both learning and learning transfer require the ability to generate and retrieve a high-level representation of the task that is not constrained by a specific digit contact distribution.
Therefore, learning manipulation using the same digits may become indistinguishable from transferring learned manipulation involving a variable number of digits, the main differences being how accurate the stored prior high-level representation is and the extent to which it needs to be updated.

Are learned manipulations always transferable?

The seamless learning transfer of our manipulation task across grip types raises the following question: is the ability of transferring learned manipulations a fundamental ability of the CNS or, conversely, is it highly dependent on the conditions of the task subjects transfer the learned manipulation to? Several lines of evidence support the latter scenario. Specifically, subjects are unable to fully transfer manipulative forces following an object rotation that changes the learned mapping between digit forces and object properties, e.g., texture (Edin et al., 1992; Quaney and Cole, 2004), mass distribution (Salimi et al., 2000, 2003; Bursztyn and Flanagan, 2008; Albert et al., 2009; Zhang et al., 2010).

The above studies suggest that the CNS might store multiple neural representations of manipulation tasks (Ingram et al., 2010). Yet, the present findings suggest the existence of a high-level, effector-independent representation of learned manipulations that can be easily transferred. However, the studies that have described failure of learning transfer all required subjects to successfully dissociate the frame of reference of the learned manipulation from a hand-centered frame of reference, whereas the present study did not. Therefore, we speculate that anticipatory control of the compensatory torque did not degrade despite changing grasp configuration because the
frame of reference of the manipulation task remained invariant relative to the hand frame
of reference.

Interestingly, however, there are instances where the congruence between
manipulation task and hand frame of reference can be broken by changing the hand
position relative to the object without interfering with transfer of learned manipulation
(Quaney and Cole 2004; Bursztyn and Flanagan 2008). These two studies, together with
the above cited work, suggest that the interference to learning transfer is not caused by
the lack of congruence between hand and manipulation frames of reference per se, but
rather by the CNS’ inability to mentally rotate the action as a function of the object’s new
orientation relative to the hand.
Chapter 5

CONTEXT-DEPENDENT LEARNING INTERFERES WITH VISUOMOTOR TRANSFORMATIONS FOR MANIPULATION PLANNING

INTRODUCTION

Dexterous manipulation is a unique and critically important human behavior that relies on integrating cognition, visual information, and sensorimotor memory for planning hand-tool interactions. When starting to learn a manipulation task, inferring object properties through vision allows humans to anticipate task dynamics and appropriate motor commands for modulating digit forces and placement (Gordon et al., 1991; Lukos et al. 2008; Fu et al., 2010). However, large discrepancies may exist between visual cues and object physical properties, e.g., a visually symmetric shape with an asymmetric mass distribution (Salimi et al., 2003; Zhang et al., 2010; Bursztyn and Flanagan, 2008), an unknown mass associated with a virtual object (Ingram et al., 2011), or a large object that is lighter than its visual size may suggest (Flanagan and Beltzner, 2000). These discrepancies result in an erroneous initial visual estimation of task dynamics and large performance errors at the beginning of the learning process. Consequently, on later trials subjects have to rely on sensorimotor memory of the experienced task dynamics to learn object manipulation rather than on these ineffective visual cues. This is because the information acquired through sensorimotor learning might be weighted more than vision as the former is more reliable (Ernst and Banks, 2002; Säfström and Edin, 2004).

It has also been shown that this sensorimotor memory acquired through hand-object interactions is specific to the object orientation at which the manipulation was
learned. Specifically, subjects fail to generalize learned manipulations to new ones following a 180° physical rotation of the object. Hence, subjects have to re-learn the task in the new context (Salimi et al., 2003; Zhang et al., 2010; Bursztyn and Flanagan, 2008; Ingram et al., 2011). The question arises about whether the physical rotation of the target object is the primary factor that prevents the generalization. Physical rotation of the object may force subjects to perform a mental rotation of the previously established sensorimotor memory (Ingram et al., 2010) similar to the mental rotation in visual object recognition which is considered computationally challenging for the brain (Zacks, 2008). Alternatively, failure to generalize learned manipulation may be an intrinsic feature of the sensorimotor system not limited to tasks involving changes of object orientation. Here we demonstrate, through novel experimental designs, that the context-dependency of the inability to generalize learned manipulation is not limited to rotation of objects with ineffective visual cues. Specifically, even with visual geometric cues congruent with object dynamics, subjects fail to generalize learned manipulations also when asked to manipulate the same object by grasping different parts of the object as well as when manipulating different objects. Furthermore, we discovered a surprising phenomenon: sensorimotor memory built in the preceding manipulation context, as well as through consecutive practice in the same context, can both interfere with subjects’ previous ability to effectively use visual cues when they start to learn manipulation in a new context, therefore preventing immediate learning generalization.
MATERIALS AND METHODS

Participants

Forty-eight healthy right-handed subjects (22 females, 26 males; 18–28 years of age) participated in this study. All participants were naïve to the purpose of the study and gave their informed consent according to the declaration of Helsinki. The protocols were approved by the Office of Research Integrity and Assurance, Arizona State University. Subjects were divided into three groups (16 subjects in each group). Each subject group participated to one of three protocols: “blocked U”, “blocked 2L”, and “random U”.

Apparatus

All subjects were instructed to lift the designated object vertically with their right hand while preventing the object from tilting, i.e., “as if trying to prevent a cup full of water from spilling”. The three protocols differed based on the shape of the object used for the manipulation and trial sequences. We used two object shapes: U-shape and L-shape, both of which have a base (19 × 5 × 5 cm³, 375 g) made of white plastic. The U-shape object has two vertical handles mounted on the two ends of the long side of the base, whereas the L-shape objects has only one vertical handle mounted on either left of right end of the base. All vertical handles (6.5 × 10 × 3 cm³, 275 g) were made of grey plastic and equipped with two hidden six-axis force–torque sensors (nano-25, ATI Industrial Automation, Garner, NC; Fig. 5.1A-C). The subjects were told and demonstrated (without lifting the object) that the handles were rigidly attached to the base. The design of the handle enables measurement of forces and torques applied by the digits. We computed the center of pressure at both vertical contact surfaces on the opposing sides of the handle and the net compensatory torque (see below) applied on the
Figure 5.1. Experimental apparatus and protocol.

A, The design of one handle instrumented with force/torque sensors. B, The two opposite actions afforded by the U-object when grasped by its left and right handles (“blocked U” and “random U” protocols). C, The two opposite actions afforded by two L-objects depending on the location of the handle relative to the base (“blocked 2L” protocol). D, The trial sequences for the two blocked protocols where subjects switched contexts after each block of eight consecutive trials of a given context. E, The trial sequences for the “random U” protocol where task context switched in a pseudo random fashion throughout the first 16 trials, followed by two blocks of eight consecutive trials of each context.
handle. Both U- and L-shaped objects provide visual geometrical cues that are congruent with the object’s mechanical properties (mass, friction, and mass distribution). Object kinematics was measured using a motion tracking system (Impulse, PhaseSpace, San Leandro, CA). Technical details of the sensors and force/torque data processing algorithms have been reported elsewhere (Zhang et al., 2010; Fu et al., 2011).

**Protocols**

The objects were located 30 cm in front of the subjects. Subjects were asked to shift their body sideways to align their right shoulder with the designated handle of the object to ensure a comfortable grasp. On hearing a ‘go’ signal, subjects reached to grasp and lift the object about 5 cm above the table and then held it in a stationary position for ~2 seconds. Subjects were required to grasp the specified handle with the tip of the thumb on the left contact surface and the tip of the index and middle fingers on the right contact surfaces of the handle (Fig. 5.1A), and to prevent the object from tilting (Fig. 5.1B and C). Subjects then replaced the object back to the table. All tasks required subjects to plan and generate torques in an anticipatory fashion to compensate the torque caused by asymmetrical mass distribution with respect to the hand (Fu et al., 2011).

Before the experiments started, the objects were visually presented to the subjects and they were allowed to touch the grip surface briefly to familiarize with the friction but without lifting the object. All protocols contained 32 trials that consist of two contexts, L and R. Subjects were instructed to perform the manipulation task in one of the contexts according to experimenter’s instructions before each trial or blocks of trials. Within each protocol, sixteen subjects were evenly divided into two groups to start with either L or R
contexts. The inter-trial and inter-block resting times were about 10 seconds. The three protocols are described below:

(1) “Blocked U” protocol: Subjects were presented with the U-shape object that affords two equal but opposite contexts L and R when lifted by grasping either the left or right handle, respectively (Fig. 5.1B). As subjects were asked to balance the object while lifting it, context L required subjects to produce a counterclockwise (CCW) compensatory torque of 550 Nmm whereas context R required a clockwise (CW) compensatory torque of 550 Nmm. The trial sequence was presented in a blocked fashion that required subjects to switch context after every eight consecutive trials in the same context (L to R, R to L; Fig. 5.1D).

(2) “Blocked 2L” protocol: Subjects were first presented with one of two L-shaped objects, both of which had a single vertical handle that affords a single action. The two objects are identical except that one has the handle on the left (left L-shape) and the other one has the handle on the right (right L-shape). Context L required subjects to lift the left L-shape object and produce a CCW compensatory torque of 320 Nmm whereas context R required lifting the right L-shape object and producing a CW compensatory torque of 320 Nmm. To ensure that subjects understood they were interacting with different objects, the left L-object and the right L-object had a label “B” and “A”, respectively, attached to the front of the handle (Fig. 5.1C). When the target object was presented (e.g., left L-shape), the other object (e.g., right L-shape) was occluded from view by a cardboard box. When subjects were asked to switch to the other object, they used both hands to lift the box and place it to cover the previously manipulated object. This procedure further ensured that subjects were aware that the
upcoming trials were to be performed on a different object, while preventing one of the
two objects to act as a distractor during grasping and lifting of the nearby object. The trial
sequence was presented in a blocked fashion that required subjects to switch context after
every eight consecutive trials in the same context (L to R, R to L, Fig. 5.1D).

(3) “Random U” protocol: Subjects were presented with the same U-shape
object used for the “blocked U” protocol (Fig. 5.1B). The trial sequence was designed to
expose subjects to L and R contexts in a pseudo random fashion for the first block of 16
trials, followed by two blocks of eight consecutive trials for each context (Fig. 5.1E).
Subjects had to switch context after the first trial, then they had to switch contexts
multiple times every 1, 2, or 3 trials before the last two blocks of trials. Each context was
presented 8 times in a pseudo random sequence.

Data Analysis

We used the compensatory torque (T_{com}) subjects generated at object lift onset
to quantify subjects’ ability to anticipate manipulative forces. In our previous work we
have validated the use of T_{com} to quantify learning of high-level representations of
manipulations independent of trial-to-trial variability of digit placement and forces
engaged in the task (Fu et al. 2010, 2011). Note that T_{com} at object lift onset is a direct
measure of anticipatory control of manipulation as it is computed before the object is
lifted. As such, T_{com} on trial 1 in all protocols is a measure of anticipatory control of
manipulation based only on visual geometric cues. T_{com} on the following trials is
expected to be influenced by both visual geometric cues and sensorimotor memory
acquired through manipulations performed on previous trials. Importantly, the
discrepancy between the T_{com} produced at lift onset and the torque required to perfectly
prevent object roll ($T_{\text{task}}$) positively correlates with the error in behavioral performance quantified as object peak roll (32 trials × 48 subjects = 1536 trials; $r = 0.71$, $p < 0.001$). We found that subjects never produced a $T_{\text{com}}$ in the wrong direction with respect to $T_{\text{task}}$. Therefore, to simplify the statistical analysis we used the absolute magnitude of $T_{\text{com}}$ ($|T_{\text{com}}|$) despite the fact that the compensatory torques were exerted in opposite directions for the L and R context in each protocol.

Statistical analyses were designed to assess $T_{\text{com}}$ within-block learning, inter-block interactions, and differences between protocols. The following statistics were used:

1. For each block of eight consecutive trials performed in the same context (all four blocks in “blocked U” and “blocked 2L”, and the last two blocks in “random U”), we performed two-way ANOVA using TRIAL as within-subject factor to examine if the production of $|T_{\text{com}}|$ improved across eight trials and GROUP as between-subject factor to examine if L and R contexts differed from each other (Fig. 5.1D and E).

2. We performed two-way ANOVA using TRIAL as within-subject factor and GROUP as between-subject factor to compare $|T_{\text{com}}|$ in trial 1 of block 1 versus the first post-switch trials (trial 9 in “blocked U” and “blocked 2L”; trial 2 in “random U”), as well as potential differences between L and R contexts, respectively (Fig. 5.1D and E). This analysis determines whether sensorimotor memory built through performing the manipulation task in Context 1 affects the ability to use visual geometry cues at the beginning of Context 2. The rationale for this analysis is that the manipulation planning error (the difference between $T_{\text{task}}$ and $T_{\text{com}}$) on the first trial could only be caused by visual estimation of object dynamics, whereas the error in the first post-switch trials...
could have been influenced by both sensorimotor memory built through practice during block 1 and the new visual estimation of task dynamics.

(3) Two-way ANOVA using TRIAL as within-subject factor and GROUP as between-subject factor to determine whether $|T_{\text{com}}|$ produced in the first trials changed across blocks 2, 3, and 4 for “blocked U” and “blocked 2L”. Note that at the beginning of blocks 3 and 4, subjects would have acquired sensorimotor memory of manipulations of both Context 1 and Context 2 performed in blocks 1 and 2 (Fig. 5.1D).

(4) One-way MANOVA using GROUP as between-subject factor to examine if starting with L or R handle caused subjects to produce $|T_{\text{com}}|$ differently in the first block of 16 random trials for “random U” (Fig. 5.1E).

(5) Two-way ANOVA using TRIAL as within-subject factor and GROUP as between-subject factor to determine whether $|T_{\text{com}}|$ changed across eight post-switch trials in the first block of 16 random trials for “random U” (Fig. 5.1E).

(6) Two-way ANOVA using TRIAL as within-subject factor and GROUP as between-subject factor to determine whether $|T_{\text{com}}|$ changed across trials following the post-switch trials in random trials (trials 3, 5, 9, 12, 14, and 16) as well as in blocked trials (trials 18 – 24) for “random U” (Fig. 5.1E).

(7) Two-way ANOVA using PROTOCOL and GROUP as between-subject factor to examine whether the extent of exposure to one context before switching to a different context influences the $|T_{\text{com}}|$ produced in the first post-switch trial (trial 9 in “blocked U” versus trial 2 in “random U”), as well as to compare the last post-switch trial (trial 25) in both protocols (Fig. 5.1D and E).
Figure 5.2. Experimental results of “blocked U” protocol.

Upper and lower part of A show the directional compensatory torque ($T_{\text{com}}$) at object lift onset and absolute peak object roll as a function of trial. Data are mean values averaged across all subjects and standard error of the mean (mid-line and height of the green squares, respectively, for $T_{\text{com}}$). The red and blue backgrounds indicate Context 1 and Context 2, respectively. B, Absolute Tcom magnitude ($|T_{\text{com}}|$) produced in the first trial (T1) and on all post-switch trials (S1, S2, and S3; see Fig. 5.1). Data are mean values averaged across all subjects and vertical lines denote standard error of the mean. Horizontal dashed lines in A and B denote task torque magnitude. Asterisks (*) in Panel A indicate a significant main effect of trial. Asterisks in Panel B indicate a significant difference at $p < 0.01$. 
RESULTS

We did not find any significant difference between the subject group that started with the R versus the L context in any of the statistical analyses for all three protocols. Therefore we report the results obtained by pooling data from group R and L and define the first context subjects started with as Context 1 and the subsequent context as Context 2, regardless of whether they started with context L or R (Fig. 5.1D and E).

“Blocked U” protocol: Learning and generalization

The effectiveness of visual cues in eliciting manipulative actions was validated in the first block of trials in which subjects produced $T_{\text{com}}$ very close to $T_{\text{task}}$ on the first trial ($|T_{\text{com}}| = 429.1 \pm 34.7 \text{ Nmm, mean } \pm \text{ SE}; |T_{\text{task}}| = 550 \text{ Nmm}$). This result indicates that subjects were able to use visual cues of object geometry to infer the direction and magnitude of the torque they needed to counteract using $T_{\text{com}}$. This was further confirmed by the fact that implicit knowledge of object mass distribution acquired through subsequent trials did not improve performance (Fig. 5.2A; no significant main effect of TRIAL, $p = 0.21$). Therefore, before lifting the object for the first time, subjects were able to use only visual geometric cues about object mass distribution and prior knowledge of material properties to predict the dynamics of the manipulation task. However, despite the almost perfect performance afforded by visual estimation, subjects failed to use it for planning a different manipulation when asked to switch to the other handle after block 1. This counter-intuitive result was revealed by significantly smaller $T_{\text{com}}$ in the first trial of block 2 ($|T_{\text{com}}| = 198.1 \pm 30.9 \text{ Nmm}$) versus the first trial of block 1 (Fig. 5.2B; significant main effect of TRIAL, $F_{(1,14)} = 20.39; p < 0.001$) as well as a significant trial-to-trial learning in block 2 (significant TRIAL effect, $F_{(7,98)} = 25.25, p <$
0.001). This suggests that, after changing the part of the (same) object grasped to perform the manipulation, sensorimotor memory not only prevented generalization across different contexts, but also produced interference on the ability to use visual estimation again for grasp planning. Remarkably, even though subjects had acquired sensorimotor memory of both manipulations at the beginning of block 3 and block 4, performance error when switching between two contexts persisted as both blocks showed significant re-learning (Fig. 5.2A; block 3 and 4: significant main effect of TRIAL; F(7,98) = 29.54 and 10.04, respectively; both p < 0.001). The interference was weakened by accumulating more practice of both manipulations, as shown by a significant reduction of error on the first trial across the last three blocks (Fig. 5.2B; significant main effect of TRIAL; F(2,28) = 11.78, p < 0.001). These results suggest that context-dependent learning interferes with the ability to use visual information each time that the context changes despite strong explicit (visual) cues about object dynamics. One may question whether this interference is object-dependent, that is, whether the inability to generalize one learned manipulation in one context to another context is due to the fact that subjects were always interacting with the same object. If so, learning a manipulation with an object should not produce interference when performing a different manipulation with another object. To examine this issue, we tested the second protocol, “blocked 2L”, in which subjects had the same blocked trial sequence (switching context every eight trials), but now the two contexts were associated with two different objects.

“Blocked 2L” protocol: Learning and generalization

In block 1, the visual cues were as efficient as the “blocked U” experiment for predicting the direction of the torque. However, subjects under-estimated the torque
magnitude, as performance was characterized by a moderate error ($|T_{com}| = 174.8 \pm 14.7$ Nmm; $|T_{task}| = 320$ Nmm) and a statistically significant learning curve (Fig. 5.3A; significant main effect of TRIAL, $F_{(7,98)} = 10.77, p < 0.001$). However, the interference caused by the sensorimotor memory of the first manipulation was again found as the $|T_{com}|$ in trial 1 of block 2 ($83.9 \pm 16.6$ Nmm) was significantly smaller than that of trial 1 of block 1 (Fig. 5.3B; significant main effect of TRIAL, $F_{(1,14)} = 12.8, p = 0.003$). This result is consistent with the above result from the U-shaped object. Importantly, this finding indicates that the interference produced by sensorimotor memory of a manipulation on planning a different manipulation is not limited to manipulations performed with the same object (U-shape) as it also occurs when switching task contexts, i.e., changing the target object. Lastly, similar to the “blocked U” experiment, with further practice the interference due to switching task contexts decreased as shown by the increase in $|T_{com}|$ across trial 1 of blocks 2, 3, and 4 (Fig. 5.3B; significant main effect of TRIAL; $F_{(2,28)} = 32.50, p < 0.001$).

“Random U” protocol: Learning and generalization

The first two protocols indicate that exposure to manipulation in one context over consecutive trials interferes with the ability to use visual information to anticipate object dynamics when switching context regardless of whether two contexts are afforded by the same or different objects. Therefore, the question arises about the neural mechanism that might underlie this surprising yet general phenomenon. The third protocol, “random U”, was designed to further our understanding about this novel interference by using a random context sequence using the U-shaped object. The rationale of this design was to prevent subjects from being exposed to the same context
Figure 5.3. Experimental results of “blocked 2L”.

Data from the “blocked 2L” protocol are shown in the same format as Figure 5.2.
consecutively over many trials (Fig. 5.1E) and therefore determine whether the above-described interference can occur after minimal exposure (1 to 3 trials) to a given manipulation context. Consistent with the results of the “blocked U” condition, subjects made very little error on the first trial ($|T_{\text{com}}| = 440.1 \pm 32.2 \text{ Nmm}; |T_{\text{task}}| = 550 \text{ Nmm}$) when using only visual estimation of object dynamics (Fig. 5.4A). However, when subjects switched to Context 2 immediately after trial 1, thus without further practice in Context 1, they produced a significantly smaller $|T_{\text{com}}|$ than on the previous trial (Fig. 5.4B; significant main effect of TRIAL; $F_{(1,14)} = 13.11, p = 0.003$). This indicates that exposure to just one trial to Context 1 creates an interference on manipulation planning on the post-switch trial. This interference was significantly smaller than the interference caused by eight consecutive trials in the “blocked U” condition, as indicated by the significantly larger $|T_{\text{com}}|$ in the first switch for the “random U” condition (Fig. 5.5; significant main effect of PROTOCOL; $F_{(3,28)} = 5.28, p = 0.029$). Similar to the “blocked U” condition, subjects tested in the “random U” protocol showed $|T_{\text{com}}|$ improvement on post-switch trials across multiple switches (Fig. 5.4B; significant main effect of TRIAL; $F_{(7,98)} = 3.32, p = 0.003$).

Subjects performed the manipulation on each handle for eight times during the first 16 trials in both “blocked U” and “random U” conditions (Figs. 2A and 4A, respectively). For the “random U” condition we found no significant differences in $|T_{\text{com}}|$ across the trials that followed each post-switch trial (trials 3, 5, 9, 12, 14, and 16; $p = 0.78$). T-tests revealed that the average $|T_{\text{com}}|$ measured for these trials were not significantly different from the last six trials of either block 1 or block 2 from the “blocked U” condition (trials 3-8 or trials 10-16, respectively; $p > 0.05$).
Figure 5.4. Experimental results using protocol “random U”.

Data from the “random U” protocol are shown in the same format as Figure 5.2. Note that this protocol is characterized by 10 context switches occurring after a variable number of trials with a given context (first 16 trials; (S1 through S8), one context switch at the beginning of the first series of 8 consecutive trials (S9), and one last context switch after 8 consecutive trials with a given context (S10).
This indicates that subjects’ performance following the context switch trial has recovered from the initial interference to a level similar to that observed through consecutive trials in the “blocked U” condition. Lastly, after the first 16 trials, subjects in both blocked and random U conditions performed another eight consecutive trials (trials 17-24). The $|T_{\text{com}}|$ in the last post-switch trial (trial 25) from these two experimental conditions was not significantly different (Fig. 5.5) and subjects in the “random U” condition showed significant re-learning (Fig. 5.4A; significant main effect of TRIAL; $F_{(7,98)} = 12.22, p < 0.001$) as also found for the “blocked U” condition.

**DISCUSSION**

*Context-dependent learning of manipulation with visual geometric cues*

Unlike previous work using objects with visual cues that are incongruent with their dynamics, we demonstrated the powerful effect of visual geometric cues on the initialization of the internal model of a new manipulation task (trial 1, all experimental conditions). It has been shown that humans can identify the center of mass of multiple separate or combined rigid bodies (Baud-Bovy and Soechting, 2001; Liby and Friedenberg, 2010). Our results indicate that this estimation can be used in the process of visuomotor transformation to generate motor commands for manipulative actions. Specifically, geometric cue-based anticipatory control was equally efficient to predict the direction of the task in both “blocked U” and “random U” protocols. However, the asymmetrical shape (L-shape) appears to be less effective for estimating torque magnitude than the asymmetrical one (U-shape), although it is still effective for predicting torque directions. This result is consistent with previous work showing that
Figure 5.5. Comparison of results from “random U” and “blocked U” protocols.

The figure shows the absolute magnitude of the compensatory torque ($|T_{\text{com}}|$) exerted on the first and last context switch for the “blocked U” and “random U” protocols. Data are mean values averaged across all subjects and vertical lines denote standard error of the mean. The horizontal dashed line denotes task torque magnitude. The asterisk indicates a significant difference at $p < 0.05$. 
subjects make larger errors when estimating the position of net center of mass of a triangular than a rectangular shape (Liby and Friedenberg, 2010).

Despite the effectiveness of visual cues, we found that failure of generalizing learned manipulation across different contexts (different parts of the same object and different objects) appears to be a general phenomenon encountered when the sensorimotor system faces the challenge of switching between two contexts that requires opposite manipulative actions (e.g., CW vs. CCW). This is demonstrated by the large error subjects made when switching to a new context for the first time. As our results were obtained without changing the orientation of the object, the present findings of context-dependency of learning generalization are consistent with, and extend beyond, the orientation-dependency of generalization of learned manipulations (Salimi et al., 2003; Zhang et al., 2010; Bursztyn and Flanagan, 2008; Ingram et al., 2011).

Sensorimotor experience interferes with the ability of using visual information

The most important and novel finding from our study is that the effectiveness of visually-based grasp planning was significantly reduced by preceding exposure to an opposite manipulation in a different context. Specifically, given the same context (R or L), the errors subjects made in anticipatory control were significantly larger when they had operated in a context that required opposite manipulative actions than when they only had visual information available (Fig. 5.2B, Fig. 5.3B, and Fig. 5.4B). In addition, longer consecutive exposure to one context induced more interference than single trial exposure (Fig. 5.5). To the best of our knowledge, our result is the first evidence that sensorimotor experience interferes with the previously demonstrated ability to transform visual input of object geometry into motor commands for manipulation planning. Interference has been
demonstrated as a reduction of learning rate in one context preceded by an opposite context using force fields (Sing and Smith, 2010) as well as visuomotor rotations (Krakauer et al., 2005). However, due to the presence of strong visual cues, our tasks are different because they are characterized by familiar dynamics, hence by a much faster learning rate than adaptation to force fields and visuomotor rotations (Ingram et al., 2011). Therefore, in our study the interference induced by previously learned context was revealed by a reduction of vision-based anticipatory control rather than a reduction in learning rate.

Even though the two contexts we studied require opposite digit force coordination patterns to produce compensatory torques in opposite directions, the present interference is unlikely to have occurred due to a bias at the level of individual digits or muscle groups. It has been shown that subjects made no performance error when switching to an opposite digit force coordination patterns following a 180° hand rotation (Bursztyn and Flanagan, 2008). It has also been shown that subjects were able to re-distribute digit forces and positions when switching across grip types to lift the same object (Fu et al., 2011). These findings suggest that manipulation can be learned in a digit-independent fashion. Specifically, opposite actions at the digit level alone do not appear to interfere with planning and execution of subsequent manipulations when the task dynamics (the direction and magnitude of the task torque) is invariant with respect to the subjects. Therefore, the interference from exposure to one preceding context found in our study is more likely to have occurred at the task level during planning manipulation, such that switching between two opposite contexts caused significant conflict in initialization of the task goal.
It has been recently shown that motor learning may involve parallel processes including error-based update of internal models (Haruno et al., 2001) and model free mechanisms such as use-dependent plasticity (Diedrichsen et al., 2010a). Using visuomotor rotation tasks, Huang and colleagues (2011) have shown that fast adaptation of an internal model channels movement toward successful error reduction, and repetition of the newly adapted movement slowly induces directional biases toward the repeated movement through use-dependent plasticity even when subjects made little performance error. If we assume the sensorimotor system learns and controls object manipulation in a similar fashion as reaching movements, we could speculate that the interference in our data arises from both model-based and model-free learning processes. Specifically, the interference induced by one trial exposure to manipulation may be caused by the updated internal model of the first context which competes with the visual-based initialization of the internal model for the second context, whereas the greater interference induced by consecutive movement repetitions may be caused by the additional involvement of use-dependent plasticity. Note, however, that object manipulation is characterized by a very different adaptation time scale than reaching movements, as for manipulation model update processes occur within a few trials because only parameter learning is required for familiar dynamics (Ingram et al., 2011).

Additional evidence for use-dependent plasticity comes from the fact that subjects in both random and blocked conditions made similar errors on the last switch (trial 25; Fig. 5.2B, Fig. 5.3B, and Fig. 5.4B). This suggests that eight repetitions of same context still caused interference on the subsequent context even when both contexts have been learned by the end of the first 16 trials. Lastly, the fact that interference persisted but
was reduced after multiple context switches suggests that subjects might have used contextual cues (i.e., associating a handle to a previously experienced manipulation) to switch to the correct internal model (Osu et al., 2004; Cothros et al., 2009).

Possible neural networks underlying the context-dependent interference

Our data suggest the existence of complex interactions and weight tuning between sensorimotor experience and visual estimation of object dynamics for generating precise motor commands, which can potentially lead to a competition between these processes and therefore sub-optimal performance. Although it is not clear where the interaction between internal model, online visuomotor control, and model free learning occurs in the brain, extensive research has shown that neural circuits underlying skilled manipulation involve a large network that transforms visual attributes of the object into goal-directed motor commands (Davare et al., 2011). The key regions consist of the anterior intraparietal area (AIP), ventral premotor (PMv), and primary motor cortex (M1). Experimental evidence from transcranial magnetic stimulation studies have shown that projections from visual cortex to AIP can affect M1-PMv functional connectivity (Davare et al., 2010), whereas PMv would be involved in facilitating M1 activity in a grasp-specific fashion (Davare et al., 2008). Furthermore, before visual information is available to the AIP-PMV-M1 circuitry, sensorimotor memory stored in the corticospinal system (M1) and/or cerebellum has the greatest influence on motor planning (Loh et al., 2010). It has also been suggested that changes in motor cortex induced by prior motor practice underlies use-dependent plasticity (Verstynen and Sabes, 2011). Our data show that the influence of sensorimotor experience can be very strong and could not be fully suppressed by visual input. Weight tuning of sensorimotor memory and vision could be
beneficial for action planning in stochastic environments in which the task goal of the upcoming context is difficult to predict (Verstynen and Sabes, 2011). At the same time, however, in a deterministic environment the sensorimotor system is somewhat limited in its ability to switch between contexts without performance degradation.

Conclusions

Our findings suggest that context-dependency is a generic feature in learning and generalization of dexterous manipulation: subjects primarily learn the action rather than the actual physical properties of the tool. Furthermore, we demonstrate that, although visual geometry cues can be very powerful for anticipatory control of dexterous manipulation, their contribution to motor planning is significantly inhibited by sensorimotor memory acquired through as little as one trial practice, therefore inducing interference. This interference may play an important role in preventing generalization of learned manipulation across different contexts. The present sensorimotor-visual interference provides novel insight into visuomotor transformations for skilled manipulation and an experimental framework for characterizing the neural circuitry responsible for linking perception and action.
Chapter 6

LEARNING SKILLED TOOL USE: PARALLEL PROCESSES UNDERLIE RETENTION AND INTERFERENCE

INTRODUCTION

Dexterous manipulation is thought to rely on building an internal representation of the task or object dynamics which can be updated through trial-by-trial learning to achieve a stable performance (Salimi et al., 2000; Flanagan et al., 2001; Nowak et al., 2007). Importantly, an object can be manipulated in different contexts, each requiring different forces and/or torques whose modulation, in turn, depends on object properties and hand-object spatial relations. However, the extent to which learning a given manipulation with the same object in one context can benefit learning manipulation in a different context is not well understood. Until recently, sensorimotor learning has been mostly studied using reaching tasks (for review, see Wolpert et al., 2011). Sensorimotor learning can be quantified as a reduction of behavioral error, i.e., endpoint accuracy, and/or increasing optimality of the motor output, i.e., less variability or energy cost. The properties of the learned representation of a motor task can then be evaluated by generalization or retrieval protocols where subjects are asked to generalize a previously learned task to a new context, or recall the learned task in the same context. Several models of sensorimotor learning based on reaching movements have been proposed, such as error-based learning which suggests that the central nervous system (CNS) updates the internal model of the task using errors made in the previous trial(s) (Smith et al., 2006), and model-free learning that are based on reinforcement and/or use-dependent plasticity (Huang et al., 2011).
Despite the insight provided by many studies of reaching movements, less is known about whether the proposed theoretical frameworks can account for sensorimotor learning underlying manipulation tasks. We have shown that a learned manipulation has an inhibitory effect on the CNS’s ability to use visual cues for planning manipulation in an opposite context, and that the strength of this interference depends on the extent of consecutive practice in the preceding context (Fu and Santello, 2012). This interference shares common features with experimental evidence from reaching studies demonstrating an anterograde interference using similar ABA paradigms where A and B denote opposite contexts. Specifically, we found the interference occurred on the “transfer trial” when subjects switched to context B the first time after learning A, as well as on the “retrieval trials” when subjects switched back to A. We hypothesized that this interference on visuomotor transformations of manipulation might have been the net result of two different learning processes running in parallel: one features error-driven updates of internal models, whereas the other depends on the repetition of successful actions. However, our previous study did not allow quantifying the role of each of these processes in the interference on manipulation transfer and retrieval. To pursue this goal, in the present study we used a series of experimental variations of the ABAB learning paradigm to thoroughly quantify the time course of the retention and interference phenomena. More importantly, these new data allowed the comparison with simulation results of sensorimotor learning theoretical models as well as experimental findings from other motor tasks.
Materials and Methods

Subjects

Sixty-four healthy right-handed subjects (18–28 years of age; 36 males) participated in this study. All participants were naive to the purpose of the study and gave their informed written consent according to the Declaration of Helsinki. The protocols were approved by the Office of Research Integrity and Assurance, Arizona State University. Subjects were randomly assigned to one of 6 groups (see below).

Apparatus

We asked subjects to grasp and lift an L-shaped object (Fu and Santello, 2012). This object consisted of a handle and a rectangular base. The handle was equipped with two force/torque (F/T) sensors (Nano25, ATI Industrial Automation; Fig. 6.1A) that were used to measure digit forces and compute the center of pressure on each side of the handle. Digit forces and center of pressure were used to calculate the compensatory torque subjects exerted on the object (Fu et al., 2010). We used an L-shaped object so as to have an asymmetrical mass distribution relative to the handle. The manipulation tasks required subjects to exert a torque to counter the external torque caused by the object’s mass distribution to prevent the object from tilting. Importantly, the object geometry also provided visual cues about the external torque direction that would allow subjects to anticipate the object’s asymmetrical mass distribution (see below).

The direction of the torque depended on the task context. Specifically, when the handle was presented on the right or left relative to the subject, the task context required a clockwise (CW) or a counterclockwise (CCW) torque (‘task torque’, $T_{\text{task}}$), respectively, of 320 Nmm (Fig. 6.1B). The two contexts were switched by instructing the subjects to
Figure 6.1. Experimental apparatus and protocol.

A, The design of the handle with embedded F/T sensors and unconstrained graspable surface. B, Two alternative presentations (R and L) of the object and their corresponding compensatory torque directions. C, The trial sequence, break time, and number of subjects for each experimental condition.
rotate the object 180 degrees about the center of the handle by grasping the base of the object on the opposite side without lifting the object. Our previous work using a L-shaped object has shown that visual cues about the object’s geometry allow subjects to anticipate the direction of the required torque even though the magnitude of the torque has to be learned by manipulating the object (Fu and Santello, 2012). The actual torque produced by the subjects at object lift onset to counter balance the task torque was defined as $T_{\text{com}}$. We also found in our previous work that the behavioral error subjects made (peak object roll) was linearly dependent on the torque error ($T_{\text{err}} = T_{\text{task}} - T_{\text{com}}$) they made at lift onset. This correlation was found in the present work, too ($r = 0.77$, $p < 0.001$, for all trials combined). Therefore, in all experiments, we measured $T_{\text{com}}$ at object lift onset to quantify subjects’ ability to predict the required compensatory torque. We also measured object peak roll using an active marker-based motion tracking system (Impulse, Phasespace Inc.) to obtain an additional motor performance index. The motion tracking system also provided measurement of object height with respect to the table surface, which was used to determine the instant at which object lift onset occurred (object height $> 0.5$ mm for at least 400 ms).

*Experimental procedures*

In all conditions, subjects sat comfortably and the object was presented 30 cm in front of them. The handle of the object was aligned with the subjects’ right shoulder to ensure a comfortable grasp with the right hand. On hearing a “go” signal, subjects reached to grasp and lifted the object $\sim$10 cm above the table, held it in a stationary position for $\sim$2 s, and replaced it on the table. Subjects were required to grasp the handle with the tip of the thumb on the left graspable surface of the handle, and the tip of the
index and middle fingers on the right graspable surfaces of the handle (Fig. 6.1B), and to prevent the object from tilting, as if ‘they are lifting a cup of water’. All tasks required subjects to plan and generate torques in an anticipatory fashion to compensate the torque caused by asymmetrical mass distribution with respect to the hand. After several lifts (see below), subjects were instructed to rotate the object 180 degrees as described above. Before the experiments started, the object was visually presented to the subjects and they were allowed to briefly touch the graspable surfaces to familiarize themselves with the frictional properties of the handle. All experimental conditions contained 4 blocks of 8 consecutive trials and each block was performed in the same context with the exception of the Rndm condition. The four blocks were always arranged in an A1B1A2B2 fashion. The experimental conditions differed in terms of the duration of the break between the first context A (Block 1) and context B (Block 2), or between context B (Block 2) and the second occurrence of context A (Block 3; Fig. 6.1C). Note that all breaks were given after the object rotation. The control group (Ctrl; n = 16) was given 10-s breaks for all context switches. To test the effect of time on the interference created by the preceding block of practice (Block 2) on the retrieval of previously learned manipulation (Block 1), different break durations were inserted between Block 2 and Block 3 since Trial 1 of Block 3 was the first retrieval trial (Fig. 6.1C). Specifically, the ‘retrieval’ groups R10m, R20m, and R1hr were given breaks of 10 minutes (n = 8), 20 minutes (n = 8), and 1 hour (n = 12), respectively. In addition, the ‘transfer’ group T1hr was tested to quantify subjects’ ability to generalize a learned manipulation from Block 1 to the new context in Block 2. The one-hour break was inserted before Block 2 since Trial 1 of Block 2 was the first time subjects encountered the second context (Fig. 6.1C). Subjects were asked to
remain seated in the chair if the break time was no more than 10 min. For longer breaks, subjects could leave the room during the break. The control group was also recalled two weeks after they performed the initial four blocks (Block 1-4) and performed another four blocks (Block 5-8) in the same order. Lastly, we also tested a group of subjects (Rndm, n = 8) that performed the first 16 trials with a pseudo random presentation of the two contexts, followed by two blocks of 8 consecutive trials in each context (Fig. 6.1C). The order of presentation of R and L contexts was counter-balanced across subjects for each experimental condition.

Data Analysis

As mentioned above, T_{err} positively correlated with the error in behavioral performance quantified as object peak roll. This allowed us to use T_{err} to quantify the anticipatory control of the task. In addition, we do not distinguish the contexts L and R since we have already shown that there was no difference between the two contexts from the perspective of torque production (Fu and Santello, 2012). Lastly, the L-shaped object used in this study provided strong visual geometrical cues that indicated the direction of the T_{com}. Subjects’ ability to correctly anticipate T_{com} direction was confirmed by data analysis revealing that T_{com} was always produced in the correct direction. Thus, the error subjects made was always due to inaccurate T_{com} magnitude produced at lift onset. We performed most of the statistical comparisons using T_{err} to avoid having to pool T_{com} with different signs as required by the two contexts. However, for graphical purposes we plotted T_{com} to show the direction of the contexts. All analyses were done using Matlab and SPSS.
Statistical analyses were designed to assess within-block learning, inter-block interactions, and the effect of break duration as follows (significance was indicated by $p < 0.05$ and Bonferroni corrections were applied when appropriate):

1. We performed two-way ANOVA using TRIAL as within-subject factor and GROUP as between-subject factor (one group starting with the L context, the other group starting with the R context) to examine if $T_{err}$ was reduced in the same fashion across eight trials within the first two blocks.

2. We performed t-tests between selected trials from all experimental conditions to quantify the interference on retrieval and transfer trials caused by preceding blocks or trials.

3. We performed one-way ANOVA on $T_{err}$ using GROUP as a between-subject factor to examine if different break durations caused different interference on retrieval of learned manipulation. Furthermore, to quantify the magnitude of the interference, we defined an ‘interference index’ ($I_{int}$) by calculating the difference between $T_{com}$ on Trial 1 of Block 3 and $T_{com}$ averaged across the last five trials of Block 1. An exponential function was fit to $I_{int}$ as a function of break duration to extract the time constant of the decay of the interference. Lastly, $I_{int}$ of manipulation retrieval was also calculated for the recall of the Ctrl group two weeks later. Specifically, $T_{com}$ on the first trial of Block 5 performed two weeks after the first experimental session was compared with $T_{com}$ averaged across the last five trials of Block 3 (context A) from the first session. Similarly, $T_{com}$ on the first trial of Block 6, also performed after the two-week break, was compared with $T_{com}$ averaged across the last five trials of Block 4 (context B) from the first session.
All tests were performed at the $p < 0.05$ significance level. Comparisons of interest exhibiting statistically significant differences were further analyzed using post hoc tests with Bonferroni corrections.

**Simulation**

To determine the extent to which our experimental results on learning, transfer, and retention could be described by current theoretical frameworks, we compared our results to two computational models of sensorimotor learning derived from manipulation and reaching tasks. Most of mathematical models of sensorimotor learning describe the learning process as error-driven updates of internal states (Wolpert et al., 2011). These models can be differentiated by the number of states, the number of time scales, and the use of context selection vectors. Since the manipulation tasks in our experiment were performed with an object with salient visual geometric cues, we selected two models that support context-selection vectors. The first model was a multi-context single rate (SR) model proposed for a virtual manipulation task in which subjects had to rotate an virtual hammer while maintaining the hand position (Ingram et al., 2011). The second model was a dual rate (DR) model that has been shown to explain many well-known motor learning phenomena found in reaching tasks, such as anterograde interference, spontaneous recovery, and savings (Lee and Schweighofer, 2009).

For both models, on each trial $n$, the motor error $e$ is determined by the difference between the motor output $y$ and the task requirement $f$:

$$ e(n) = f(n) - y(n) $$  \hspace{1cm} \text{Equation 6.1} $$

For the SR model, the state update process follows:

$$ y(n) = x(n)^T c(n) $$  \hspace{1cm} \text{Equation 6.2} $$
and

\[ x(n+1) = A \cdot x(n) + B \cdot e(n) \cdot c(n) \]  \hspace{1cm} \text{Equation 6.3} 

where \( x \) is a 2-d vector that represents the internal estimate of the task dynamics of the two contexts, \( e \) is the context selection vector that takes the value of \((1,0)^T\) or \((0,1)^T\) depending on the context on trial \( n \). This model assumes that the contexts are well separated and therefore little generalization or interference across the contexts should occur. \( A \) and \( B \) are the forgetting and learning rates, respectively.

For the DR model, the state update process follows:

\[ y(n) = x_f(n) + x_s(n)^T \cdot c(n) \]  \hspace{1cm} \text{Equation 6.4} 

and

\[ x_f(n+1) = A_f \cdot x_f(n) + B_f \cdot e(n) \]  \hspace{1cm} \text{Equation 6.5} 

\[ x_s(n+1) = A_s \cdot x_s(n) + B_s \cdot e(n) \cdot c(n) \]  \hspace{1cm} \text{Equation 6.6} 

where \( x_s \) is a 2-d vector that represents the internal states of the two contexts in a slow-learn-slow-forget process, \( x_f \) is a single state of a fast-learn-fast-forget process, and \( c \) is the context selection vector.

The purpose of our simulation was to examine whether existing models could capture the main features of our experimental results. We chose the parameters that best reproduced the results from the Ctrl group, i.e., a fast learning curve leading to a performance plateau within the first 2-3 trials, as follows: the task requirements \( f(n) \) was set to be 1 for context A and −1 for context B representing the opposite dynamics to balance the L-shaped object. For the SR model, we chose \( A = 0.94 \) and \( B = 0.7 \). For the DR model, we chose \( A_s = 0.995, B_s = 0.2, A_f = 0.7, \) and \( B_s = 0.5 \). Note that, whereas the forgetting rate \( A \) is comparable to the rates used in the literature, we used much larger
learning rates $B$. This choice was motivated by the fact that learning rate in our experiment is very fast (within 3 trials) relative to other tasks such as reaching against force fields (Smith et al., 2006) or virtual manipulation (Ingram et al., 2011). Another small, but important modification to existing models was their initialization. Unlike reaching tasks, the object manipulation task has salient visual geometric cues about the object mechanical properties and therefore the dynamics of the task (Fu and Santello 2012). Therefore, the initial motor output $y(1)$ in the first trial of our simulations was about half the task torque instead of zero (Fig. 6.2A). To do so, we set the initial value of $x(1)$ in the SR model to $(0.5, -0.5)^T$. For the DR model, motor output $y(1)$ is the sum of the initial estimate from both the fast and slow states. Since the fast state is context-independent, it is reasonable to assume that the visual context cues do not apply to the fast state. Therefore, we set the $x_f(1)$ to $(0.5, -0.5)^T$ and $x_s(1)$ to 0. Note that we performed the above simulations to illustrate the main features of these theoretical models for comparison with our data rather than to reproduce our experimental values.

**RESULTS**

Subjects learned our object lifting and balancing task very quickly and in the first block of eight trials exhibited similar learning rates in all blocked conditions (Ctrl, R10m, R20m, R1hr, and T1hr). Specifically, subjects started with a moderate error on the first trial by under-estimating the task torque ($T_{err} = 131.33 \pm 12.48$ Nmm, Mean ± SE, n = 56), but quickly minimized the error within the first three trials (Fig. 6.2A). One-way ANOVA showed no difference across all blocked conditions on $T_{err}$ for Trial 1 of Block 1 ($F_{(4,51)} = 1.258, p = 0.299$). In addition, there were no significant main effects of Trial ($F_{(4,204)} = 1.260, p = 0.287$) or Condition ($F_{(4,51)} = 0.565, p = 0.689$) across the last 5 trials.
of Block 1 on $T_{err}$. This result is consistent with our previous study (Fu and Santello, 2012) and was expected because the L-shaped object provided visual geometric cues about the direction of the task torque. Therefore, subjects only needed to improve the estimation of the torque magnitude and its timing with respect to object lift onset. It should be pointed out that the visual geometric cues only significantly reduced the initial error in the first trial, but did not make the learning curve to change much faster. It has been shown that, even with an inverted T-shaped object that does not have salient visual geometric cues, subjects could learn to exert the correct compensatory torque within 2-3 trials (Fu et al., 2010).

*Interference occurred at both transfer trials with minimal break*

After learning context A through Block 1, subjects rotated the object 180°, thus switching the manipulation context to B (Figs. 1B and C). Subjects in the control (Ctrl) and retrieval conditions (R10m, R20m, and R1hr) performed the first lift immediately after the object rotation and performed a total of eight consecutive manipulations in context B. Although the object had the same visual geometric cues, subjects made a large error in the first trial of the Block 2 (transfer trial, Fig. 6.2A; $T_{err} = 233.43 \pm 8.37$ Nmm). The error was significantly greater than the error subjects made in the first trial of Block 1 (repeated-measures ANOVA; significant main effect of Trial, $F_{(1,40)} = 49.383, p < 0.001$). This suggests that subjects not only failed to generalize what they had learned in context A, but also performed worse than when starting without prior manipulation experience, indicating anterograde interference. Despite the anterograde interference on the first trial, subjects were still able to learn context B quickly to the same extent as context A (Fig. 6.2A). We found no significant difference between the averages of $T_{err}$ of
Figure 6.2. Experimental results from control and retrieval groups.

A. From top to bottom, the trial-to-trial $T_{com}$ production in Block 1-4 for Ctrl, R10m, R20m, and R1hr groups, respectively. The $T_{task}$ (black dashed line) is defined to be positive for the first context (A) and negative for the second (B). B. The trial-to-trial $T_{com}$ production in Block 5-8 for Ctrl group after two weeks break. C. The interference indices plotted against time. The black solid line is the best exponential fit to the data. Data are averages of all subjects (± SE).
the last 5 trials of Block 1 versus Block 2 (no effect of Trial $F_{(4,160)} = 0.617, p = 0.651$; no effect of Condition $F_{(3,40)} = 0.744, p = 0.515$; no effect of block $F_{(1,40)} = 1.733, p = 0.196$).

After Block 2, subjects in the Ctrl condition were asked to rotate the object again after performing context B to switch back to context A (Fig. 6.1C). After a very short break (10 s), subjects made an error on Trial 1 of Block 3 even though they could have retried the previously learned context A. We asked whether this retrograde interference could have been due to (a) learning of context B causing context A to be unlearned, or (b) learning of B temporarily blocking the retrieval of A without erasing learning of context A. To distinguish between these two alternative phenomena, we asked subjects in R10m, R20m, and R1hr conditions to take breaks of different durations after they rotated the object at the end of Block 2 (Fig. 6.1C). Interestingly, when subjects came back to perform Block 3, we found that the duration of the break weakened the strength of the retrograde interference (Fig. 6.2A), i.e., subjects made a significantly smaller error in the retrieval trial if they had taken a longer break. Specifically, $T_{err}$ in Trial 1 Block 3 was 197.26 ± 15.22 Nmm, 137.40 ± 21.53 Nmm, 238.02 ± 21.53 Nmm, and 81.98 ± 17.56 Nmm, for Ctrl, R10m, R20m, and R1hr conditions, respectively (one-way ANOVA; significant main effect of condition, $F_{(3,40)} = 14.201 , p < 0.001$). Thus, learning of B only temporarily blocked the retrieval of learned context A without erasing it.

**Effect of time on the magnitude of interference on retrieval trials**

To better quantify the interference effect on the retrieval trial, we defined the index of the strength of the interference (Iint) as the difference between $T_{com}$ on Trial 1 of Block 3 and $T_{com}$ averaged across the last 5 trials of Block 1. We then fitted an
exponential function $I_{\text{int}} = c + ae^{-bt}$ to the mean $I_{\text{int}}$ averaged across subjects for $t = 0$, 10, 20, and 60 minutes. The results of the curve fitting indicated that the half-life of the decay of the interference was 10.91 minutes (Fig. 6.2C; adjusted $R^2 = 0.95$). This further indicates that subjects in the R1hr condition could retrieve context A in Trial 1 of Block 3 almost perfectly with minimal interference. One-sample t-test confirmed that $I$ for $t = 60$ minutes was not significantly different from zero ($t = 1.595, p = 0.139$). To examine how long the learned context could be retained, we also asked the subjects in Ctrl condition to come back two weeks after they first performed the tasks and repeat the experimental sequence. Independent T-test showed no significant difference in the strength of the interference when comparing Trial 1 of Block 3 of the R1hr condition and Trial 1 of Block 5 of the Ctrl condition ($t = 0.366, p = 0.717$; Fig. 6.2B), thus indicating that the learned context A was well retained even after two weeks. This result extended the previously found 24 hour retention of object lifting (Gordon et al., 1993; Nowak et al., 2007), and it was comparable with the retention of reaching movements in force field (Shadmehr and Brashers-Krug, 1997) and visuomotor rotation (Krakauer et al., 2005).

Interestingly, we found interference again when subjects switched contexts after Block 5 (Fig. 6.2B), as indicated by the large error found again in Trial 1 of Block 6 when subjects had to retrieve context B. The strength of this interference after two weeks was similar to that found in the retrieval trial of the Ctrl condition (Figs. 6.2A and 6.2B; independent sample t-test, $t = 0.511, p = 0.613$). This result indicates that the most recent manipulations in context A induced interference again on the subsequent manipulation context.
Figure 6.3. Experimental results from transfer and random groups.

**A**, Trial-to-trial $T_{\text{com}}$ production for T1hr group. **B**, Comparisons between the Ctrl and T1hr groups using first trials and transfer trials. **C**, Trial-to-trial $T_{\text{com}}$ production for T1hr group. **D**, Comparisons between the Ctrl and Rndm groups using first trials and transfer trials. Data are averages of all subjects (± SE).
Time-dependent anterograde interference on the transfer trial

We have demonstrated that learning manipulation in context B temporarily interferes with the retrieval of previously learned manipulation in context A. This raises the question of whether learning context A in the first block would exert a similar interference on the subsequent manipulation in context B. We hypothesized that if a long enough was given after Block 1, subjects could have started learning context B with a smaller initial error. In the T1hr condition, subjects performed one block of eight trials and rotated the object at the end of the block (Fig. 6.1C). After one-hour break, subjects came back and started to learn the manipulation in context B (Fig. 6.3A). As expected, $T_{err}$ in Trial 1 Block 2 was found to be 160.65 ± 16.17 Nmm and was significantly larger than $T_{err}$ in the transfer trial of the Ctrl condition (Fig. 6.3B; $t = 3.857$, $p = 0.001$). This suggests that, although learning manipulation A still induced a temporary anterograde interference on the subsequent context, its strength was inversely proportional to the time between the first and second context. Furthermore, $T_{err}$ in the transfer trial was statistically indistinguishable from $T_{err}$ in the first trial of Block 1 (Fig. 6.3B; $t = 0.775$, $p = 0.455$). This result suggests that subjects started learning context B without any transfer from the previously learned context A, even when one-hour break was long enough for the interference effect to decay to a minimum level. This phenomenon is consistent with those reported by previous studies (Bursztyn and Flanagan, 2008; Zhang et al., 2010; Fu and Santello, 2012) by showing no task-level learning transfer from context A to B. Furthermore, here we demonstrate that lack of learning generalization in manipulation tasks was not due to lack of context cues or anterograde interference caused by learning a context immediately preceding the new context.
Effect of repetitive manipulations on interference

The last condition, Rndm, consisted of random presentation of the two manipulation contexts. This design prevented subject from being exposed to the same context for more than three consecutive trials (Fig. 6.3C). An important feature of the context presentation was that the first context switch occurred after the first trial. We found that subjects made a smaller error ($T_{err} = 137.58 \pm 22.81$ Nmm) when switching context after only one trial experienced in the preceding context than after eight consecutive trials performed in the preceding context (Fig. 6.3D; $t = 4.86, p < 0.001$). This error was still slightly larger than the error subject made in the first trial ($T_{err} = 117.74 \pm 34.47$ Nmm), thus suggesting that one trial was sufficient to induce interference on the next context while further practice in the same context would have increased the strength of the interference.

Comparison between experimental and simulation results

Our data clearly revealed several important features of retention and interference in learning of dexterous manipulation tasks. Specifically, if manipulation A is learned, learning of the second manipulation B does not erase the learned manipulation A, but rather builds a temporary memory component. Such component competes with the memory component built through learning task A if A is to be retrieved, thus creating interference. Furthermore, the initial learning of task A may also build a memory component that competes with the learning of B. Lastly, the magnitude of this interference increases with the number of repetitions in the same manipulation context but decays with increasing time between context switches. The question arises about whether existing computational models of motor learning could capture these features.
Figure 6.4. Simulation results.

A, Simulation results using single rate model with block ABAB paradigm. B, Simulation results using dual rates model with block ABAB paradigm. C, Simulation results using dual rates model with pseudo-random context sequence. The value of ±1 on the y-axes denotes full adaptation (T_{com} = T_{task}).
The simulation results of the multi-context single rate SR model could replicate the retrograde interference in Ctrl condition as a significant error in Trial 1 of Block 3 (Fig. 6.4A). However, there are several differences between the results predicted by the SR model and our data. First, the SR model cannot reproduce the anterograde interference occurring on Trial 1 of Block 2. Since context A and B had same visual cues, the initialization of the internal representation of the context would be the same, therefore leading to the same initial error for Block 1 and Block 2 in the SR model. Furthermore, the retrograde interference found for the first context switch in the SR model was caused by the forgetting of the inactive context A in Block 2 depicted by a gradual decay while learning the active context B in Block 2 (Fig. 6.4A). This model would predict that a break given between Block 2 and Block 3 would not reduce the interference as A has been forgotten to some extent and thus cannot be ‘relearned’ during the break.

The simulation results of the DR model replicate the data from the Ctrl condition reasonably well by reproducing the effect of the interference in both transfer and retrieval trials (Fig. 6.4B). This model explains the interference by capturing subjects’ inability to change the fast component after the context switch as the fast process is context-independent (Fig. 6.4B). It is also interesting to see that, as one practices a manipulation in one context over a longer period of time, motor output becomes increasingly dominated by the slow component. Note that the slow component has a very slow forgetting rate whereas the fast component has a very fast forgetting rate. Thus, the model would predict that most of the fast component would be gone if a break were given between blocks, whereas the previously learned slow component could still be retrieved well. However, the temporal characteristics of the DR model failed to match
the results from the Rndm condition. Since the fast process in the DR model is more sensitive to error than the slow process, the initial stage of learning (where error is larger) could be dominated by the fast process. However, as the fast process is also context-dependent, the model would predict that switching after one trial would cause similar or more interference (Fig. 6.4C) than switching after eight trials. In contrast, our data demonstrated a smaller interference for the switch after one trial (Fig. 6.3D). The fact that this DR model cannot predict the positive correlation between the number of consecutive trials and the strength of anterograde interference is due to the fundamental structure of the model, i.e., the fast state is modeled as context-independent. Interestingly, this positive correlation is not limited to our manipulation task, but it is also found in force-field adaptation tasks (Sing and Smith, 2010). However, these authors have explained this result with a context-insensitive dual-rate learning model, which does not support our context-sensitive results.

DISCUSSION

Effect of previous motor experience on current manipulation

In simple lifting tasks with constrained digit placement, digit forces are scaled to the object weight experienced in the previous trial if no information about object weight in the current trial is available (Quaney et al., 2003). Similarly, in object balancing tasks with unconstrained digit placement, the compensatory torque is biased by the object weight distribution experienced in the previous trial when the weight distribution in the current trial cannot be predicted (Lukos et al., 2013). In bimanual manipulation tasks with unpredictable presence of mechanical linkage between two hands, the scaling of the finger forces depends on the presence of the linkage experienced in the previous trials,
with three consecutive presentations of the linkage causing more force scaling bias than one presentation (Witney et al., 2000). These findings indicate that previous hand/digit actions influence the next action performed by the same hand if the upcoming task dynamics is unpredictable. Moreover, this motor bias, traditionally termed as ‘sensorimotor memory’ (Johansson and Westling, 1988b), seems to be independent of the actual task context in which it is established, as demonstrated by the observation that squeezing an object could bias the grip force used to lift an object in the next trial (Quaney et al., 2003). However, these studies often used no context cues and/or were performed with constrained digit placement.

Our result supports the existence of a ‘sensorimotor memory’ at the task level for manipulation, whose influence on the subsequent action positively correlates with repeated exposure to the same context. It should be emphasized that such influence is a general phenomenon for manipulation tasks and therefore not limited to object rotation tasks. Our previous work (Fu and Santello, 2012) showed similar interferences using a U-shaped object in A1B1A2B2 and random context switching paradigm resembling the Ctrl and Rndm condition, respectively, used in the present study. In that study, the context switches consisted of asking subjects to grasp one of the handles located on either side of the object. Despite the different means of eliciting context switch relative to the present study, both anterograde and retrograde interferences were also found. Since both U- and L-shaped object are characterized by salient visual geometric cues, these results strongly argue that sensorimotor memory of previous manipulations could bias the motor output even when subjects could have anticipated the task dynamics through visual cues about object geometry. Most importantly, we revealed that such bias caused by sensorimotor
memory lasts a relatively short time (i.e., half-life of about 10 minutes), and it could influence both learning transfer and retrieval.

**Learning retention and interference in other sensorimotor learning tasks**

Studies of reaching have provided a large body of experimental evidences using tasks such as visuomotor rotations and reaching against force fields. However, it was unclear whether these models could have also explained motor retention and interference of real-life dexterous manipulation tasks. Using an experimental design similar to the classic A\_1B\_1A\_2 paradigm, we compared our results with both experimental data and model predictions based on reaching studies. It should be emphasized that learning of our manipulation task, which takes about 2–3 trials, is a much faster process than learning reaching movements in novel environments (tens of trials) due to the presence of richer visual contextual cues (Ingram et al., 2011). Therefore, the interference reported in reaching studies has often been described as a reduction in learning rate, whereas in tasks like the one we studied the interference is manifested as an error on the first trial after the context switch. Nevertheless, both means of interference quantification denote a negative influence from the manipulation learned prior to switching context.

We found common features that are shared across learning of hand and arm movements. For reaching in force field tasks, the strength of anterograde interference on context B\_1 increased with the number of consecutive practice in context A\_1 (Sing and Smith, 2010). Furthermore, the anterograde interference gradually decreased with time, such that subjects learn B\_1 as if starting fresh if enough break time (>5.5 hours) was given between A\_1 and B\_1 (Shadmehr and Brashers-Krug, 1997). However, we found significant differences in the temporal characteristics of the retrograde interference
between our task and reaching tasks. Specifically, several studies have found that if B₁ is learned immediately after learning A₁, and provided that the trial numbers are equal for learning of both contexts, the context retrieval in A₂ would be always interfered by the learning of B₁ regardless of the duration between B₁ and A₂ (Brashers-Krug et al., 1996; Caithness et al., 2004; Krakauer et al., 2005). In contrast, we showed that a short break between B₁ and A₂ could greatly decrease the strength of the interference (Fig. 6.2A). Additionally, we also showed that context A could be retained well after two weeks even if the last context subjects performed was B (Fig. 6.2B).

Reaching studies have also raised an interesting issue about retrograde interference. If recall of A failed, did learning of B erase the memory of A, or prevent the recall of A while keeping the memory of A intact? Recent experimental evidence favors the second explanation. Criscimagna-Hemminger and Shadmehr (2008) reported that after a short exposure to B after learning of A, the performance on the retrieval trial was brought back to baseline showing apparent extinction of A. However, the inhibitory effect of B was shown to be fragile as it disappeared within minutes, and spontaneous recovery (i.e., performance changed back to a level close to that after having learned A) was demonstrated using error-clamp trials in null fields. This result is consistent with ours, i.e., the effect of the interference gradually decayed with time. However, the same study also demonstrated that context B became more stable after a longer break and spontaneous recovery was not observed if more than one hour was given after context B. In contrast, our results showed continuous decay of the interference with time and retrieval of context A was not affected after one hour.

*Possible mechanisms underlying the retention and interference for manipulation tasks*
Two existing theoretical models were tested against our data. Both of them could capture some of our basic findings but failed to account for other important features. The single-rate model did not support the protection of the inactive context when learning the active one, whereas the multiple-rate model did not support the positive correlation between number of consecutive trials and strength of the interference. One possible explanation is that most of the current theoretical motor learning/adaptation models are based on motor errors made in each trial. However, error-driven updates may not be the only process underlying motor learning, especially when the experimental design includes repetitive practice in one context after the initial learning stage. During the later stage of motor learning, in which performance error is usually small, other mechanisms may play more significant roles. Recent studies have proposed use-dependent plasticity and reinforcement learning as possible candidate mechanisms running in parallel with error-driven updates (Huang et al., 2011). Our results strongly suggest that both retrograde and anterograde interference in manipulation tasks may be caused by a non-error driven processes since significant interference could re-emerge after a block of trials without significant error (Fig. 6.2B, Block 5).

We speculate that such practice-induced context-independent sensorimotor memory competes with error-driven context-dependent internal models. While the neural correlates of internal models remain unclear (Franklin and Wolpert, 2011), the cerebellum (Nowak et al., 2004, 2009) is thought to maintain and update such models for manipulation due to its role in comparing motor and sensory signals, hence in supporting error-driven learning. Furthermore, premotor and parietal cortices are thought to recall stored internal representations with contextual cues (Grafton, 2010; Davare et al., 2011).
With regard to repetition-based sensorimotor memory, there is evidence strongly suggesting that it could be stored in the primary motor cortex (M1). Specifically, repetitive transcranial magnetic stimulation (rTMS) over M1 disrupts anticipatory finger force scaling (Chouinard et al., 2005). Additionally, a recent study found that motor evoked potentials (MEP) in M1 were scaled based on lifting forces experienced in the previous trial, but such MEP modulation could be over-written 150 ms after visual information about the object weight was available (Loh et al., 2010). Since our data showed that visually-based anticipatory grasp control was significantly interfered by consecutive practice, it is possible that increasing the number of repetitions results in stronger weighting of sensorimotor memory that cannot be fully suppressed by visually-selected internal models. Although our number of repetitive manipulations may be small compared to the number of repetitions that have been found to produce use-dependent learning (Classen et al., 1998; Diedrichsen et al., 2010b), it is worth pointing out that our tasks feature a 2-second holding phase that requires subjects to produce a significantly large constant torque in addition to a short object lifting movement. This isometric force production phase may play an important role in our tasks for building up the motor bias or ‘sensorimotor memory’. This proposition, however, requires further investigation.
Chapter 7

SUMMARY AND CONCLUSIONS

GENERAL FINDINGS

Dexterous manipulation is one of the most important and intricate sensorimotor human behaviors. The ability to acquire and use objects as tools to sense, interact with, and change the environment is crucial to the evolution of the brain and the establishment of our civilization (Wilson, 1999). Decades of research have provided numerous data about the neural control of hand and fingers, but our knowledge of how dexterous manipulations are learned and executed is still limited. The purposes of this dissertation were to provide more behavioral data for understanding human manipulation, and more importantly, to push the boundaries and fill several critical gaps between different fields of motor neuroscience. The major contributions of the dissertation are described below.

Novel apparatus and experimental protocols

Surprisingly, most studies in the past three to four decades have focused on either hand kinematics during reach-to-grasp, or finger forces applied at constrained contact sites. However, most of our activities of daily living (e.g., self-feeding, tool use, etc.) involve the coordination between hand kinematics and kinetics, i.e., between how we choose digit placement and digit force distribution.

The first major contributions of this dissertation are the experimental apparatus and protocols that enabled quantification of both digit positions and forces in more natural manipulation tasks without constraining subjects to position their digits at fixed locations. The advantage of these new tasks over previous work is to allow subjects to
adapt digit positions to task requirement while allowing the experimenter to measure digit forces in response to digit position modulation.

It should be pointed out that, in most of our tasks, the main goal was to balance the object by producing a torque through a combination of digit positions and forces. If the contact sites are constrained, the torque production task is reduced to digit force production tasks as the solution is limited to a small range of local forces. While such constraints are great to study local force control for grasp stability, it prevent us to further assess the learning and control of high level task goals since learning and control of local digit forces could directly lead to correct execution of the task. In theory, one can use memory of forces from previous trials when digit positions are constrained. However, this process is unlikely to be used in natural object/tool use on a daily basis.

*Mutual dependence of digit positions and forces control*

Through the use of the unconstrained manipulation and torque production tasks, we revealed that, the first time in the motor neuroscience literature, the ability of the CNS to plan and control local variables (i.e., digit forces and positions) in a coordinated fashion to accomplish high-level task goals (i.e., torque production) consistently. This finding was supported by the first three studies (Chapter 2-4). Specifically, when subjects were asked to lift an inverted T-shaped object with a hidden mass that could cause mismatch between object apparent and actual center of mass, they gradually learn to produce a compensatory torque at lift onset to minimize object roll during lift (Fig. 2.4). It was found that subjects also changed their digit positions through learning (Fig. 2.5), thus reducing the digit forces necessary for successful manipulation. Specifically, the increased vertical distance between thumb and index finger made the grip forces also
contribute to the torque production (Fig. 2.6). As a result, the frictional load forces could be more evenly distributed across two digits, thus requiring less grip force to maintain local contact stability. This suggests that subjects did not only learn the task, but also tended to optimize the motor output from the perspective of energetic cost. More importantly, in the first study, we showed that subjects exhibited significant digit position variability which was compensated for by the change digit load forces (Fig. 2.8).

To further understand the control process underlying digit position and force covariation, we used a virtual reality setup in the second study (Chapter 3) to evaluate how subjects control digit forces in response to predictable and unpredictable change in digit relative positions. It was found that, when digit positions can be predicted before contact occurred, subjects could plan the appropriate forces and release the force command soon after initial contact. In contrast, if the digit positions could not be predicted, subjects had to use sensory feedback after making contact with the object to update the force command erroneously programmed before contact (Fig. 3.7). This result provided additional evidence to the sensorimotor control point framework that the CNS programs digit forces in an anticipatory fashion depending on the object properties and task requirements, then compares the expected and actual sensory information at specific action goals, i.e., transition between contact and object rotation. If the mismatch occurs, the correction is made to the digit forces within 100-200 ms.

*Context-dependent high level representations of manipulation*

The ability to control digit positions and forces as a unit that satisfy task goal was extended to multi-digit manipulations in the third study (Chapter 4). After learning a manipulation using a set of digits, subjects were able to immediately switch grip type by
adding or removing a digit to/from the set used during learning, and produced the same
task torque (Fig. 4.3). Given the significant change in digit position (Fig. 4.4), this result
suggested that the CNS could re-compute the new digit forces and positions based on the
memory of the task torque. Furthermore, the positive transfer of a learned manipulation
across different grip types raised an interesting issue about learning and representation of
dexterous manipulations. After comparing with literature, we found that the ability to
generalize a learned manipulation to a new one depends on the frame of reference in
which the changes in task conditions occur. Changes at the “digit level” (i.e., hand
orientation or grip type, etc.), could be compensated for, thus exhibiting good
generalization. In contrast, changes occurring at the “task level” (i.e., object orientation),
which require a change of the direction of the task torque, seem to cause poor
generalization (Zhang et al., 2010; Fu and Santello, 2012). These observations raised the
question about why subjects failed task level generalization, and whether subjects learned
the object physical properties (i.e., mass distribution) or the manipulative action.

We speculated that subjects learned the object properties, but ‘mental rotation’
was required to generalize such implicit knowledge, acquired through haptic interactions,
to a new manipulation. Because most of past research used visually symmetrical objects
that were not congruent with the actual object dynamics. In the fourth study (Chapter 5),
we introduced a new experimental design with visual geometric cues congruent with
object dynamics. In addition, the change of manipulation context was induced without
physically rotating the object. Instead, we used a U-shaped object consisting of a base
with two vertical handles, each affording a distinct manipulative action. We found that
the congruent visual cues were very effective in allowing subjects to identify the task
dynamics. This was revealed by an initial torque production close to the required task torque (Fig. 5.2). However, lack of positive transfer was still found despite the existence of visual geometric cues as well as lack of physical object rotation when the context was switched (Fig. 5.2). This result suggested that subjects primarily learned the action in a specific context rather than learning the actual physical property of the object.

*Learning retention and interference of dexterous manipulation*

We noticed that the findings in the fourth study resembled some of the characteristics of motor learning reported using tasks that were more related to arm and/or wrist. This gave us a great opportunity to bridge the gap between the control of the hand and arm. In fact, since our experimental design has brought the focus of research on manipulation from local digit force control to task-level torque control, it should be pointed out that subjects did not use their hand and digits isolated from arm, and their arms also plays important role to support task level torque/forces and motion. Therefore we could reasonably speculate that the encoding of the manipulation task as supination/pronation may be similar to the encoding of a translational force field or other task performed by the arm.

The last experiment (Chapter 6) was designed to further quantify the learning of manipulation in the sense of retention and interference by using experimental approaches similar to those in the literature of arm control for aiming tasks. This allowed us to reveal similarities and differences between manipulation and other motor tasks in a systematic fashion. Specifically, we found both anterograde and retrograde interference in an ABAB blocked learning and context switching paradigm (Fig. 6.2 and 6.3). By varying the duration of break time between blocks, and by varying the number of consecutive trials
within same context, we revealed parallel mechanisms underlying learning of manipulation. One learning process was dependent on the error and the acquired memory could be retained and retrieved for long period of time. In contrast, the other process was dependent on the repetition of successful actions (lifting the object while preventing it from tilting) and it could produce a short-term inhibitory effect when subjects were asked to retrieve the internal representation acquired through first process. This finding strongly suggests that the current theoretical models need to be improved to explain the learning of dexterous manipulation.

**Future work**

Although we have revealed that the CNS has the ability to plan the digit positions and forces as a unit, as well as to correct digit forces based on sensing of digit positions, it remains unclear what neural circuits are underlying these functions. Our experimental protocols and result provided possibilities to investigate the neural mechanism for dexterous manipulation with the aid of transcranial magnetic stimulation (TMS) and Functional magnetic resonance imaging (fMRI) facility, as well as anesthesia of the digits. Full digital anesthesia could be achieved by injecting anesthetic (e.g., mepivacaine, lidocaine) at the base of the digits around metacarpal-interphalangeal joints (Monzée et al., 2003). This blocks the cutaneous sensation preventing subjects to accurately perceive center of pressure and forces. It has been shown that the digit force control could be significantly altered with anesthesia by increase in the overall grip force applied to the object during loading, lifting, and holding (Johansson and Westling, 1984; Häger-Ross and Johansson, 1996; Jenmalm and Johansson, 1997). However, it remains unknown whether absence of afferent signals from mechanoreceptors in the fingertips
would significantly impair subjects’ ability to compensate the variability of digit centers of pressure through force modulation for learning and executing dexterous manipulation. The CNS may fail to show effective covariation between digit positions and forces, or it might use other strategies to compensate for the loss of tactile sensation. For instance, subjects may try to position their digits more consistently under visual guidance and rely more on reproducing the forces that have successfully performed the task as the muscle spindles and GTOs within digital muscles are still intact.

fMRI has been successfully implemented to investigate motor equivalence (Rijntjes et al., 1999). When signing with fingers and toes, the secondary sensorimotor cortices of the dominant hand area were found to be activated independent from the actual effector used to perform the motor action. This suggests that fMRI may provide insightful anatomical evidence about where the high-level representation of the task could be stored and decomposed. To address this question, fMRI could be used when subjects perform the grip type switching task (Chapter 4). After subjects learn to balance the object with one grip type and are asked to change to the other grip type, the brain may exhibit distinct activation pattern to re-compute a new digit position-force relationship.

Last but not the least, TMS could be used with variable frequencies and timings to assess the planning and control of digit positions and force with better temporal resolution. For instance, single pulse TMS could be delivered to the primary cortex to measure corticospinal excitability (CSE) when subjects perform tasks that involve digit positioning and/or digit force production. Furthermore, rTMS could be used to generate virtual lesion in AIP to assess its functional role in the coordination of digit position and forces.
As our last three studies shifted to the learning and internal representation of manipulation tasks, they also open several new paths to further reveal the possible corresponding neural mechanisms. For the extensions of this dissertation, an interesting behavioral experiment would be to examine the ability of across-hand transfer. Since we have proposed that part of the learning process occurred in M1 and this part of the learning could interfere with the subsequent manipulations, it could be hypothesized that the interference can be greatly reduced if the context switch involves change of hand. In fact, our preliminary data has supported this hypothesis. However, more experiments are necessary to quantify the influence of learning on the contralateral hand.

Additionally, fMRI and TMS are also of great importance to probe the neural structure of learning manipulation. For instance, TMS could be used measure whether CES changes after blocked learning of novel object dynamics, which was hypothesized to indicate use-dependent plasticity. rTMS could also be used to create temporary lesion in different areas of the sensorimotor cortex to assess their functional relevance in maintaining the internal representation of the learned manipulation tasks. Furthermore, fMRI could be used to provide anatomical evidence (especially brain regions that are hard to access through TMS, e.g., basal ganglia and cerebellum) about the brain region involved with context switching paradigms. Lastly, we could also recruit patients with neurological disorders (e.g., Parkinson Disease) to participate in the experimental designs that were performed by normal people and observe whether impairment to specific brain regions could alter the characteristics of the learning and control of unconstrained manipulation. A recent study in our lab has already showed that PD patients modulated digit positions and forces less effectively during unconstrained manipulation (Lukos et
Further experiments are needed to understand whether PD patients may exhibit different extent of retention and interferences.

This dissertation also provided the foundation to bridge the gap between dexterous manipulation and other sensorimotor tasks. However, there were still some major differences between the task structures. For instance, the reaching task usually has a very limited time window for subjects to accomplish the task goal, therefore forcing subjects to learn a ballistic force production profile (Sing and Smith, 2010). Whereas the manipulation tasks usually did not have time constraints and contained a prolonged static holding phase, although subjects sometimes exhibited feed-forward force control during when the task is familiar. To better compare the dexterous manipulation tasks and reaching tasks, it is necessary to construct novel robotic devices similar to the well-known planar manipulandum that could provide flexible and quantitative adjustment for the task design. A special feature that has to be implemented in this new robotic/haptic device is the rotation degrees of freedom (Howard et al., 2009), because object rotation is an important manipulation usually performed by hand/wrist rather than the arm (e.g., opening door knob or bottle cap). With such devices, we could provide more evidences in a more controlled environment, therefore leading to better computational models for learning and control of dexterous manipulation.

CONCLUSIONS

The work presented here provided new evidence and insights about the sensorimotor learning and control of manipulation. Although much remains to be understood about the underlying neural mechanisms, this dissertation contributed to the motor neuroscience field by bridging the gap between local digit force control and high-
level goal directed hand actions. This contribution was made possible by removing physical constraint on digit placement, introducing context specific task goals, as well as comparing with the other motor control areas. This work created a new general platform for neuroscientists to further investigate how the brain learn, store, and control dexterous manipulation tasks.
REFERENCES


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urophysiology 101:569–579.


APPENDIX A

SUPPLEMENTARY MATERIAL FOR CHAPTER 2
Task mechanics

Subjects had to learn how to coordinate digit forces and positions to comply with the task requirement of minimizing object roll during lift. To better understand the relation between the subjects’ response (modulation of digit forces and positions) and the behavioral outcome (object roll minimization), it is useful to first describe the mechanical characteristics of the objects and task. The free-body diagrams of the _unconstrained_ and _constrained_ grip devices are shown in Figure A and B, respectively. The two objects share the same mechanics. However, note that the area and position of the grasp surfaces of the _constrained_ device forces digit placement to be nearly collinear (the implications of this constraint on force modulation are explained below).

Attainment of successful object roll minimization can be described as the subjects’ ability to generate a moment on the object that is of equal magnitude and opposite direction to that of the external torque ($T_{ext} = F\cdot l$) caused by added mass about the CM of the unloaded object ($CM_0$). Because of sensory feedback delays, subjects learn to minimize object roll by anticipating $T_{ext}$ rather than reacting to it, accurate anticipatory control being acquired usually through a few object lifts and resulting from the formation of sensorimotor memories. Perfect anticipation of $T_{ext}$ can therefore be defined as the production of a net digit torque at object lift onset that is of equal magnitude as, and exerted in the opposite direction to, $T_{ext}$. We will refer to this net digit moment as the _compensatory moment_ ($T_{com}$) and define it as:

$$T_{com} = \frac{W}{2} F_{1y} - \frac{W}{2} F_{2y} + (y_1 + y_0)F_{1z} - (y_2 + y_0)F_{2z}$$  \hspace{1cm} (2)
where \( w \) is the grip width, \( F_{i_y} \) and \( F_{i_z} \) are the load and grip forces exerted by thumb and index finger (\( i = 1 \) and 2, respectively), \( w/2 \) is the moment arm of the moment generated by digit load forces about \( CM_0 \) (load moment), \( y_i \) is the vertical coordinate of the digit center of pressure relative to center of the sensors, and \( y_0 \) is the vertical distance between the center of the sensors and the center of mass of the object without the added mass. Thus, \( y_0 + y_i \) corresponds to the moment arm of the grip force moment about \( CM_0 \).

Since the horizontal (side-to-side) movement of the object was very small throughout object lift, digit grip forces were always nearly equal and opposite to each other and therefore positively covaried (Pearson’s correlation coefficients > 0.98 across all subjects). Therefore the right side of equation (2) can be simplified with the assumption that \( F_{1_z} \approx F_{2_z} \approx F_{GF} = (F_{1_z} + F_{2_z})/2 \) is true:

\[
T_{com} = \frac{w}{2} d_{LF} + d_y F_{GF} \tag{3}
\]

where \( d_{LF} = F_{1_y} - F_{2_y} \) is the difference between thumb and index finger load forces (load force asymmetry) and \( d_y = y_1 - y_2 \) is the vertical distance between thumb and index finger centers of pressure. This equation shows that the compensatory moment \( T_{com} \) is comprised of two moment components: the moment generated by grip forces \( (T_{GF} = d_y F_{GF} ) \) and the moment generated by load forces \( (T_{LF} = \frac{w}{2} d_{LF} ) \). The right side of equation (3) depends on three variables: \( d_{LF}, d_y, F_{GF} \). Let us assume that the subject, after having lifted the object a few times, learns the magnitude and direction of \( T_{com} \) necessary to compensate \( T_{ext} \) at object lift onset. A given compensatory moment can be attained by an infinite number of combinations of \( d_{LF}, d_y, \) and \( F_{GF} \). The example in the
supplementary figure shows a combination based on positioning the thumb much higher than the index finger, this combination being possible only for the *unconstrained* device. Subjects could choose to use the same combination of these three variables across trials or, alternatively, choose different but equally valid combinations from trial to trial.

Note that previous work on two-digit grasping has not examined the relationship between digit position and forces with the assumption that $d_y$ is zero ($y_1 = y_2$ in Fig. 2.3; $d_y = 0$). This assumption arises from the fact that the fingertips were constrained to be collinear by the position of the force sensors (Fig. B). Therefore, in grasp studies examining learning of object roll minimization, the research question and analysis are reduced to subjects learning how to generate a compensatory moment using an asymmetrical distribution of load forces only, i.e., $T_{com} = T_{LF}$. However, when grasping the *constrained* device we expected the assumption of $d_y = 0$ to be violated as small modulation of $d_y$ might have occurred within the small area of the sensor (this is shown in Fig. B as thumb normal force being exerted at a slightly higher point than index finger normal force). Therefore, we measured digit CoPs also for the *constrained* device. However, based on our previous work we expected $d_y$ to be significantly larger when grasping the *unconstrained* device.

As mentioned above, perfect anticipation of $T_{ext}$ occurs after subjects have learned the relation $T_{com} = -T_{ext}$ at object lift onset. In such case, object roll that would have otherwise resulted from object lift is prevented. Note, however, that subjects might be unable to implement perfect anticipation of $T_{ext}$ due to suboptimal retrieval and/or implementation of sensorimotor memories. Alternatively, subjects may choose to
consistently implement a given value of $T_{com}$ at object lift onset that, despite not matching exactly $-T_{ext}$, is sufficiently good to achieve an acceptable level of object roll minimization.

Supplementary figure. Task mechanics. Panels A and B show the free-body diagram of the unconstrained and constrained grip devices, respectively, for a left center of mass condition. $CM_o$ is the center of mass (CM) of the object without the added mass and is located along the vertical midline 32 mm below the $z$-axis of the sensors (not shown) passing through their centers (dashed horizontal line); $CM_w$ is the CM of the added mass; $G$ and $F$ are the gravitational forces acting on the object (3.92 N) and the added mass (3.88 N), respectively; $y_1$ and $y_2$ are the vertical coordinates of the centers of pressure of the thumb and index finger, respectively, on the grasp surface with respect to the center of the sensors; $y_i$ is the vertical distance between the center of each sensor and the CM of
the object without the added mass; $F_{1y}$ and $F_{1z}$ are the load and grip forces generated by thumb; $F_{2y}$ and $F_{2z}$ are the load and grip forces generated by index finger; $w$ is the distance between the two grasp surfaces (60.7 mm); $l$ is the distance between the vertical midline of the object and the CM of the added mass ($l = -65$ mm, 0 mm, and 65 mm for left, center and right CM, respectively); $T_{ext}$ is the external torque caused by the added mass and is equivalent to the product $F \times l$. $CM_o$ was computed based on the object physical dimensions using Solidworks (Solidworks, Concord, MA).
APPENDIX B

IRB APPROVALS AND HUMAN SUBJECTS CONSENT FORMS
To: Marco Santello  
ECG  

From: Carol Johnston, Chair  
Biosci IRB  

Date: 12/27/2012  

Committee Action: Renewal  

Renewal Date: 12/27/2012  

Review Type: Expedited F12  

IRB Protocol #: 0712002437  

Study Title: Collaborative Research: Sensory Integration and Sensorimotor Transformations for Dexterous Manipulation  

Expiration Date: 12/28/2013  

The above-referenced protocol was given renewed approval following Expedited Review by the Institutional Review Board.  

It is the Principal Investigator’s responsibility to obtain review and continued approval of ongoing research before the expiration noted above. Please allow sufficient time for reapproval. Research activity of any sort may not continue beyond the expiration date without committee approval. Failure to receive approval for continuation before the expiration date will result in the automatic suspension of the approval of this protocol on the expiration date. Information collected following suspension is unapproved research and cannot be reported or published as research data. If you do not wish continued approval, please notify the Committee of the study termination.  

This approval by the Biosci IRB does not replace or supersede any departmental or oversight committee review that may be required by institutional policy.  

Adverse Reactions: If any untoward incidents or severe reactions should develop as a result of this study, you are required to notify the Biosci IRB immediately. If necessary a member of the IRB will be assigned to look into the matter. If the problem is serious, approval may be withdrawn pending IRB review.  

Amendments: If you wish to change any aspect of this study, such as the procedures, the consent forms, or the investigators, please communicate your requested changes to the Biosci IRB. The new procedure is not to be initiated until the IRB approval has been given.  

Please retain a copy of this letter with your approved protocol.
SUBJECT CONSENT FORM

Collaborative Research: Sensory Integration and Sensorimotor Transformations for Dexterous Manipulation
SCHOOL OF BIOLOGICAL AND HEALTH SYSTEMS ENGINEERING,
ARIZONA STATE UNIVERSITY

INTRODUCTION
The purposes of this form are to provide you (as a prospective research study participant) information that may affect your decision as to whether or not to participate in this research and to record the consent of those who agree to be involved in the study.

RESEARCHERS
Dr. Marco Santello, Ph.D., (Professor, School of Biological and Health Systems Engineering), Dr. Wei Zhang, Ph.D., (Postdoctoral Research Associate, School of Biological and Health Systems Engineering), Qiushi Fu, M.S., (Graduate Student Research Assistant, School of Biological and Health Systems Engineering), Jason Choi (Graduate Student Research Assistant, School of Biological and Health Systems Engineering), Daisuke Shibata, M.S. (Graduate Student Research Assistant Student, Kinesiology program), Dr. Veronica Santos, Ph.D. (Assistant Professor, School of Biological and Healthy Systems Engineering), Michael De Gregorio (Graduate Student Research Assistant, School of Biological and Health Systems Engineering), Dr. Pranav Parikh, Ph.D. (Postdoctoral Research Scholar, School of Biological and Health Systems Engineering), and Keivan Mojtabaei (Graduate Student, School of Biological and Health Systems Engineering) have invited your participation in a research study.

STUDY PURPOSE
The purpose of the research is to obtain information about how sensory information from the fingertips is used during coordination of various movements of the hand. This information may be useful to professionals who work with people who have some form of physical disability and require therapy.

DESCRIPTION OF RESEARCH STUDY
If you decide to participate, then as a study participant you will join a study in which you will be asked to grasp a lightweight object (less than 2 pounds) with your whole hand while seated, and either squeeze lightly for several seconds, or to lift it a few inches above the table, hold it there for several seconds, and return it to the table. You will be asked to position your grasp on the object so that your thumb and each finger are placed over each pad. Certain properties of the object will be occasionally changed (such as center of mass, weight, or texture). In some instances you might be asked to position the fingertips of the thumb and index finger of one hand at a given distance from each other and then match that distance using the thumb and index fingertips of the other hand. Vision of both hands may not be allowed during this task. Additionally, you may be asked to squeeze a grip device with one or both hands while trying to match the fingertip distance of one hand using the fingertips of the other hand. If you say YES, depending on the tasks, your participation will last for 60-90 minutes during one session or for 2-3 hours over 2-day sessions, including instructions and rest periods between trials and tasks. In some instances the object may be a virtual object displayed on computer monitor that you will grasp with the ends a three-hinge linkage system, which may in some instances automatically move the object. The linkage system can also rotate the object about any of these directions. In some instances you will be asked to resist the movements imposed by the linkage system and in other instances the linkage system will resist your movements. Properties of the movement and resistance may be changed (such as direction of resistance or movement, strength of the resistance or movement). Minimal force (< 1.5 lb) is exerted by the linkage system when it moves or resists your movement; therefore, you should not feel any discomfort.
other instances you will be asked to grasp and lift a cylindrical metal object (height: 16cm diameter: 5cm). You may be asked to close your eyes during portions of the experiment, including times in which you reach to and grasp the objects. In some instances you may be asked to wear liquid crystal spectacles. The lenses of the goggles can change from transparent to opaque which removes your ability to see in front of you during various time points during the experiment. The object and if you consent, your hand and arm movements during each experimental session will be videotaped for the purpose of data and movement analysis. Experiments will be performed at the PEBE building in room 168 on the Tempe campus of Arizona State University. You may be excluded from this study if you do not meet the inclusion criteria based on screening tools to be completed. Approximately 500 subjects will be participating in this study.

RISKS
You should not participate in this study if you have any known neurological illness or orthopedic condition. Because you are in good health and have had no prior injury or health condition affecting your muscles, joints, or nerves, the risks of injury or discomfort in this research are minimal. There is a possibility that the linkage system will move you at an uncomfortable speed, however, several safety precautions have been implemented to reduce this risk. Specifically, the maximal speed of the movement imposed by the linkage system is set below human physiological limits. If these speeds are exceeded the linkage system is designed to immediately shutdown. Although your fingers you will be attached to the device via Velcro-like straps, you will be able to remove your fingers from the device if you feel any discomfort to let go of the object to protect yourself from potential discomfort, pain, or injury. The metal cylindrical object is powered and connected to the USB port of a pc with proper shielding and grounding. The risk of getting static shock is no different than using metal objects in daily life. However, as with any research, there is some possibility that you may be subject to risks that have not yet been identified.

BENEFITS
If you are enrolled in kinesiology and related program and your instructor previously consents to give extra credit for your participation in this research, you will be eligible for extra credit even you are excluded from this study after coming to the laboratory. Otherwise this study will be of no direct benefit to you. However, your participation may contribute to a broader understanding of processes underlying hand function with implications for development of therapeutic intervention in people with impaired hand function due to injury or illness. You will not receive payment for your participation.

NEW INFORMATION
If the researchers find new information during the study that would reasonably change your decision about participating, then they will provide this information to you.

CONFIDENTIALITY
All information obtained in this study is strictly confidential unless disclosure is required by law. The results of this research study may be used in reports, presentations, and publications, but the researchers will not identify you. To ensure confidentiality, a code will be used instead of your name for data analysis. Your identity will not be associated with any published results. All characteristics that could identify you in the records, including the videotape, will be stored fully confidential in a locked filing cabinet in the principal investigator’s office at Arizona State University. The videotape will be destroyed following the completion of the study.

WITHDRAWAL PRIVILEGE
It is ok for you to say no. Even if you say yes now, you are free to say no later, and withdraw from the study at any time. Your decision will not affect your relationship with Arizona State University or otherwise cause a loss of benefits to which you might otherwise be entitled. Participation is voluntary and nonparticipation or withdrawal from the study will not affect your grade or employment status.

COSTS AND PAYMENTS
There is no payment for your participation in the study.
COMPENSATION FOR ILLNESS AND INJURY
If you agree to participate in the study, then your consent does not waive any of your legal rights. However, no funds have been set aside to compensate you in the event of injury.

VOLUNTARY CONSENT
Any questions you have concerning the research study or your participation in the study, before or after your consent, will be answered by Marco Santello, Ph.D., Neural Control of Movement Laboratory, School of Biological and Health Systems Engineering, PEBE room 107B, University of Arizona, (480) 965-8279.

If you have questions about your rights as a subject/participant in this research, or if you feel you have been placed at risk; you can contact the Chair of the Human Subjects Institutional Review Board, through the ASU Research Compliance Office, at 480-965 6788.

This form explains the nature, demands, benefits and any risk of the project. By signing this form you agree knowingly to assume any risks involved. Remember, your participation is voluntary. You may choose not to participate or to withdraw your consent and discontinue participation at any time without penalty or loss of benefit. In signing this consent form, you are not waiving any legal claims, rights, or remedies. A copy of this consent form will be given (offered) to you.

I ( ) consent to be video taped.
I ( ) do NOT consent to being video taped.

The written, video taped materials will be viewed only by the principal investigator and members of the research team.

Written, video taped materials
( ) may be viewed in an educational setting outside the research
( ) may NOT be viewed in an educational setting outside the research.

- My signature means that I agree to participate in this study.

__________ Subject's Signature  ____________ Printed Name  ____________ Date

INVESTIGATOR'S STATEMENT
"I certify that I have explained to the above individual the nature and purpose, the potential benefits and possible risks associated with participation in this research study, have answered any questions that have been raised, and have witnessed the above signature. These elements of Informed Consent conform to the Assurance given by Arizona State University to the Office for Research Integrity and Assurance to protect the rights of human subjects. I have provided (offered) the subject/participant a copy of this signed consent document."

Signature of Investigator______________________________ Date________________

ARIZONA STATE UNIVERSITY IRB
APPROVED BY IRB
DATE: 2/16/13
NAME: JMT

195
To: Wei Zhang

From: Carol Johnston, Chair
BioSci IRB

Date: 05/04/2010

Committee Action: Amendment to Approved Protocol

Approval Date: 05/04/2010
Review Type: Expedited P6 F7
IRB Protocol #: 0712002437
Study Title: Dextrous Control During Multi-Digit Grasping
Expiration Date: 10/07/2010

The amendment to the above-referenced protocol has been APPROVED following Expedited Review by the Institutional Review Board. This approval does not replace any departmental or other approvals that may be required. It is the Principal Investigator's responsibility to obtain review and continued approval of ongoing research before the expiration noted above. Please allow sufficient time for reapproval. Research activity of any sort may not continue beyond the expiration date without committee approval. Failure to receive approval for continuation before the expiration date will result in the automatic suspension of the approval of this protocol on the expiration date. Information collected following suspension is unapproved research and cannot be reported or published as research data. If you do not wish continued approval, please notify the Committee of the study termination.

This approval by the BioSci IRB does not replace or supersede any departmental or oversight committee review that may be required by institutional policy.

Adverse Reactions: If any untoward incidents or severe reactions should develop as a result of this study, you are required to notify the BioSci IRB immediately. If necessary a member of the IRB will be assigned to look into the matter. If the problem is serious, approval may be withdrawn pending IRB review.

Amendments: If you wish to change any aspect of this study, such as the procedures, the consent forms, or the investigators, please communicate your requested changes to the BioSci IRB. The new procedure is not to be initiated until the IRB approval has been given.

Please retain a copy of this letter with your approved protocol.
SUBJECT CONSENT FORM

Coordination of multi-digit forces during grasping objects of varied properties

DEPARTMENT OF KINESIOLOGY, ARIZONA STATE UNIVERSITY

INTRODUCTION
The purposes of this form are to provide you (as a prospective research study participant) information that may affect your decision as to whether or not to participate in this research and to record the consent of those who agree to be involved in the study.

RESEARCHERS
Dr. Wei Zhang, Ph.D., (Postdoctoral Research Associate, Dept. of Kinesiology) and Dr. Marco Santello, Ph.D., (Associate Professor, Dept. of Kinesiology) and Qiushu Fu, M.S., (Graduate Student Research Assistant, Dept. of Kinesiology) and Dr. Mark Jesunathadas, Ph.D., (Postdoctoral Research Associate, Dept. of Kinesiology) have invited your participation in a research study.

STUDY PURPOSE
The purpose of the research is to obtain information about how sensory information from the fingertips is used during coordination of various movements of the hand. This information may be useful to professionals who work with people who have some form of physical disability and require therapy.

DESCRIPTION OF RESEARCH STUDY
If you decide to participate, then as a study participant you will join a study in which you will be asked to grasp a light-weight object (less than 2 pounds) with your whole hand while seated, and either squeeze lightly for several seconds, or to lift it a few inches above the table, hold it there for several seconds, and return it to the table. You will be asked to position your grasp on the object so that your thumb and each finger are placed over each pad, Certain properties of the object will be occasionally changed (such as center of mass, weight, or texture). If you say YES, depend on the tasks, your participation will last for 60-90 minutes during one session or for 2-3 hours over 2-day sessions, including instructions and rest periods between trials and tasks. If you consent, your hand and arm movements during each experimental session will be videotaped for the purpose of data and movement analysis. Experiments will be performed at the PEBE building in room 168 on the Tempe campus of Arizona State University. You may be excluded from this study if you do not meet the inclusion criteria based on screening tools to be completed. Approximately 200 subjects will be participating in this study.

RISKS
You should not participate in this study if you have any known neurological illness or orthopedic condition. Because you are in good health and have had no prior injury or health condition affecting your muscles, joints, or nerves, the risks of injury or discomfort in this research are minimal. However, as with any research, there is some possibility that you may be subject to risks that have not yet been identified.

BENEFITS
If you are enrolled in kinesiology and related program and your instructor previously consents to give extra credit for your participation in this research, you will be eligible for extra credit even

Updated by 2009-09-30 Subject’s Initials:_____ 1
you are excluded from this study after coming to the laboratory. Otherwise this study will be of no direct benefit to you. However, your participation may contribute to a broader understanding of processes underlying hand function with implications for development of therapeutic intervention in people with impaired hand function due to injury or illness. You will not receive payment for your participation.

**NEW INFORMATION**

If the researchers find new information during the study that would reasonably change your decision about participating, then they will provide this information to you.

**CONFIDENTIALITY**

All information obtained in this study is strictly confidential unless disclosure is required by law. The results of this research study may be used in reports, presentations, and publications, but the researchers will not identify you. To ensure confidentiality, a code will be used instead of your name for data analysis. Your identity will not be associated with any published results. All characteristics that could identify you in the records, including the videotape, will be stored in a locked filing cabinet in the principal investigator's office at Arizona State University. The videotape will be destroyed following the completion of the study.

**WITHDRAWAL PRIVILEGE**

It is up to you to say no. Even if you say yes now, you are free to say no later, and withdraw from the study at any time. Your decision will not affect your relationship with Arizona State University or otherwise cause a loss of benefits to which you might otherwise be entitled. Participation is voluntary and nonparticipation or withdrawal from the study will not affect your grade or employment status.

**COSTS AND PAYMENTS**

There is no payment for your participation in the study.

**COMPENSATION FOR ILLNESS AND INJURY**

If you agree to participate in the study, then your consent does not waive any of your legal rights. However, no funds have been set aside to compensate you in the event of injury.

**VOLUNTARY CONSENT**

Any questions you have concerning the research study or your participation in the study, before or after your consent, will be answered by Wei Zhang, Ph.D., P.T., Neural Control of Movement Laboratory, Department of Physiology, PEBE room 152, University of Arizona, (480) 965-6629, or Marco Santello, Ph.D., Neural Control of Movement Laboratory, Department of Physiology, PEBE room 107B, University of Arizona, (480) 965-8279.

If you have questions about your rights as a subject/participant in this research, or if you feel you have been placed at risk, you can contact the Chair of the Human Subjects Institutional Review Board, through the ASU Research Compliance Office, at 480-965 6788.

This form explains the nature, demands, benefits and any risk of the project. By signing this form you agree knowingly to assume any risks involved. Remember, your participation is voluntary. You may choose not to participate or to withdraw your consent and discontinue participation at any time without penalty or loss of benefit. In signing this consent form, you are not waiving any legal claims, rights, or remedies. A copy of this consent form will be given (offered) to you.

Updated by 2009-09-30

Subject's Initials:________
I ( ) consent to be video taped.
I ( ) do NOT consent to being video taped.
The written, video taped materials will be viewed only by the principal investigator and members of the research team.

Written, video taped materials
( ) may be viewed in an educational setting outside the research
( ) may NOT be viewed in an educational setting outside the research.
• My signature means that I agree to participate in this study.

Subject’s Signature _____________________________ Printed Name _____________________________ Date _____________________________

INVESTIGATOR’S STATEMENT
"I certify that I have explained to the above individual the nature and purpose, the potential benefits and possible risks associated with participation in this research study, have answered any questions that have been raised, and have witnessed the above signature. These elements of Informed Consent conform to the Assurance given by Arizona State University to the Office for Research Integrity and Assurance to protect the rights of human subjects. I have provided (offered) the subject/participant a copy of this signed consent document."

Signature of Investigator _____________________________ Date _____________________________

Updated by 2009-09-30 Subject’s Initials: _____

3
To: Wei Zhang

From: Carol Johnston, Chair
Biosci IRB

Date: 10/09/2009

Committee Action: Renewal

Renewal Date: 10/09/2009

Review Type: Expedited F6 F7

IRB Protocol #: 0712002437

Study Title: Coordination of multi-digit forces during grasping objects of varied properties

Expiration Date: 10/07/2010

The above-referenced protocol was given renewed approval following Expedited Review by the Institutional Review Board.

It is the Principal Investigator’s responsibility to obtain review and continued approval of ongoing research before the expiration noted above. Please allow sufficient time for reapproval. Research activity of any sort may not continue beyond the expiration date without committee approval. Failure to receive approval for continuation before the expiration date will result in the automatic suspension of the approval of this protocol on the expiration date. Information collected following suspension is unapproved research and cannot be reported or published as research data. If you do not wish continued approval, please notify the Committee of the study termination.

This approval by the Biosci IRB does not replace or supersede any departmental or oversight committee review that may be required by institutional policy.

Adverse Reactions: If any untoward incidents or severe reactions should develop as a result of this study, you are required to notify the Biosci IRB immediately. If necessary a member of the IRB will be assigned to look into the matter. If the problem is serious, approval may be withdrawn pending IRB review.

Amendments: If you wish to change any aspect of this study, such as the procedures, the consent forms, or the investigators, please communicate your requested changes to the Biosci IRB. The new procedure is not to be initiated until the IRB approval has been given.
SUBJECT CONSENT FORM

Coordination of multi-digit forces during grasping objects of varied properties

DEPARTMENT OF KINESIOLOGY, ARIZONA STATE UNIVERSITY

INTRODUCTION
The purposes of this form are to provide you (as a prospective research study participant) information that may affect your decision as to whether or not to participate in this research and to record the consent of those who agree to be involved in the study.

RESEARCHERS
Dr. Wei Zhang, Ph.D., (Postdoctoral Research Associate, Dept. of Kinesiology) and Dr. Marco Santello, Ph.D., (Associate Professor, Dept. of Kinesiology) and Qiaoshi Fu, M.S., (Graduate Student Research Assistant, Dept. of Kinesiology) have invited your participation in a research study.

STUDY PURPOSE
The purpose of the research is to obtain information about how sensory information from the fingertips is used during coordination of various movements of the hand. This information may be useful to professionals who work with people who have some form of physical disability and require therapy.

DESCRIPTION OF RESEARCH STUDY
If you decide to participate, then as a study participant you will join a study in which you will be asked to grasp a light-weight object (less than 2 pounds) with your whole hand while seated, and either squeeze lightly for several seconds, or to lift it a few inches above the table, hold it there for several seconds, and return it to the table. You will be asked to position your grasp on the object so that your thumb and each finger are placed over each pad. Certain properties of the object will be occasionally changed (such as center of mass, weight, or texture). If you say YES, depend on the tasks, your participation will last for 60-90 minutes during one session or for 2-3 hours over 2-day sessions, including instructions and rest periods between trials and tasks. If you consent, your hand and arm movements during each experimental session will be videotaped for the purpose of data and movement analysis. Experiments will be performed at the PEBE building in room 168 on the Tempe campus of Arizona State University. Approximately 80 subjects will be participating in this study.

RISKS
You should not participate in this study if you have any known neurological illness or orthopedic condition. Because you are in good health and have had no prior injury or health condition affecting your muscles, joints, or nerves, the risks of injury or discomfort in this research are minimal. However, as with any research, there is some possibility that you may be subject to risks that have not yet been identified.

BENEFITS
Participation in this study will not be of any personal benefit to you. However, your participation may contribute to a broader understanding of processes underlying hand function with implications for development of therapeutic intervention in people with impaired hand function due to injury or illness. You will not receive payment for your participation.

Updated by 2009-09-30

Subject's Initials:

1
NEW INFORMATION
If the researchers find new information during the study that would reasonably change your decision about participating, then they will provide this information to you.

CONFIDENTIALITY
All information obtained in this study is strictly confidential unless disclosure is required by law.
The results of this research study may be used in reports, presentations, and publications, but the researchers will not identify you. To ensure confidentiality, a code will be used instead of your name for data analysis. Your identity will not be associated with any published results. All characteristics that could identify you in the records, including the videotape, will be stored fully confidential in a locked filing cabinet in the principal investigator’s office at Arizona State University. The videotape will be destroyed following the completion of the study.

WITHDRAWAL PRIVILEGE
It is ok for you to say no. Even if you say yes now, you are free to say no later, and withdraw from the study at any time. Your decision will not affect your relationship with Arizona State University or otherwise cause a loss of benefits to which you might otherwise be entitled.
Participation is voluntary and nonparticipation or withdrawal from the study will not affect your grade or employment status.

COSTS AND PAYMENTS
There is no payment for your participation in the study.

COMPENSATION FOR ILLNESS AND INJURY
If you agree to participate in the study, then your consent does not waive any of your legal rights. However, no funds have been set aside to compensate you in the event of injury.

VOLUNTARY CONSENT
Any questions you have concerning the research study or your participation in the study, before or after your consent, will be answered by Wei Zhang, Ph.D., P.T., Neural Control of Movement Laboratory, Department of Physiology, PEBE room 168, University of Arizona, (480) 965-6629, or Marco Santello, Ph.D., Neural Control of Movement Laboratory, Department of Physiology, PEBE room 107B, University of Arizona, (480) 965-8279.

If you have questions about your rights as a subject/participant in this research, or if you feel you have been placed at risk; you can contact the Chair of the Human Subjects Institutional Review Board, through the ASU Research Compliance Office, at 480-965 6788.

This form explains the nature, demands, benefits and any risk of the project. By signing this form you agree knowingly to assume any risks involved. Remember, your participation is voluntary. You may choose not to participate or to withdraw your consent and discontinue participation at any time without penalty or loss of benefit. In signing this consent form, you are not waiving any legal claims, rights, or remedies. A copy of this consent form will be given (offered) to you.

I ( ) consent to be video taped.
I ( ) do NOT consent to being video taped.
The written, video taped materials will be viewed only by the principal investigator and members of the research team.

Updated by 2009-09-30
Subject’s Initials:_______
• Written, video taped materials
  () may be viewed in an educational setting outside the research
  () may NOT be viewed in an educational setting outside the research.
• My signature means that I agree to participate in this study.

Subject's Signature ____________________________ Printed Name ____________________________ Date ____________

INVESTIGATOR'S STATEMENT
"I certify that I have explained to the above individual the nature and purpose, the potential benefits and possible risks associated with participation in this research study, have answered any questions that have been raised, and have witnessed the above signature. These elements of Informed Consent conform to the Assurance given by Arizona State University to the Office for Human Research Protections to protect the rights of human subjects. I have provided (offered) the subject/participant a copy of this signed consent document."

Signature of Investigator ____________________________ Date ____________

Updated by 2009-09-30

Subject's Initials: ________
APPENDIX C

COPYRIGHT PERMISSIONS FOR PUBLISHED MATERIALS
PERMISSIONS FROM MANUSCRIPT COAUTHORS

Dr. Ziaul Hasan, coauthors of “Transfer of learned manipulation following changes in degrees of freedom” published in *Journal of Neuroscience* in Sep. 2011, has given permission to Qiushi Fu for use of this manuscript in this dissertation.

Dr. Wei Zhang, coauthors of “Anticipatory planning and control of grasp positions and forces for dexterous two-digit manipulation” published in *Journal of Neuroscience* in Jul. 2010, has given permission to Qiushi Fu for use of this manuscript in this dissertation.

Dr. Marco Santello, coauthors of the above two manuscript as well as “Context-dependent learning interferes with visuomotor transformations for manipulation planning” published in *Journal of Neuroscience* in Oct. 2012, has given permission to Qiushi Fu for use of this manuscript in this dissertation.