

Sensory-Motor Integration for Control of  
Digit Position in Grasping and Manipulation

by

Daisuke Shibata

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Graduate Supervisory Committee:

Marco Santello, Chair  
Natalia Dounskaia  
Jeffrey Kleim  
Stephen Helms Tillery  
Michael McBeath

ARIZONA STATE UNIVERSITY

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## ABSTRACT

Dexterous manipulation is a representative task that involves sensorimotor integration underlying a fine control of movements. Over the past 30 years, research has provided significant insight, including the control mechanisms of force coordination during manipulation tasks. Successful dexterous manipulation is thought to rely on the ability to integrate the sense of digit position with motor commands responsible for generating digit forces and placement. However, the mechanisms underlying the phenomenon of digit position-force coordination are not well understood. This dissertation addresses this question through three experiments that are based on psychophysics and object lifting tasks. It was found in psychophysics tasks that sensed relative digit position was accurately reproduced when sensorimotor transformations occurred with larger vertical fingertip separations, within the same hand, and at the same hand posture. The results from a follow-up experiment conducted in the same digit position-matching task while generating forces in different directions reveal a biased relative digit position toward the direction of force production. Specifically, subjects reproduced the thumb CoP higher than the index finger CoP when vertical digit forces were directed upward and downward, respectively, and vice versa. It was also found in lifting tasks that the ability to discriminate the relative digit position prior to lifting an object and modulate digit forces to minimize object roll as a function of digit position are robust regardless of whether motor commands for positioning the digits on the object are involved. These results indicate that the erroneous sensorimotor transformations of relative digit position reported here must be compensated during dexterous manipulation by other mechanisms, e.g., visual feedback of fingertip position. Furthermore, predicted

sensory consequences derived from the efference copy of voluntary motor commands to generate vertical digit forces may override haptic sensory feedback for the estimation of relative digit position. Lastly, the sensorimotor transformations from haptic feedback to digit force modulation to position appear to be facilitated by motor commands for active digit placement in manipulation.

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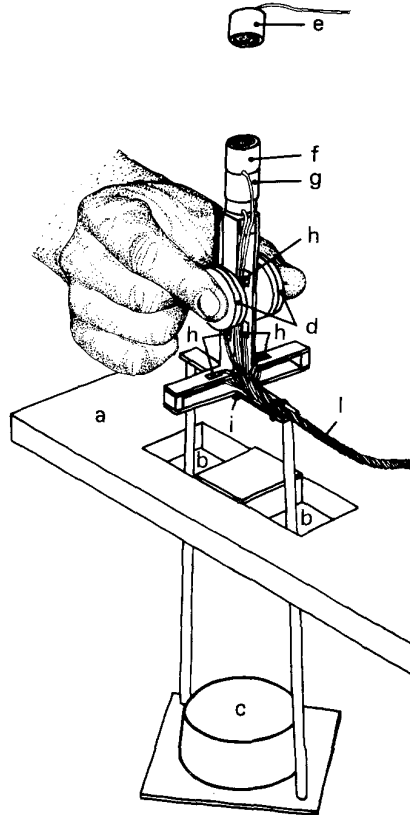
## CHAPTER 1

### INTRODUCTION

#### CONTROL OF DIGIT FORCES AND POSITION FOR OBJECT MANIPULATION

Dexterous manipulation requires fine modulation of forces applied by the digits onto an object. Digit forces have to be coordinated as to fulfill specific task requirements, e.g., moving or holding an object against gravity. Forces normal and tangential to the contact surface must be coordinated to prevent the object from slipping. However, such modulation of digit forces as a function of the task and/or object properties (e.g., friction, mass) may also take into account other constraints, such as preventing muscle fatigue or damage to the object. The coordination of digit normal and tangential forces has been extensively studied in object lifting and holding, in which the digit placement was constrained to fixed small areas (Johansson & Westling, 1984, 1988a). Specifically, as a digit tangential force increased, a digit normal force simultaneously increased to prevent the digits from slipping as a function of surface friction coefficients (Johansson & Westling, 1984). Sensory feedback facilitates not only this digit force coordination during the manipulation, but also an anticipatory control of forces *before* the onset of manipulation, i.e., onset of object motion. Specifically, prior experience with manipulation of the same or similar objects provides information about its properties as well as the forces that are appropriate for manipulation. This allows humans to recall sensorimotor memory of previous manipulations and adjust digit forces before feedback about object properties can be acquired. For example, subjects scale digit forces to object mass before the object is lifted, as indicated by the modulation of peak grip force rate (Johansson and Westling, 1984).

Over the past 30 years, research on grasping has mostly focused on a relatively simple, yet elegant experimental approach: subjects are asked to grasp, lift, and hold an object using the precision grip between the index finger and thumb. This task has provided significant insight, including the contribution of afferent signals from the finger pads as a function of the coefficient of contact surface friction (Johansson & Westling, 1984), and the anticipatory control of digit forces when manipulating familiar or unfamiliar object with different weights (Gordon et al., 1993). However, this approach is characterized by a major limitation: subjects are asked to place their fingertips on pre-determined locations on the object, often coinciding with the position of force sensors (Figure 1). In fact, manipulation performed during activities of daily living often do not constrain digit placement. Specifically, contact points are chosen based on intended manipulation, object geometry, and the extent to which subjects are familiar with object properties (Lukos et al., 2007, 2008; Fu et al., 2010). Without digit placement constraints, a given digit placement in the current trial may be different from that used in previous trials. This trial-to-trial variability of digit position prevents subjects from using the same digit forces that are estimated from previous trials for anticipatory control. Therefore, for a given manipulation to be successfully performed despite grasping the objects at different locations, digit forces must be modulated as a function of digit position. This problem of digit force-to-position modulation has only been recently addressed using an experimental approach that removes digit placement constraints, thus allowing subjects to choose digit placement (Fu et al., 2010, 2011; Lukos et al., 2013). Specifically, subjects were asked to grasp and lift an inverted T-shaped object without digit placement constraints using a precision grip. The object has an asymmetrical mass distribution, and



*Figure 1.1.* An example of object used by Johansson and Westling in 1984.

a – table; b – holes in table; c – exchangeable weight shielded from the subjects view by the table; d – exchangeable discs; e and f – vertical position transducer with an ultrasonic receiver (e) and an ultrasonic transmitter (f); g – accelerometer; h – strain gauge force transducers for measurement of grip and load force (vertical lifting force); i – peg with an hemispherical tip on which the object rests while placed on the table (legend and figure reprinted from Johansson and Westling, 1984).

subjects were asked to lift the object while minimizing object roll. These studies found that subjects adjusted digit forces as a function of variable digit placement on a trial-to-trial basis. This behavior allowed subjects to generate a net torque on the object at lift onset in a consistent fashion (Fu et al. 2010). The phenomenon of digit position-force coordination suggests that the central nervous system (CNS) integrates the sense of digit position with motor commands responsible for distributing forces among the digits. However, the underlying mechanisms are not well understood.

#### **ANTICIPATORY AND REACTIVE MECHANISMS FOR GRASP CONTROL**

Digit forces can be planned before feedback about object properties is available. Specifically, it has been shown that grip forces could be scaled with object weight before object mass could be sensed, i.e., before object lift onset (Johansson and Westling, 1984). In addition, choice of digit position can also be planned according to the object geometry and intended manipulation (Friedman and Flash, 2007; Lukos et al., 2008; Crajé et al., 2011; Sartori et al., 2011; Gilster et al., 2012).

Johansson and colleagues have proposed a model that describes how the CNS adjust motor commands for digit forces by comparing predicted and actual sensory signals, i.e., ‘sensorimotor control points’ (Johansson and Flanagan, 2009). This theory can be used to monitor task progression and detect performance errors for each transition across specific action phases of the manipulation task, i.e., between end of reach and object contact, or between exerting load forces required to lift the object and onset of object’s vertical motion. These events can be detected through specific afferent signals. When the finger pads make a contact with the object surface, a class of mechanoreceptors (see below for details) is activated to provide the CNS with information about the

occurrence of contact. Another group of mechanoreceptors is responsible for detecting the moment of object lift-off. These sensory events are predicted by generating motor commands for manipulation and each action phase so that the CNS can detect the achievement of task sub-goals. At the same time, predicted and actual sensory feedback are also compared, and corrective actions are triggered if a mismatch occurs. Therefore, the sensorimotor control point theory emphasizes the importance of feedback provided by tactile afferents through object contact as well as the crucial role of expecting specific afferent signals. It could be argued that, in addition to the tactile afferents, visual feedback would also play a role in the corrective actions in manipulation tasks. Prior to movement initiation and contact, object material, texture, and shape are perceived through vision. However, recent studies has shown that removal of visual feedback of thumb position or hand before object contact does not significantly affect thumb position relative to the index finger (Voudouris et al., 2012) or force production (Lukos et al., 2013). These findings indicate that visual feedback would be primarily used to plan hand shape and fingertip trajectories before making contact with the object.

This dissertation focuses on the mechanisms underlying the phenomenon of anticipatory digit force-to-position modulation found for dexterous manipulation tasks. Specifically, the aim of this dissertation is to provide insight into humans' ability to sense digit position, and integrate it with motor commands for digit force modulation. The new knowledge provided by this dissertation is expected to improve our understanding of sensorimotor integration mechanisms underlying the control of complex movements.

## **ROLE OF AFFERENT SENSORY FEEDBACK IN POSITION SENSING**

To address the phenomenon of digit force-position modulation and underlying sensorimotor mechanisms, it is important to assess the extent to which humans can sense limb position, e.g., elbow flexion versus extension. Such ability has been extensively studied by blocking visual feedback of the involved limb, eliminating tactile sensation with anesthesia, inducing artificial skin stretch, perturbing the output of muscle receptors with mechanical vibration, and blocking the input into muscles with paralysis. These approaches have provided significant insight into the contributions of voluntary motor commands and sensory feedback to the limb position sensing (for review see Proske and Gandevia, 2009, 2012).

*Skin receptors.* Skin deformation, stretch, touch, pressure, and vibration can be detected by afferent signals through four cutaneous mechanoreceptors embedded in glabrous and hairy skin (Johnson, 2001; Edin, 2004). These receptors can be categorized according to whether their response to a stimulus returns to their baseline state quickly (i.e., fast adapting, FA) or slowly (slow adapting, SA), and whether they are located superficially (type I) or deeply (type II) in the skin. SA-I afferents terminate in Merkel cell and are sensitive to static sustained skin deformation at a low frequency (<5 Hz). FA-I afferents terminate in Meissner's corpuscles of the superficial skin and are sensitive to dynamic skin deformation at a high frequency (5-50 Hz), but insensitive to static force. FA-II afferents terminate in Pacinian corpuscles and are most sensitive to high-frequency vibrations. SA-II afferents terminate in Ruffini endings of the deep skin and are sensitive to skin stretch. Together, these receptors respond to skin deformation of the finger pad and dorsal region of the hand as the finger pads make contact with an object and the hand



posture changes. Of particular relevance to the questions addressed by this dissertation is the role of SA receptors as sensors of skin stretch caused by changes in digit posture. Specifically, the discharge rate of cutaneous mechanoreceptors, particularly the SA receptors, increases as a function of skin stretch for the receptors located near the metacarpo-phalangeal joint of the index finger (Edin and Abbs, 1991). Furthermore, a psychophysics study has shown that changes in the skin stretch contributed to an accurate estimation of the static proximal inter-phalangeal joint angle (Edin and Johansson, 1995).

*Joint receptors.* In addition to skin receptors, joint receptors contribute to sensing limb and digit position. These receptors are relatively less active at the mid-range of motion of joint but become significantly active towards the limits of the joint range of motion (Ferrell, 1980; Burgess et al., 1982; Burke et al., 1988; Edin, 1990). Thus, joint receptors are thought of as “limit detectors”. During object manipulation, as finger span – the distance between fingertips – increases to shape the hand for grasping an object (Santello and Soechting, 1997), afferent signals from joint receptors might provide additional information relative to visual feedback about hand configuration and relative position of the fingertips.

*Muscle receptors.* Muscle receptors consist of muscle spindles and Golgi tendon organs (GTOs). Muscle spindles located in a muscle belly are sensitive to static and dynamic changes in muscle length (Brown and Butler, 1973), whereas GTOs within the tendon-muscle junction increase their discharge rate to changes in tension occurring at the tendons and muscles (McCloskey et al., 1974; Gregory et al., 2001). Goodwin et al. (1972) demonstrated that vibration onto the tendon of the elbow flexor induced illusion of the static angle and movement at the elbow. When the muscle tendon or belly was

vibrated at 80-100 Hz to increase their activity of particularly primary spindles as well as secondary spindles and GTOs (Fallon and Macefield, 2007), the CNS interprets this increased afferent activity as muscle stretch. As a result, subjects perceive elbow angle as more extended than what it actually is, and an opposite phenomenon occurs when elbow extensors are stimulated. There is now general agreement that, muscle receptors, particularly muscle spindles, significantly contribute to sensing limb static position and dynamic movement (for review see Proske and Gandevia, 2009, 2012).

#### **SENSORIMOTOR TRANSFORMATIONS UNDERLYING MATCHING VERTICAL DISTANCE BETWEEN FINGERTIPS**

The above psychophysics work examined somatosensory feedback associated with mechanoreceptors sensing a joint angle, and it well suited to address questions about the role of somatosensory feedback for upper or lower limb sensorimotor control. However, and as discussed above, execution of grasping tasks would rely on sensing contact of each digit on the object surface, as well as determining the relative location of contact points. The ability to sense relative contact point locations has been examined in the horizontal plane (Santello and Soechting, 1997). However, this study did not examine the role of physical contact with an object, hence afferent signals from the finger pads, as a potential contributor to sensing fingertip position as it occurs during grasping. Furthermore, it should be noted that digit placement for precision grips often requires placement of the fingertips that are vertically separated, e.g., when a torque has to be generated (Fu et al., 2010). Therefore, the extent to which the findings from psychophysical studies examining only single joints or horizontal relative digit position

can apply to sensing vertical relative digit position for force modulation during grasping remains to be established. This question was addressed by Study #1.

### **ROLE OF CENTRALLY-GENERATED EFFERENT SIGNALS IN POSITION SENSING**

In addition to afferent sensory feedback described above, centrally-generated efferent signals (i.e., motor commands) to muscles are thought to play a significant role in movement execution. It has been shown that voluntary motor commands can influence central processing of afferent signals conveying information about the joint angle (Gandevia, 1987; Gandevia et al., 2006; Smith et al., 2009). Specifically, Smith et al. (2009) blocked the voluntary motor commands by paralysis to affect muscles below the elbow while afferent signals remained intact. When attempting to flex the wrist under this condition, subjects reported their wrist to be in a flexed position. This finding suggests that voluntary motor commands for force production at a given limb posture can interfere with humans' the ability to sense joint angle.

This mechanism has been proposed to operate within internal forward models whose role is to predict sensory consequences of motor actions based on a copy of motor commands and an estimate of the current state of the body (Wolpert et al., 1995; Kawato, 1999). The internally-predicted sensory consequences are then compared with incoming actual sensory afferent signals to estimate sensory state in the immediate future. A mismatch between the predicted and actual sensory signals, if any, would trigger to adjust motor commands and predicted sensory states for a more accurate estimation.

Furthermore, it has been recently documented that sensitivity to stimuli that are generated by external environment was attenuated during voluntary finger tapping and grasping movements, but not at rest (Bays et al., 2006; Voss et al., 2006; Seki and Fetz, 2012).

This finding suggests that voluntary motor commands for tapping and grasping influence sensitivity to externally-generated stimuli possibly because of the comparison of predicted and actual sensory feedback within the forward models.

Another effect of digit force production derived from voluntary motor commands in grasping and manipulation is skin deformation of the finger pads in multiple directions following object contact. A force normal to the contact surface induces a compression of the finger pad, whereas a force tangential to the contact surface necessary for lifting an object lead to a lateral skin deformation of the finger pad, and subsequent shift of the center of pressure of the finger pad on the object surface (Birznieks et al., 2001; Jenmalm et al., 2003). Thus, skin deformation of the finger pad is normally coupled with digit force production and induced by both normal and tangential digit forces in manipulation task. However, previous studies have examined subjects' ability to match the sensed joint angle by exerting a force only normal, rather than tangential, to the contact surface (Gandevia, 1987; Gandevia et al., 2006; Smith et al., 2009).

The extent to which voluntary motor commands responsible for digit force production during grasping and prior to the onset of manipulation (e.g., without lifting an object) may influence subjects' perception of the digit position and ability to reproduce the sensed relative digit position remains to be established. It is important to understand voluntary motor commands without visual feedback of the hand because the contact points at which the digits apply forces on an object could be inferred through tactile feedback from the finger pad when vision of the contacts is blocked. This question was addressed by Study #2.

## **PERCEPTION-ACTION COUPLING: INTEGRATION OF SENSED DIGIT POSITION WITH FORCE MODULATION FOR DEXTEROUS MANIPULATION**

Psychophysics studies 1 and 2 discussed in previous sections have examined how accurately subjects could reproduce the sensed and remembered relative digit position using tactile and proprioceptive feedback. As noted above, however, this matching task protocol has not been used to study actions normally involved with dexterous manipulation, i.e., static force production followed by object movement. Moreover, previously studied matching tasks were designed to have discrete sensing and matching phases with an interspersed 10 s resting phase. These tasks required retaining memory of digit position during the sensing phase, and retrieving remembered digit placement to reproduce it during the matching phase. However, object manipulation involves transitioning from initial object contact to vertical force production for object lifting with a time delay of few hundred milliseconds required to stabilize the object between digits (for review see Johansson and Flanagan, 2009). As noted above, this sequence of actions – contact, static force production, estimation of relative digit position to modulate forces – would require integrating sensed relative digit position for digit force production without having to recall remembered digit position. Object manipulation with unconstrained digit placement would result in variable relative digit position, which may need to be sensed accurately for appropriate force modulation. Thus, to further understand the sensorimotor integration mechanisms underlying digit force-position coordination, it is important to examine how accurately subjects can sense the relative digit position within a single object lift without memory recall, and how well subjects can perform a grasp-lift task for a given digit position.

Another gap between psychophysics work and the study of object manipulation tasks is whether a limb is moved voluntarily or involuntarily to a target point. Some studies required subjects to indicate the sensed limb position after their limb was *passively* placed to a given position by an experimenter or an apparatus. In object manipulations, subjects *actively* place their digits on the object for its manipulation. It has been shown that an estimation of limb endpoint after active reaching movements was more precise than after passive reaching movements (Adamovich et al., 1998; Gritsenko et al., 2007; Bhanpuri et al., 2013). Furthermore, predictable sensory consequence of active movement appears to benefit position sensing. Specifically, a recent study has shown that a predictable physical contact of the hand after an active arm movement results in an accurate estimation of hand endpoint (Bhanpuri et al., 2013). Conversely, endpoint estimation was less accurate when contact could not be predicted due to passive arm movement or a perturbation during the active movement. Hence, not only the active arm movement but also the corresponding sensory consequences (i.e., the predictable physical contact in the cited study; see also above discussion on feedforward models) may facilitate subjects' ability to estimate the limb endpoint. In an object manipulation, an active digit positioning and sensory consequence of the digit contact with the object surface can be predicted. This phenomenon may facilitate sensing a relative digit position and subsequent action in object manipulation. However, the extent to which voluntary motor commands for active digit placement influences perception-action coupling (sensing relative digit position-digit forces) remains to be investigated. This question was addressed by Study #3.

## CHAPTER 2

# HAPTIC-MOTOR TRANSFORMATIONS FOR THE CONTROL OF FINGER POSITION

### INTRODUCTION

Dexterous manipulation relies on the ability to coordinate digit forces (Johansson and Westling, 1988b; Johansson and Flanagan, 2009) and positions (Lukos et al., 2007, 2008; Fu et al., 2010, 2011; Zhang et al., 2010; Crajé et al., 2011). Choice of digit placement plays an important role in manipulation, as indicated by its sensitivity to task, object geometry, and intended manipulation (Friedman and Flash, 2007; Lukos et al., 2007; Fu et al., 2010; Crajé et al., 2011; Sartori et al., 2011; Gilster et al., 2012). It has recently been shown that when subjects are asked to manipulate objects that do not constrain digit placement at specific locations, trial-to-trial variability in digit placement is compensated by concurrent modulation of digit forces such that manipulation can be performed in a consistent fashion (Fu et al., 2010). These findings indicate that the central nervous system integrates the sense of digit position with motor commands responsible for distributing forces among the digits (Johansson and Cole, 1992; Johansson and Edin, 1993; Johansson and Flanagan, 2009).

Although it could be argued that vision of hand placement on the object would play a key role in the modulation of digit forces as a function of position, the position of one or more digits is often occluded by the object as it happens when grasping a bottle or holding a cup. However, a recent study has shown that removal of visual feedback of thumb position before object contact does not significantly affect thumb placement relative to the index finger (Voudouris et al., 2012). Furthermore, psychophysical

evidence from matching finger span to visually or haptically perceived object size indicates that the horizontal distance between the finger pads can be accurately sensed without visual feedback of the hand in the absence of contact forces (Santello and Soechting, 1997). Similarly, the horizontal distance between the thumb and two fingers was accurately matched even when the matching task was performed with the contralateral hand while holding an object so as to prevent it from slipping without visual feedback of both hands and the object (Van Doren, 1998). These observations suggest that visuomotor transformations mapping object graspable surfaces to relative fingertip position or grip axis orientation can be accurately implemented using only somatosensory feedback.

The above studies, however, constrained grasp aperture to change only on one axis (horizontal) (Santello and Soechting, 1997; Van Doren, 1998) or focused on the orientation of contacts on the horizontal plane (Voudouris et al., 2012). Therefore, the extent to which the above findings apply to tasks involving *non-collinear* contacts, eliciting different patterns of mechanoreceptor activity than collinear contacts, remains to be established. Non-collinear contacts occur when normal forces exerted by opposing digits are used to generate a torque while grasping an object. This is achieved by an offset between the contact points in the plane of the contact surfaces. This is an important question because object manipulation often does not constrain the finger pads to be positioned collinearly relative to each other (Fu et al., 2010; Zhang et al., 2010). Another gap in previous literature is that digit force was not measured, hence not controlled for, by studies that allowed contact forces (Van Doren, 1998; Drewing and Ernst, 2006; Voudouris et al., 2012). Therefore, it is not known whether subjects' ability to accurately



reproduce digit contact orientation without visual feedback might have been associated with exerting specific force magnitudes.

Another open question is whether the ability to reproduce digit position depends on whether sensing occurs through the same versus the opposite hand. Lastly, although the effects of non-congruent arm position on perception of hand shape using the opposite hand were previously addressed (Pesyna et al., 2011), it is not known whether congruence of relative position of the digits affects subjects' ability to match finger pad distance haptically perceived with the opposite hand. It should be emphasized that the haptic-motor transformations associated with reproducing finger pad distance rely on different abilities depending on whether the posture of the hand used for sensing finger pad distance is the same or different from the posture of the hand used for matching. Specifically, when the posture of the 'sensing' and 'matching' hand are the same, subjects can use the memory of somatosensory feedback acquired at a given posture to reproduce the same posture of the 'matching' hand, hence finger pad distance. In contrast, when the postures of the 'sensing' and 'matching' hands differ, somatosensory feedback arising from muscles, tendons, and skin afferents needs to be processed to create an appropriate internal representation of the relative position of the finger pads independent from postural sensory cues.

The present study was designed to address the above gaps by determining the factors that affect subjects' ability to sense and reproduce the vertical distance between finger pads. Specifically, we asked subjects to sense the vertical distance between the center of pressure (CoP) of the thumb and index finger pads ( $d_y$ ) of the right hand ("reference" hand) and, after a brief delay, match it using the same or opposite hand

(“test” hand). In addition, we asked subjects to perform the matching task using an inverse test hand posture relative to the reference hand to prevent them from merely matching hand postures (Fig. 1C and 2A). An inverse hand posture is generated by changing the relative vertical position of the two digits without involving wrist supination or pronation.

We hypothesized that the matching error (difference between reference and test hand  $d_y$ ) would be greater (1) in the collinear ( $d_y = 0$  mm) than non-collinear ( $d_y \neq 0$  mm) digit position (Fig. 2.1C), (2) when the postures of the reference and test hand were inversed (Asymmetric, middle column, Fig. 2.2A), and (3) when subjects reproduced finger pad distance using the opposite hand (top row, Fig. 2.2A) as opposed to using the same hand (bottom row, Fig. 2.2A). The rationale for the first hypothesis is that somatosensory afferent responses from skin, joints, muscles, and tendons would provide signals with higher signal-to-noise ratio about finger pad distance when finger pads are further apart than when they are collinear (Burke et al., 1988; Edin and Abbs, 1991; Edin, 1992; Edin and Johansson, 1995). The second hypothesis is based on the expectation that matching finger pad distance would be facilitated by matching (remembered) sensory feedback from reference hand to sensory feedback from test hand when hand postures are congruent. Therefore, this hypothesis also implies that subjects’ ability to match finger pad distance would be challenged by perceiving and reproducing finger pad distance dissociated from hand postural cues, i.e., reproducing a posture-independent internal representation of finger pad distance, for incongruent hand postures (Symmetric vs. Asymmetric, Fig. 2.2A). The rationale for the third hypothesis is that transferring sensory information across cerebral hemispheres to generate motor commands with the opposite

hand would add sensorimotor transformation errors relative to those associated to perceiving and reproducing finger pad distance with the same hand (Adamo and Martin, 2009; Adamo et al., 2012).

## **MATERIALS AND METHODS**

### *Subjects*

Fifteen right-handed volunteers (10 males and 5 females, mean age and standard deviation:  $23.5 \pm 4.5$  yrs) participated in this study. Hand dominance was assessed using the 10-item Edinburgh Handedness Inventory (Oldfield, 1971). All subjects were classified as right-handed (mean Laterality Quotient and standard deviation:  $83.3 \pm 22.3$ ). Subjects were naïve to the purpose of the study and had no previous history of orthopedic, neurological trauma, or pathology of the upper limbs. Subjects gave their written 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.

### *Apparatus*

Subjects sat on an adjustable chair with both forearms resting on a table. A tabletop, in which a computer monitor was placed at subjects' eye level, was used to prevent vision of the forearms, hands, and the two identical handles used to measure digit forces and torques exerted by thumb and index finger (Fig. 2.1A; see below for details). After matching the position and orientation of the arms and hands, the forearms and wrists were constrained with straps and rigid dowels anchored to the platform to minimize movements across trials and throughout the experiment (Fig. 2.1A). The relation between the hand posture and the handle position was also maintained constant by anchoring the handles to the table. The positioning of the object and platform was

adjusted for each subject and fixed after we confirmed that subjects' digits were placed on the handle in a comfortable posture. The CoP of the thumb pad and index finger pad of each hand was computed as described in Fu et al. (2010) using two six-component force/torque sensors mounted on each side of both handles (ATI Nano-25 SI-125-3, ATI Industrial Automation, Garner, NC; force range: 125, 125, and 500 N for  $x$ -,  $y$ - and  $z$ -axes, respectively; force resolution: 0.06 N; torque range: 3000 N•mm; torque resolution: 0.378 N•mm; "a", Fig. 2.1B). The CoP was defined as the vertical coordinates of the center of pressure of the contact between the finger pad and the graspable surface (Fig. 1B) relative to the center of the sensor. Calibration of each sensor with its contact surface revealed that the vertical ( $y$ ) coordinate of each digit CoP could be computed with a maximum error across all measurements and sensors of  $\pm 1.1$  mm (maximum average error  $\pm$  standard deviation:  $0.2 \pm 0.5$  mm) when three forces (0.6, 1.0, and 1.4 N) were applied perpendicular to the contact surface mounted on the sensor. The actual normal force that subjects exerted with a digit during the experimental tasks fell within the 0.6-1.4 N in 95% of all trials. Error in CoP reconstruction was similar across the four sensors. The contact surfaces of the handles were covered with 100-grit sandpaper (static friction coefficient range: 1.4-1.5) to allow subjects to maintain a relaxed posture of the digits without having to exert significant forces on the handles to prevent the digits from slipping. As a result, tangential forces were very small and ranged between 0.1 and 0.2 N. Force and torque data were acquired, recorded, and stored in a computer with a 12-bit A/D converter board (PCI-6225, National Instruments, Austin, TX; sampling frequency: 1 kHz) through a custom data acquisition interface (LabVIEW version 8.0, National Instruments).

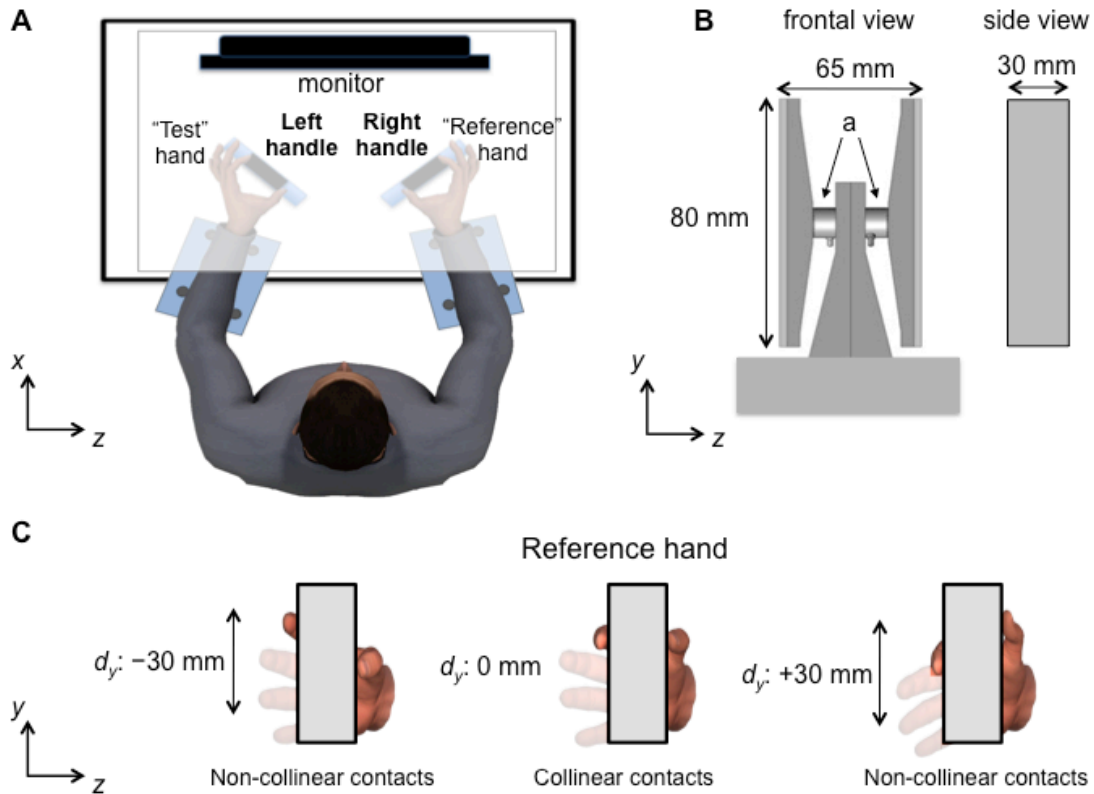


Figure 2.1. Experimental setup.

Panel A shows a top view of the experimental setup. In this figure, the subject is shown performing the matching task using the left hand (“Test” hand) to reproduce the vertical distance ( $d_y$ ) between the thumb and index finger pad of the right hand (“Reference” hand) (see text for more details). Note that the table top (gray) prevented the subjects from seeing their forearms and hands but is shown as transparent for graphical purposes only. Forearms and wrists were strapped to the table to prevent movements within and across trials while the handles were anchored to the table. Panel B shows a frontal view of one of the two handles used for the study (“ $a$ ” denotes force/torque sensors). Panel C shows the frontal view of the handle with the three  $d_y$ s of the reference hand used for the study. Note that  $d_y$  is defined as positive or negative when the thumb pad is higher or lower than the index finger pad, respectively.

## *Experimental Procedures*

We asked subjects to match the vertical distance ( $d_y$ ) between thumb and index CoP of the right (dominant) hand (“reference” hand) using the same hand or the opposite hand (both are defined as “test” hand). At the beginning of the experiment, subjects performed several practice trials to familiarize themselves with the task. Note that feedback about matching performance was not provided during the practice or experimental trials.

*Reference hand.* We tested three  $d_y$ s at the reference hand: +30, 0, and -30 mm, defined as higher, same, or lower thumb CoP relative to index finger CoP (Fig. 1C). During the practice trials, we confirmed that all subjects could comfortably achieve these non-collinear  $d_y$ s (+30 and -30 mm) within their range of motion regardless of variability of hand size. We measured three parameters of reference hand: (1) length, defined as the distance from the wrist crease to the tip of middle finger (average length  $\pm$  standard deviation:  $184.2 \pm 10.6$  mm); (2) width, defined as the distance between the radial aspect of the second metacarpo-phalangeal (*mcp*) joint and the ulnar aspect of the fifth *mcp* joint (average width  $\pm$  standard deviation:  $83.1 \pm 4.8$  mm); and (3) thumb-index distance, defined as the distance between outstretched thumb and index fingertips (average length  $\pm$  standard deviation:  $163 \pm 13.1$  mm). No outliers were found for any of these three parameters across subjects.

The experimenter asked subjects to relax the digits of the reference hand while passively moving them to one of the three  $d_y$ s (“passive  $d_y$  adjustment”, Fig. 2.2B). During this procedure and while matching  $d_y$  (see Fig. 2.1C), subjects were required to keep the middle, ring, and little fingers extended. One of the experimenters monitored the

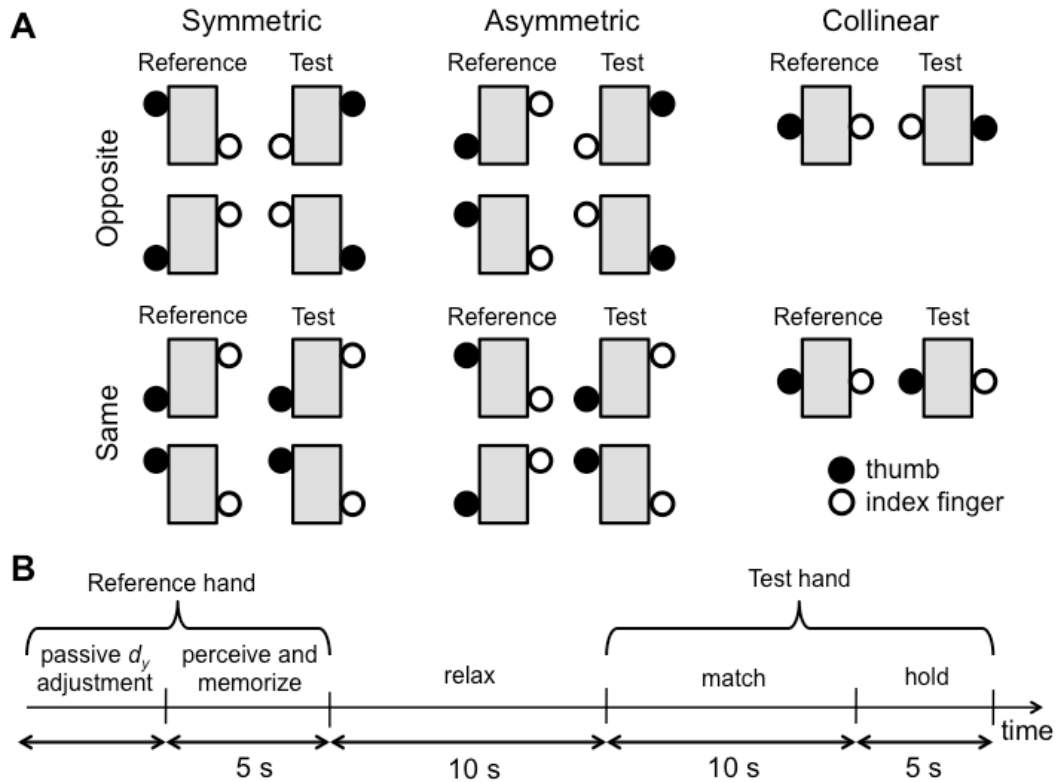


Figure 2.2. Experimental conditions and trial timeline.

Panel A shows all experimental conditions. The thumb and index finger of the reference hand were positioned at one of the three target vertical distances ( $d_y$ ; see Figure 1) and subjects were asked to reproduce  $d_y$  after a 10-second delay using either the opposite hand (test hand) (“Opposite” condition) or the same hand (reference hand) (“Same” condition). For both Opposite and conditions, subjects were asked to either reproduce  $d_y$  using the congruent reference hand posture (“Symmetric” condition) or an inverse posture (“Asymmetric” condition) (see text for more details). Note that the collinear  $d_y$  requires subjects to use the same posture with both hands. Panel B shows the trial timeline. In the phase of “passive  $d_y$  adjustment”, the digits were passively placed to one of three digit positions. Once the desired  $d_y$  was reached and digit force was controlled, recoding of reference hand  $d_y$  started while subjects tried to perceive and memorize the reference hand  $d_y$  for 5 seconds. During the “relax” phase, subjects were asked to retain the remembered  $d_y$  while relaxing their hands for 10 seconds, followed by the “match” phase in which they had to reproduce that  $d_y$  with test hand within 10 seconds. The test hand  $d_y$  was then recorded for 5 seconds while subjects kept the digit position and digit force level (“hold” phase).

CoP for each digit and the resultant  $d_y$  of the reference hand on a second computer monitor that was not visible to the subject. Another experimenter visually verified that subjects maintained the desired hand posture (thumb and index fingertips in contact with the device while keeping the other fingers extended) until the desired  $d_y$  was reached. While keeping a given  $d_y$ , we asked subjects to generate very small normal forces with the thumb and index finger of reference hand. This criterion was enforced by providing visual feedback of digit normal forces to the subject on a computer monitor placed on the tabletop (Fig. 2.1A). The normal force range was between 0.4 and 1 N, the lower bound being the minimum force required for accurate computation of digit CoP (Fu et al., 2010). Once this force criterion was met, we asked subjects to maintain reference hand  $d_y$  for 5 seconds within a tolerance window of  $\pm 5$  mm from the desired  $d_y$  in order to start recording reference hand  $d_y$  (“perceive and memorize”, Fig. 2.2B). Throughout the experiment, subjects were able to maintain each of the three prescribed  $d_y$ s within the  $\pm 5$  mm tolerance window. After the 5-seconds period, we gave subjects a verbal signal to release the digits of reference hand from the handle and place the hand flat (all digits straight, adducted, and with the palm in a horizontal orientation) on the table. Note that neither hand was in contact with the handle for 10 seconds (“relax”, Fig. 2.2B). After the 10 seconds delay, we gave another verbal signal to match the remembered reference hand  $d_y$  using test hand within 10 seconds (see below for details). Note also that, when one hand was in contact with the handle, the other hand was placed flat on the table.

*Test hand.* Subjects were asked to actively place test hand to the remembered  $d_y$  on its respective handle after the verbal signal was given within 10 seconds (“match”, Fig. 2.2B). During the “match” period, subjects were required to exert normal forces



between 0.4 and 1 N (see above). The trial was repeated if subjects were unable to exert digit forces within the required target during the “match” period. When the force criterion was met within the 10-second period, subjects were given a verbal signal to hold  $d_y$  for 5 seconds to record the test hand thumb and index finger CoP (“hold”, Fig. 2.2B). Finally, subjects were asked to release the test hand from the handle after another verbal signal was given.

We tested four matching conditions that differed depending on whether test hand and reference hand were required to assume a congruent or inverse posture (“Symmetric” and “Asymmetric” conditions, respectively) and whether matching tasks were to be performed with the same hand used as the reference hand or the opposite hand (“Same” and “Opposite” conditions, respectively). For each of these four conditions, we tested the above-described three  $d_y$ s (Fig. 2.1C).

In the Symmetric condition (Fig. 2.2A, left column), subjects matched the reference hand  $d_y$  with the test hand by keeping the relative digit position congruent across the two hands. Specifically, when subjects detected the thumb CoP to be higher or lower than the index finger CoP of the reference hand, they were asked to position the thumb CoP higher or lower than the index finger CoP of the test hand, respectively, while matching the reference hand  $d_y$ . For the Asymmetric condition (Fig. 2.2A, middle column), subjects were asked to match reference hand  $d_y$  by using an inverse relative digit position with the test hand. Specifically, when subjects detected the thumb CoP to be higher or lower than the index CoP of the reference hand, they were asked to position the thumb CoP lower or higher than the index CoP of the test hand, respectively. Note that for the collinear digit position ( $d_y = 0$ ), the test hand  $d_y$  (Fig. 2.2A, right column)

reflects the perceived reference hand  $d_y$ . Therefore, even though the actual reference hand  $d_y$  is  $\sim 0$ , they might have perceived  $d_y$  to be non-zero. If so, subjects would reproduce  $d_y$  with test hand by positioning thumb and index finger CoP in a non-collinear configuration that might be symmetrical or asymmetrical depending on the perceived relative position of reference hand  $d_y$ .

Subjects were notified whether the postures of test hand and reference hand were required to be congruent or inverse and whether the test hand was the opposite or same hand before starting the block of consecutive trials. Each block of the four experimental conditions consisted of 15 consecutive trials (5 trials per  $d_y$ ; Fig. 2.1C) for a total of 60 trials. For each experimental condition, the order of presentation of reference hand  $d_y$  was randomized across trials and subjects. The presentation of experimental conditions was counterbalanced across subjects.

### *Data processing*

Force data were filtered using a moving average filter every 50 samples over the duration of data recording and used for computing and displaying online normal force magnitude and digit CoPs and  $d_y$  for both reference and test hand using LabVIEW. The CoP of each digit was defined as the vertical coordinate of the CoP of the contact between the finger pad (thumb or index finger) and the surface of the handle relative to the center of the force/torque sensor (Fig. 1B). After data collection, CoP data for each digit were analyzed off-line with custom-written software (Matlab, The MathWorks, Natick, MA). The vertical coordinate of digit CoP was averaged within each trial for each digit and was used to compute  $d_y$  for statistical analysis.

Error in matching performance was defined as  $d_y$  of test hand during the “hold” phase minus reference hand  $d_y$  during the “perceive and memorize” phase (Fig. 2.2B) and was computed as either absolute or relative error. The relative error takes into consideration the sign of  $d_y$  of the reference and test hand, and therefore can take a positive or negative value. The sign of the relative error denotes whether subject made over- or under-estimation of the reference hand  $d_y$  in the non-collinear conditions. In contrast, absolute error was computed by taking the absolute value of positive and negative relative errors. Over- and under-estimation of reference hand  $d_y$  were defined as longer and shorter distances, respectively, between the thumb and index finger CoP of test hand relative to that of the reference hand. The sign of the relative error for non-collinear  $d_y$  depends on the sign convention used for reference hand  $d_y$ . Specifically, when reference hand thumb was passively placed non-collinearly and higher than the index finger ( $d_y \approx 30$  mm), negative and positive relative error indicate under- and over-estimation of reference hand  $d_y$ , respectively. In contrast, when reference hand thumb was placed lower than the index finger ( $d_y \approx -30$  mm), negative and positive relative error indicate over- and under-estimation of reference hand  $d_y$ , respectively. Analysis of relative error in the collinear reference hand  $d_y$ s was excluded from analysis because, unlike the non-collinear reference hand  $d_y$ s (above), reference hand  $d_y$  could fluctuate between positive and negative values across trials.

### *Statistical analysis*

After data processing for the computation of absolute and relative error, we determined whether there were outliers within each subject and experimental condition. Outliers were defined as data above or below three standard deviations of the mean. We

found only one outlier datum and excluded it from statistical analysis. Statistical analysis with and without the outlier datum did not change the statistical main effects and interactions.

To determine the extent to which actual reference hand  $d_y$  could be grouped within each of the three desired  $d_y$ s for statistical analyses, we performed linear regression analysis on reference hand  $d_y$  versus test hand  $d_y$  on separate group of trials ( $n = 5$ ) from each desired  $d_y$ , experimental condition, and subject. This analysis was performed to determine the extent to which trial-to-trial deviations from the desired reference hand  $d_y$  within the  $\pm 5$  mm tolerance window were large enough to be perceived by the subject as detectable by systematic changes in test hand  $d_y$ . Furthermore, to determine whether trial-to-trial fluctuation of reference hand force induced systematic changes in the test hand force and matching error, linear regression analyses were also performed on the reference hand force versus the test hand force across subjects ( $n = 15$ ) and matching error within subjects ( $n = 60$ ). We also performed linear regression analysis on the absolute error over 60 trials within subjects to determine whether subjects' ability to match the digit positions varied systematically throughout the duration of the experiment.

$E_{abs}$  was analyzed using 3-way analysis of variance (ANOVA) with repeated measures within  $d_y$  (3 levels: +30, 0, -30 mm), test hand posture (2 levels: Symmetric, Asymmetric), and Hand (2 levels: Opposite, Same). These within-subject factors were used to test the effect of each experimental condition on  $d_y$  matching accuracy. This 3-way ANOVA was performed at the  $p \leq 0.05$  significance level to test the hypotheses that the matching error would be greater ( $I$ ) for collinear than non-collinear digit positions,

(2) when the postures (relative positions of thumb and index finger) of the reference and test hand were inversed, and (3) when subjects reproduced finger pad distance using the opposite hand as opposed to using the same hand. A *post hoc* test was used to test the hypothesis that the matching error would be greater in the collinear ( $d_y = 0$  mm) than non-collinear ( $d_y \neq 0$  mm) digit position. *Post hoc* tests were run using paired sample *t*-tests with Bonferroni corrections when appropriate. Relative error from non-collinear  $d_{y,s}$  was analyzed by two-tailed *t*-tests for each experimental condition and non-collinear reference hand  $d_{y,s}$  to determine whether the mean relative error was significantly different from zero.

Sphericity assumptions were tested for all analyses of absolute and relative error (Greenhouse-Geisser analysis). Violations of normality equality assumptions were tested using Shapiro-Wilk test and Levene's test, respectively ( $p > 0.05$ ). Values in the text are reported as means  $\pm$  standard error.

## **RESULTS**

### *Validation of experimental protocol*

*Effect of small trial-to-trial fluctuations in reference hand  $d_y$ .* Linear regression analysis on reference hand  $d_y$  versus test hand  $d_y$  revealed that virtually all linear fits (>95%) were not statistically significant ( $p > 0.05$ ). Therefore, as the small trial-to-trial fluctuations in reference hand  $d_y$  did not elicit systematic changes in test hand  $d_y$ , for statistical purposes we allocated measured reference hand  $d_y$  values to its corresponding category (0, + 30 mm, or -30 mm).

*Effect of small trial-to-trial fluctuations in reference hand force.* The average normal forces of the thumb and index finger exerted by reference and test hand were

virtually identical ( $0.78 \pm 0.05$  N and  $0.80 \pm 0.05$  N, respectively). The linear regression analysis revealed that the reference and test hand normal forces were highly correlated ( $r^2 = 0.92$ ,  $p < 0.01$ ). Linear regression analysis on the reference hand normal force versus matching error within subjects revealed that linear fits from 14 out of 15 subjects were not statistically significant ( $p > 0.05$ ). For the only subject for whom the linear fit was statistically significant ( $p < 0.05$ ) the  $r^2$  value was only 0.11. Thus, these two linear regression analyses indicate that there was no systematic change in the test hand force or matching error as a function of the small trial-to-trial fluctuations of reference hand normal force.

*Effect of experiment duration.* The linear regression analysis on the matching error over 60 trials within subjects revealed that 10 out of 15 (66.6%) linear fits were not statistically significant ( $p > 0.05$ ). The remaining 5 out of 15 (33.4%) linear fits that were statistically significant ( $p < 0.05$ ) were characterized by an inconsistent sign of the regression coefficients. Most importantly, 13 out of 15 (86.7%) of the  $r^2$  of the significant linear fits was very small ( $< 0.1$ ), whereas the maximum  $r^2$  of the remaining 2 out of 15 (13.3%) significant fits was only 0.13. Therefore, matching error did not systematically vary as a function of trial. Thus, we could rule out effects of the duration of experiment, such as fatigue or familiarization with task, on matching error.

#### *Absolute error*

Figure 2.3 shows the averages of absolute matching error of 5 trials from all subjects as a function of the vertical distance between thumb and index finger CoP ( $d_y$ ) for each experimental condition. The matching errors per vertical distance were connected using different colors for each subject, and the thick black line denotes the

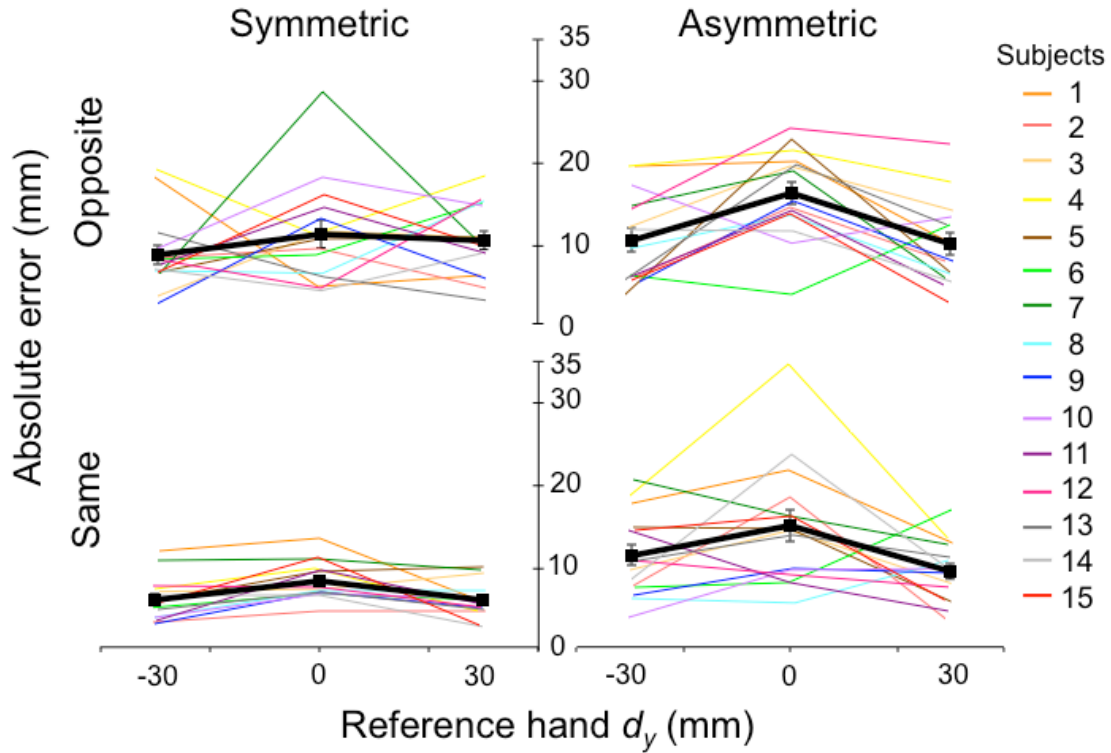


Figure 2.3. Absolute error: individual subjects.

Averages of absolute error of 5 trials from all subjects are shown as a function of reference hand  $d_y$  (+30, 0, and -30mm) for the four matching conditions, and connected with different colors for each subject. The thick black line denotes the mean absolute error averaged across 15 subjects with standard error of the mean. Top panels show the opposite condition, in which subjects were asked to reproduce  $d_y$  using the opposite hand after a brief delay. Bottom panels show the same condition, in which subjects used the same hand to reproduce  $d_y$  after a brief delay. These two conditions are shown separately for the symmetric (left) and asymmetric (right) condition, in which postures of the reference and test hand were congruent and inverse, respectively.

mean absolute error averaged across 15 subjects. Overall, subjects tended to make greater absolute error when asked to match collinear  $d_y$  ( $d_y = 0$  mm) than when the thumb CoP was placed higher ( $d_y = 30$  mm) or lower ( $d_y = -30$  mm) than the index finger CoP. Furthermore, greater absolute error were produced when the postures of the test and reference hand were inversed (Asymmetric condition) and when the matching task was performed with the opposite hand (Opposite condition). The performance of two subjects (#7 and #4) was characterized by large errors for collinear  $d_y$  in Opposite-Symmetric and Same-Asymmetric conditions (dark green and yellow lines, respectively, in Fig. 2.3). Thus, we performed the statistical analyses both with and without these two subjects. The statistical main effects were not altered by removing these two subjects, thus all statistical analyses reported below were performed on all subjects.

Greater absolute error in the collinear than non-collinear  $d_y$  was observed in both symmetric and asymmetric matching conditions (black and gray bars, Fig. 2.4A). Three-way ANOVA confirmed that absolute error was significantly greater in the collinear than non-collinear conditions ( $12.6 \pm 0.9$  mm for  $d_y = 0$  mm;  $9.0 \pm 0.9$  mm for  $d_y = -30$  mm;  $8.8 \pm 0.7$  for  $d_y = 30$  mm; main effect of Distance:  $F_{[2,28]} = 10.8$ ;  $p < 0.01$ ; Fig. 2.4A), and in the asymmetric than symmetric condition ( $12.0 \pm 0.9$  mm and  $8.3 \pm 0.5$  mm, respectively; main effect of Posture:  $F_{[1,14]} = 26.5$ ;  $p < 0.01$ ; Fig. 2.4B, left). We also found a significant interaction Posture  $\times$  Distance ( $7.1 \pm 0.8$  mm for Symmetric at  $d_y = -30$  mm;  $9.6 \pm 1.0$  mm for Symmetric at  $d_y = 0$  mm;  $8.1 \pm 0.7$  mm for Symmetric at  $d_y = 30$  mm;  $10.8 \pm 1.1$  mm for Asymmetric at  $d_y = -30$  mm;  $15.5 \pm 1.4$  mm for Asymmetric at  $d_y = 0$  mm;  $9.6 \pm 1.0$  mm for Asymmetric at  $d_y = 30$  mm;  $F_{[2,28]} = 4.02$ ;  $p < 0.05$ ; Fig. 2.4A).



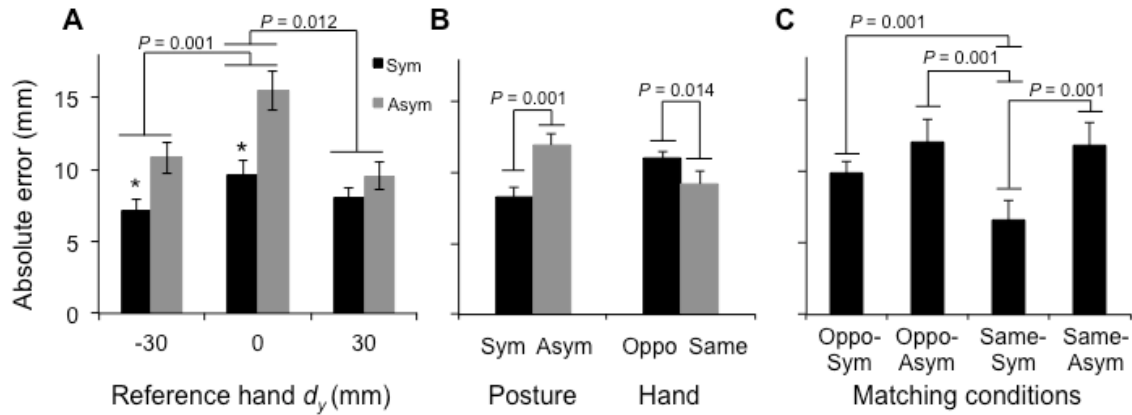


Figure 2.4. Absolute error: averaged data.

Absolute errors were compared across reference hand  $d_{y,s}$ , postures, hands, and matching conditions. Panel A shows average absolute error for symmetric and asymmetric conditions (black and gray bars, respectively) across reference hand  $d_{y,s}$ . Panel B, left, shows average absolute error for symmetric and asymmetric conditions (black and gray bars, respectively) as a function of hand posture (Sym, Asym: Symmetric and Asymmetric conditions, respectively). Panel B, right, shows average absolute error when reference and test hand differed or were the same (Oppo, Same: Opposite and Same conditions, respectively). Panel C shows absolute error averaged for each condition. For all panels, absolute errors were averaged across all subjects within the given comparisons groups ( $\pm$  SE). The asterisks denote significant difference ( $p < 0.05$ ) between the symmetric and asymmetric conditions.

Absolute error was significantly greater in the Asymmetric than Symmetric condition for  $d_y = 0$  and  $-30$  mm (*post hoc t*-test: Symmetric at  $d_y = 0$  mm vs. Asymmetric at  $d_y = 0$  mm;  $t_{[14]} = -3.54$ ,  $p < 0.003$ ; Symmetric at  $d_y = -30$  mm vs. Asymmetric at  $d_y = -30$  mm;  $t_{[14]} = -6.17$ ;  $p < 0.001$ ; adjusted  $\alpha = 0.003$ ; Fig. 2.4A). This indicates that the main effect of Posture (Fig. 4B, left) arose from the difference in the absolute error between the symmetric and asymmetric conditions during the  $d_y = 0$  and  $-30$  mm, but not 30 mm. Moreover, greater absolute error were found when matching was performed by the opposite hand than by the same hand ( $11.0 \pm 0.8$  mm and  $9.2 \pm 0.7$  mm respectively; main effect of Hand:  $F_{[1,14]} = 7.907$ ;  $p < 0.05$ ; Fig. 2.4B, right).

We also found a significant interaction Hand  $\times$  Posture ( $10.0 \pm 0.7$  mm for Opposite-Symmetric;  $12.1 \pm 1.6$  mm for Opposite-Asymmetric;  $6.6 \pm 1.4$  mm for Same-Symmetric; and  $11.8 \pm 1.6$  mm for Same-Asymmetric;  $F_{[1,14]} = 5.411$ ;  $p < 0.05$ ; Fig. 2.4C). *Post hoc* paired *t*-tests with Bonferroni corrections found that subjects made significantly smaller  $E_{abs}$  when matching was performed by the same hand in the symmetric condition (Same-Symmetric) than the Opposite-Symmetric, Opposite-Asymmetric and Same-Asymmetric conditions ( $t_{[14]} = -4.808$ ,  $-5.724$ , and  $-5.878$ , respectively;  $p < 0.001$  for all conditions; adjusted  $\alpha = 0.008$ ; Fig. 2.4C). Note that no significant difference was found for pairwise comparisons across the other three experimental conditions. This indicates that subjects' ability to match reference hand  $d_y$  was greatest when sensing and matching was performed with the same hand and using the same hand posture.

### *Relative error*

Figure 2.5 shows the averages of relative matching error of 5 trials from all subjects as a function of  $d_y$  without the collinear digit position for each experimental condition. Similar to Figure 2.3, each line denotes one subject, and the thick black line denotes the mean relative error averaged across 15 subjects. Overall, under-estimation relative error occurred when reference hand thumb was placed higher or lower than the index finger ( $d_y = 30$  or  $-30$  mm), respectively, in all four conditions. Note that the relative error in the collinear condition was excluded from the analysis of directional bias (see Methods). For all but the Same-Symmetric condition, two-tailed  $t$ -tests revealed under-estimation relative error that was significantly different from zero ( $d_y = -30$  mm:  $3.1 \pm 1.0$  mm;  $t_{[14]} = -3.081$ ;  $p < 0.01$ ;  $d_y = 30$  mm:  $-2.8 \pm 1.1$  mm;  $t_{[14]} = -2.457$ ,  $p < 0.05$ ; Fig. 2.6A) and in the three matching conditions (Opposite-Symmetric:  $t_{[14]} = -2.146$ ;  $p < 0.05$ , Opposite-Asymmetric:  $t_{[14]} = -3.098$ ;  $p < 0.01$ , Same-Asymmetric:  $t_{[14]} = -4.234$ ;  $p < 0.01$ ; Fig 2.6B). Thus, these findings indicate that subjects tended to underestimate reference hand  $d_y$  in all conditions with the exception of Same-Symmetric condition.

### **DISCUSSION**

The main findings of this study, summarized in Table 2.1, are that errors in haptic-motor transformations of finger pad distance are sensitive to (1) the congruence between the posture of the hand used for sensing and that used for reproducing finger pad distance (greater error for inverse than congruent postures), (2) whether finger pad distance is reproduced with the same hand used for sensing (greater error for matching performed with the opposite than same hand), and (3) the relative position of contacts

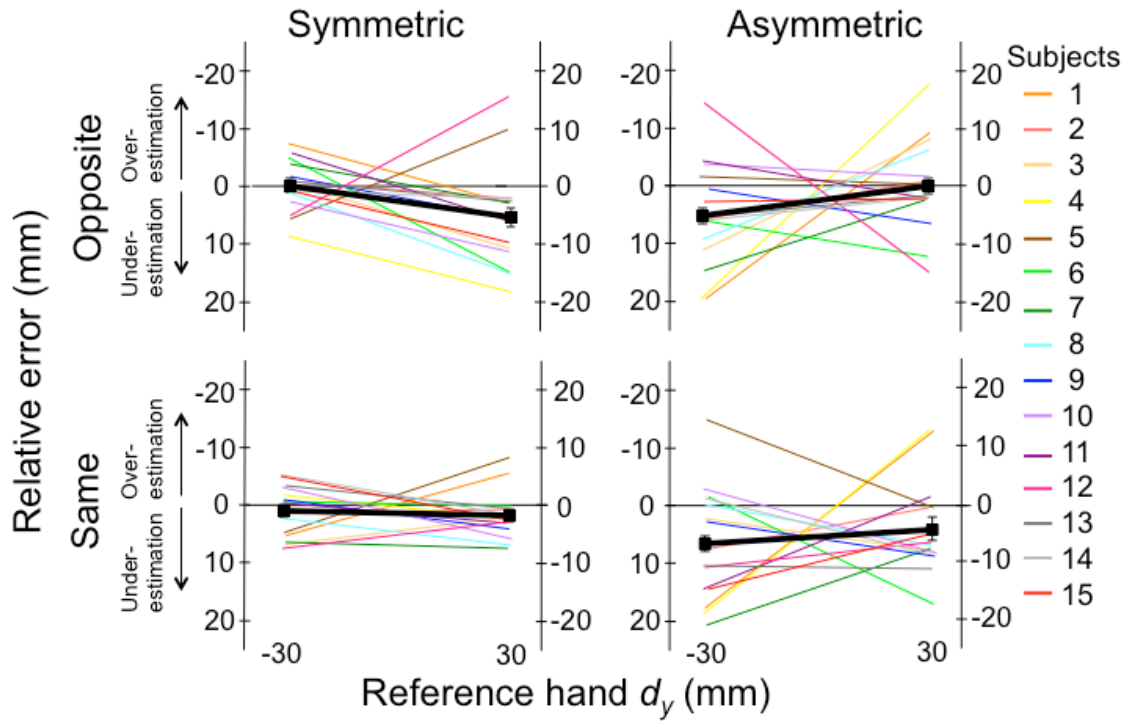


Figure 2.5. Relative error: individual subjects.

Averages of relative errors of 5 trials from each subject are shown as a function of reference hand  $d_y$  ( $-30$  and  $+30$ mm) for each of the four matching conditions. The thick black line denotes the mean relative error averaged across 15 subjects with standard error of the mean. Data from the collinear condition were excluded (see text for more details). The left- and right-hand  $y$ -axes for each plot refer to relative errors obtained for reference hand  $d_y$  of  $-30$  and  $30$  mm, respectively, in which positive or negative relative error are defined as under-estimation errors, respectively.

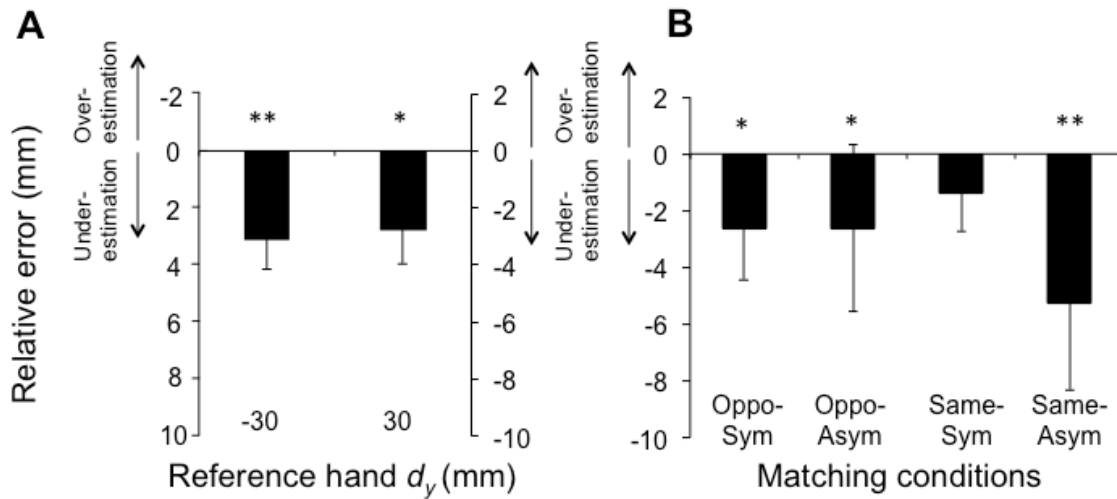


Figure 2.6. Relative error: averaged data.

Relative errors were compared across reference hand  $d_y$ s and matching conditions (panels A and B, respectively). For Panel A, the relative errors with respect to the under- and over-estimation are shown in the same format as Figure 2.5. For Panel B, relative error values were pooled across non-collinear  $d_y$ . For both panels, data are averages of all subjects within a given group ( $\pm$  SE). Note that relative error from the collinear condition was excluded from statistical analysis across matching conditions (see text for more details). Single and double asterisks denote a statistically significant difference from zero ( $p < 0.05$  and  $0.01$ , respectively). Note that, since the opposite signs of relative error were defined as under- and over-estimation, the sign of relative error when reference hand thumb was placed lower ( $d_y = -30$  mm) is inverted for the relative error pooled across the four conditions (Panel B) for graphical purpose only such that the negative relative error always denotes underestimation.

Table 2.1. Task differences across experimental conditions and rank of matching error

	Experimental conditions			
	Same-Sym	Oppo-Sym	Same-Asym	Oppo-Asym
Incongruent postures between $R_{hand}$ and $T_{hand}$ ?	NO	NO	YES	YES
Transfer across hemispheres?	NO	YES	NO	YES
Rank of matching error (smallest to largest)	1	2	3	4

Sym: Symmetric; Asym: Asymmetric; Oppo: Opposite;  $R_{hand}$ : Reference hand;  $T_{hand}$ :

Test hand

(greater errors for collinear than non-collinear finger pad positions). We discuss these results in the context of the role of digit placement sensing for force modulation required for dexterous manipulation.

*Effect of hand posture: congruent vs. inverse hand configurations (Table 2.1, top row)*

The greater absolute error in the asymmetric condition indicates that congruent sensory feedback arising from similar hand postures facilitates the reproduction of sensed  $d_y$ . Specifically, when reference and test hand postures were congruent, subjects might have merely tried to duplicate reference hand configuration by matching the remembered feedback rather than perceived  $d_y$ , thus bypassing higher-order processing of CoP distance based on sensing CoP of each digit. Therefore, the Asymmetric condition is a more reliable measure of subjects' ability to integrate sensory feedback to estimate  $d_y$  regardless of postural sensory cues. It follows that higher-level processing of sensory inputs to estimate finger pad distance leads to greater haptic-motor transformation errors. This conclusion predicts that tasks that require transferring sensory information about digit placement from one hand to another would be performed with greater accuracy when hand postures are mirror symmetric. Examples of such tasks are unimanual tasks where an object is transferred across hands, or bimanual tasks that involve symmetrical application of forces/torques with both hands through similar contact distributions.

*Effect of hand used for sensing and reproducing finger pad distance: opposite versus same matching (Table 2.1, middle row)*

We found that absolute error was greater in the matching condition using the opposite than same hand. Furthermore, we found that absolute error was smaller in the Symmetric condition using the same hand (Same-Sym) than the other three matching

conditions (Fig. 2.4C). These findings indicate that the perceived sensory information is less accurately transferred across than within hands. This result is consistent with previous studies in which subjects matched wrist (Adamo and Martin, 2009) and elbow (Goble and Brown, 2007, 2008; Goble et al., 2009) flexion and extension angles across limbs. However, our task can be considered more complex due to the requirement of integrating the spatial relation between digits' CoP to estimate their vertical distance. It has been suggested that transferring sensory information across hemispheres may increase noise and potential loss of information due to the asymmetry of hemispheric activation during hand movement (Gordon et al., 1994; Adamo et al., 2012). This asymmetric activation of hemispheres might have contributed to the greater error found for the Opposite condition, although further work is needed to identify the underlying neural mechanisms.

#### *Relative error*

Computation of relative error revealed a tendency for underestimating reference hand  $d_y$  in most of matching conditions except the Symmetric condition performed with the same hand (Fig. 2.6). This phenomenon has been observed when the wrist angle of the right hand is matched using the left hand (Adamo and Martin, 2009). Despite the task differences (see above), it would appear that transfer of sensory information from the left to the right cerebral hemisphere leads to under-estimation of joint angle, as well as higher-order sensorimotor transformations required when hand postural sensory cues cannot be used to match  $d_y$  across hands (Opposite-Asymmetric condition).

Regarding the retrieval of remembered sensory information and matching with the same hand used for sensing  $d_y$  (Same condition), there was no directional bias when the



matching task was performed *symmetrically* using the same hand, which is also consistent with previous findings on wrist angle matching (Adamo and Martin, 2009). However, we also found underestimation in reference hand  $d_y$  when the matching task was performed *asymmetrically* using the same hand, which is a condition that cannot be tested in the single joint angle matching task. Thus, we speculate that higher-level processing of finger pad distance based on digit CoP sensing is the primary source of underestimation error when the matching task was performed asymmetrically using the same hand.

*Effect of relative digit position: collinear vs. non-collinear contacts*

We found that subjects make greater errors in reproducing finger pad distance ( $d_y$ ) when sensing collinear than non-collinear contacts. Here we discuss potential neural mechanisms that might underlie these results.

*Skin afferents.* It is possible that subjects sensed and reproduced non-collinear  $d_y$  with greater accuracy due to the greater extent of skin stretch on the dorsal region of the hand. Skin afferent input is likely to play a significant role in sensing digit position in the present experiment as we prevented visual feedback of the hand and ensured consistent deformation of the finger pads by having subject exert similar contact forces across all conditions. Previous studies (Edin and Abbs, 1991; Edin and Johansson, 1995) have shown that the discharge rate of cutaneous receptors, particularly the slowly adapting receptors, increases as a function of skin stretch for the receptors located near the metacarpo-phalangeal ('*mcp*') joint of the index finger. Matching performance in our task might have resulted not only from feedback delivered by skin afferents from the dorsal region of the hand, but also on tactile input elicited by deformation of the glabrous skin

of the finger pad. However, the contribution of the cutaneous receptors within the contact area to sense CoP should have been largely comparable across all experimental conditions as we controlled contact forces and verified that small trial-to-trial force fluctuations had no influence on matching error. Furthermore, Edin and Johansson (1995) reported that the changes in the skin stretch contributed to an accurate estimation of the static proximal inter-phalangeal joint angle even when tactile feedback provided unreliable information due to anesthesia. Therefore, it is likely that the contribution of skin stretch afferent responses can account for our results, if we assume that our non-collinear  $d_y$  elicited a greater discharge from skin afferents, hence a greater afferent signal-to-noise ratio of finger pad position, than collinear  $d_y$ .

*Joint receptors.* Joint receptors of the *mcp* joint of index finger and carpometacarpal ('*cmc*') joint of thumb might also have contributed to sensing  $d_y$  as they are relatively less active at the mid-range of motion of joint but significantly active towards the limits of the joint range of motion (Ferrell, 1980; Burgess et al., 1982; Burke et al., 1988; Edin and Abbs, 1991). The joint in the collinear digit position is thought to be at a mid-range of motion of the *mcp* and *cmc* joints, whereas the non-collinear digit positions are closer to the limit of the thumb and index finger *mcp* and *cmc* joint range of motion.

*Central commands.* In addition to the above-mentioned afferents contribution in sensing the digit position, it has been reported that central motor commands contribute to position sense (Gandevia, 1987; Winter et al., 2005; Gandevia et al., 2006; Proske, 2006; Proske and Gandevia, 2009; Smith et al., 2009; Walsh et al., 2009). Physiological evidence indicates that central and peripheral signals are strongly correlated due to alpha-

gamma co-activation (Vallbo, 1971, 1974; Allen et al., 2008) Furthermore, it has been proposed that predicted future sensory states are implemented through the muscle spindles to update the motor commands during point-to-point movements (Wolpert et al., 1995; Flanagan and Wing, 1997; Dimitriou and Edin, 2008, 2010). Since we passively positioned the digits and controlled for digit contact forces, the extent to which central commands might have been involved in estimating digit position was likely constant across experimental conditions.

In summary, based on the above arguments we speculate that the smaller error found for non-collinear digit positions might have resulted primarily from the integration of sensory inputs from skin and joint receptors.

*Haptic-motor transformations: sensing and reproducing finger pad distance*

To successfully perform our matching task, subjects had to first accurately sense the CoP of each digit of the reference hand, integrate that feedback into an internal representation of distance between CoPs, hold the representation in memory, transfer it to the contralateral cerebral hemisphere (Opposite condition only), and lastly send motor commands to the test hand for controlling the position of each finger pad such as to reproduce the sensed  $d_y$ . The errors we report in this process of transforming digit position could have arisen at one or more of these stages, ranging from purely sensing to motor, or at the high-level computation of CoP vertical distance. The fact that Asymmetric and collinear contacts conditions were characterized by greater matching errors suggests sub-optimal transformations at both the high-level computation levels and sensing, respectively. Similarly, tasks involving  $d_y$  sensing and reproduction with the same hand might have an advantage as no across-cerebral hemisphere transfer of sensed

$d_y$  is required, thus suggesting that retrieval of  $d_y$  internal representations is characterized by less noise than retrieving and transferring it to the contralateral hemisphere. However, since our matching task did not involve a significant digit force production when subjects perceived the digit position such as to prevent an object from slipping, further work is needed to address potential contributions of motor commands responsible for digit force production.

#### *Role of digit position sensing for dexterous manipulation*

The present study revealed maximum absolute errors of up to  $\sim 1.6$  cm (Fig. 2.4A), and smaller errors for particular combinations of task conditions, e.g., Same-Symmetric ( $\sim 0.6$  cm). These findings not only provide insight into the capability of the central nervous system (CNS) to use somatosensory feedback for haptic-motor transformation errors, but also about potential mechanisms that the CNS would have to use to ensure successful performance of dexterous manipulation.

For small position sensing errors, the compliance of finger pads might be sufficient to compensate for digit force magnitude and/or direction modulated to the perceived, as opposed to actual, digit contact distribution. However, for greater digit position errors that might occur when contacts of one or more digits are blocked from view by the object (i.e., a scenario similar to our present study), one would expect greater and more detrimental manipulation performance errors. This is because, for a desired set of net forces and torques on the object, the CNS has to compensate for potential trial-to-trial variability in digit position by modulating contact forces accordingly (Fu et al., 2010). Conversely, if the CNS only used sensorimotor memories of previously used forces and retrieved them on subsequent manipulations but exerted them at different

contacts, object dynamics would differ from that experienced on previous trials. As subjects do modulate forces as a function of variable digit placement (Fu et al., 2010, 2011), the present observations point to the involvement of sensorimotor mechanisms, and these might potentially include vision, capable of compensating for haptic-motor transformation errors. Besides vision of contacts, which does not seem to play a significant role in sensing the orientation of contacts (Voudouris et al., 2012), another potential source of feedback that might reduce digit position sensing errors at the onset of manipulation is the intensity and/or pattern of tactile feedback elicited by exerting contact forces.

Trial-to-trial variability in digit placement when grasping was followed by object lifting was smaller than the matching errors found in the present study (Fu et al., 2010). This phenomenon may be task-sensitive since there was no requirement to lift the object in the present study. Furthermore, a major difference between previous and present work is that the digits were passively moved by the experimenter at given distances and with no visual feedback of the hand and object. In contrast, in grasp-to-lift tasks subjects are actively changing the vertical distance between the fingertips and are likely to use vision to guide digit placement. When actively modulating fingertip distance, subjects might use a feedforward control strategy whereby a sense of digit placement might already be established before contact with the object (hence, tactile feedback) occurs. We speculate that availability of visual feedback and voluntary modulation of fingertip distance are the main causes underlying the differences in accuracy of digit placement between grasp-and-lift tasks and the present matching task.

In summary, the present errors associated with haptically-based reproduction of finger pad distance indicate that the CNS must implement mechanisms to compensate for errors in sensing finger pad distance to ensure that digit forces are distributed according to the required manipulation task requirements. The extent to which these mechanisms might include vision of the hand and/or tactile feedback is the subject of ongoing investigation.

## CHAPTER 3

### MOTOR COMMANDS DISTORT SENSORIMOTOR TRANSFORMATIONS

#### UNDERLYING CONTROL OF RELATIVE FINGERTIP POSITION

##### INTRODUCTION

Dexterous object manipulation requires coordination of digit forces (Johansson and Westling, 1988b; Johansson and Flanagan, 2009) and positions (Lukos et al., 2007, 2008; Fu et al., 2010, 2011; Zhang et al., 2010; Crajé et al., 2011). It has been shown that when subjects can choose digit placement on an object, they modulate digit forces to compensate for trial-to-trial variability in digit position. This behavior is thought to be instrumental for ensuring a consistent manipulation performance and might explain humans' ability to perform the same manipulation task despite variability in where or how the object is grasped (Fu et al., 2010, 2011). Although the mechanisms underlying digit position-force coordination are not well understood, they are likely to involve integration of visual and haptic sensing of digit position, i.e., where the digits are relative to each other and the object, and motor commands responsible for distributing forces among the digits.

To understand the sensorimotor transformations responsible for the above phenomenon of digit position-force coordination, our previous study examined subjects' ability to match the remembered relative vertical distance between the center of pressure of thumb and index finger pads without visual feedback of the hand (Shibata et al., 2013). This study revealed that sensorimotor transformations are more accurate for (a) larger vertical separations between the digits' center of pressure, and (b) when fingertips' vertical distance is reproduced with the same hand and at the same posture as those used

when sensing the fingertip distance. It was speculated that the more accurate fingertip distance matching performance found for larger fingertip distances could have resulted from a combination of factors, including afferent responses from joint receptors and higher signal-to-noise ratio of afferent signals from skin receptors in the dorsal region of the hand, which are thought to provide proprioceptive information about digit position (Edin and Abbs, 1991; Edin and Johansson, 1995; Edin, 2001, 2004; Collins et al., 2005). Moreover, it was proposed that reproduction of fingertips' vertical distance with the same hand and at the same posture would bypass higher-order processing of fingertip distance that would otherwise be involved with transferring remembered sensory feedback to the contralateral hand or a different hand posture.

It should be noted that in our previous study (Shibata et al. 2013) we passively positioned the subjects' fingertips to given distances and required them to exert negligible contact forces. This was done to control for the potential effect that voluntary motor commands for positioning the digits or generating forces might have had on fingertip distance matching performance. Specifically, it has been shown that when subjects are asked to match static joint angle, voluntary motor commands for force production at a given limb posture can negatively influence matching performance by biasing the error in the direction of the attempted movement (Gandevia, 1987; Gandevia et al., 2006; Smith et al., 2009). Additionally, this perceptual bias is greater when only motor commands are available following anesthesia and paralysis (Gandevia et al., 2006) than when motor commands and afferent signals are available while muscles are paralyzed (Smith et al., 2009). These findings suggest that voluntary motor commands for force production can influence the central processing of afferent signals conveying information about limb



posture. This mechanism has been proposed to operate within internal forward models whose role is to predict sensory consequences of motor actions based on a copy of motor commands and an estimate of the current state of the body (Wolpert et al., 1995; Kawato, 1999). The internally-predicted sensory consequences are then compared with incoming sensory afferent signals to estimate sensory state in the immediate future.

Previous matching tasks involving force production (Collins et al., 2005; Gandevia et al., 2006; Smith et al., 2009; Proske and Gandevia, 2012) did not require the perception of relative contact points or sensorimotor transformations required by the retrieval and reproduction of remembered limb postures. Specifically, these studies required subjects to indicate which direction the finger, hand, or limb was pointing to using the opposite hand while the target body parts remained at the target location. Such a matching task could be performed using proprioceptive feedback about the joint angle or posture without having to retrieve the sensory feedback of the perceived joint angle stored in memory. However, these tasks differ from grasping and manipulation tasks where the above-described digit position-force coordination might rely on sensing the fingertips' relative position rather than digit or wrist joint angles *per se*. Furthermore, sensorimotor control of digit forces relies on prior experience with same or similar objects (Johansson and Westling, 1984, 1988a; Gordon et al., 1993; Quaney et al., 2003). This prior experience in the form of *sensorimotor memory* persists for at least 24 hours (Gordon et al., 1993).

Besides the above-described effect that digit force generation might have on perception of fingertip distance, digit force production associated with grasping and manipulation is accompanied by skin deformation of the finger pads following object

contact. The resultant activation of tactile afferents provide information about the magnitude and direction of force acting on the finger pads (Birznieks et al., 2001; Jenmalm et al., 2003; Barbagli et al., 2006; Johansson and Flanagan, 2009; Panarese and Edin, 2011). More importantly, the contact points at which the digits apply forces on an object could be inferred through tactile feedback from the finger pad when vision of the contacts is not available. The center of pressure on the finger pad is likely to shift as the tangential digit force leads to skin deformation of the finger pad. Since our previous study involved a negligible tangential digit force (less than 0.2 N; (Shibata et al., 2013)), the contribution of lateral skin deformation induced by a shear force on the finger pad on the accuracy of matching the relative distance between contact points remains unknown.

The gaps in the above-reviewed work raise the following question: To what extent motor commands responsible for digit force production affect subjects' ability to transform sensory feedback of relative contact points to motor commands for placing the digits to their remembered locations? To address this question, we asked subjects to perceive and reproduce fingertip distance after a short delay using the same hand. The delay was used to introduce a memory component to the matching task similar to the above-mentioned sensorimotor memory component underlying grasping tasks.

Furthermore, to prevent subjects from merely matching the pressure on the finger pad and hand posture, one subject group performed the matching task without significant digit force production when matching the remembered contact points. The present study also examined subjects' ability to reproduce the remembered digit contact points when tangential forces of the thumb and index finger were produced in the same or opposite direction. An object manipulation may require a vertical translation and/or a rotation of a

grasped object. To perform a vertical translation, the digit tangential forces are produced in the same direction, whereas these forces are exerted in opposite directions to rotate an object.

We hypothesized that (1) when the tangential forces of the thumb and index finger are produced in opposite directions, the reproduction of memorized fingertip distance would be biased toward the directions of the tangential forces exerted while perceiving and memorizing the digits placement, and (2) the magnitude of the biased error would be greater when the remembered relative contact points associated with the production of relatively large digit forces are matched while exerting negligible forces. The rationale for the first hypothesis is that voluntary motor commands for force production would distort the matched joint angle and limb position in the direction of the attempted movement (Gandevia et al., 2006; Smith et al., 2009). When the direction of digit tangential forces was the same, we expected no directional bias in matching error of the relative vertical fingertip distance. The second hypothesis is based on the expectation that matching relative contact points would be facilitated by the congruent skin deformation of the finger pad used to match the remembered points with that used to perceive and remember the relative contact points. Thus, this hypothesis implies that fingertip distance matching ability would be challenged by reproducing the remembered points while experiencing different digit forces and tactile feedback associated with skin deformation on the finger pad. To test the second hypothesis, we asked subjects to match the remembered relative distance between contact points while exerting negligible or significant force.

## **MATERIAL AND METHODS**

### *Subjects*

Two groups of fifteen healthy subjects each participated in this study. Group 1 (11 females; mean  $\pm$  SD:  $23.2 \pm 7.0$  yrs.) participated in Experiment 1, and Group 2 (5 females; mean  $\pm$  SD:  $22.7 \pm 4.3$  yrs.) participated in Experiment 2. We used the 10-item Edinburgh Handedness Inventory (Oldfield, 1971) to assess subjects' hand dominance. All subjects were classified as right-handed based on the mean Laterality Quotient and standard deviation (Group 1:  $77.8 \pm 18.9$ ; Group 2:  $78.0 \pm 19.2$ ). Subjects were naïve to the purpose of the study. Subjects gave their written 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.

### *Apparatus*

We used a custom-made grip handle to measure digit forces and center of pressure (CoP) of the thumb and index finger pad for both Experiments 1 and 2 (Fig. 3.1A). The sensorized handle has been described in detail elsewhere (Shibata et al., 2013). Briefly, two six-component force/torques sensors were mounted on each side of the handle (ATI Nano-25 SI-125-3, ATI Industrial Automation, Garner, NC; force range: 125, 125, and 500 N for  $x$ -,  $y$ - and  $z$ -axes, respectively; force resolution: 0.06 N; torque range: 3000 N•mm; torque resolution: 0.378 N•mm; Fig. 3.1A). The vertical coordinate ( $y$ ) of the CoP of each digit on the contact surface (red dots, Fig. 3.1B) was computed from the force-torque sensor output. We performed calibration of each sensor by applying forces (3, 4, 5, and 6 N) perpendicular to the contact surface mounted on the sensor. This calibration revealed that the force and torque output of the two sensors could

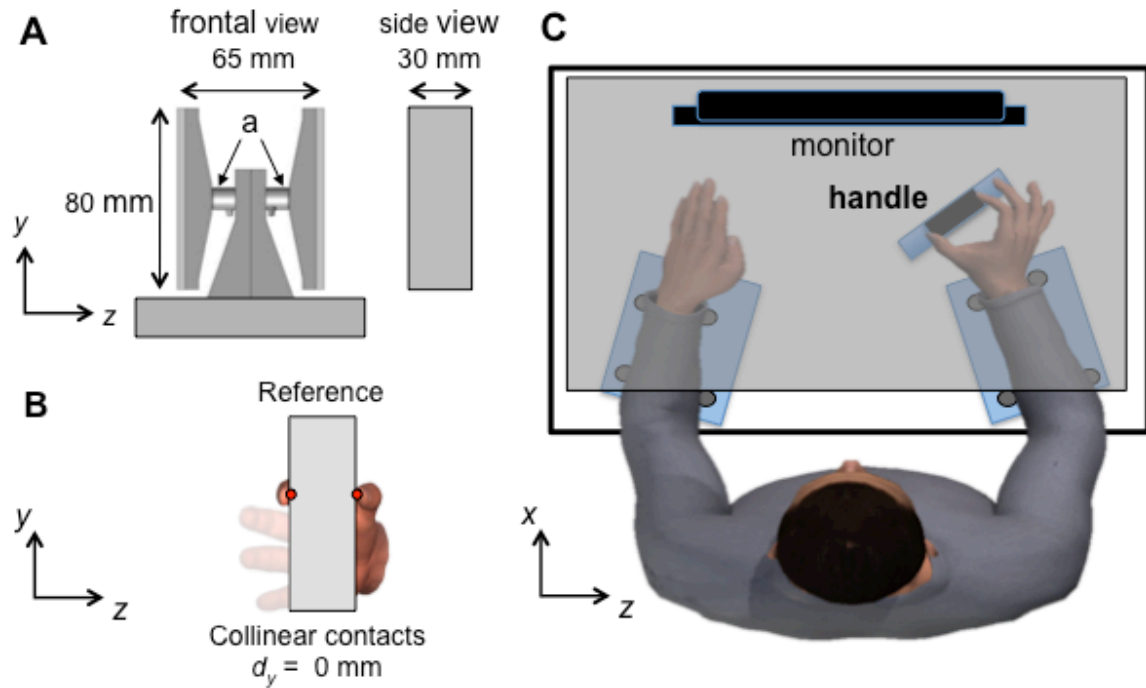


Figure 3.1. Experimental setup.

Panel A shows frontal and side views of the handle used for the study (“ $a$ ” denotes force/torque sensors). Panel B shows the frontal view of the handle with thumb and index fingertip center of pressure of the reference hand located at the same  $y$ -coordinates (vertical height relative to the base of the object) on the graspable surfaces of the handle (collinear  $d_y$ ). The red dots denote the center of pressure of each digit. Panel C shows a top view of the experimental setup. The subject is shown contacting the handle with thumb and index fingertip, while the left hand was kept flat on the table. When relaxing in between trials, both hands were kept flat and relaxed. Note that the table top (gray) was opaque and prevented subjects from seeing their forearms and hands but is shown as transparent for graphical purposes only. Forearms and wrists were strapped to the table to prevent movements within and across trials while the handle was anchored to the table.

be used to compute the vertical coordinate of each digit CoP with a maximum error across all measurements and sensors of  $\pm 1.2$  mm (maximum average error  $\pm$  SD:  $0.3 \pm 0.4$  mm). Error in CoP reconstruction was similar between the two sensors and to the errors found when applying smaller normal forces (i.e., 0.6, 1.0, and 1.4 N; Shibata et al., 2013). During the experimental tasks, subjects exerted normal force with a digit within the 0.6 – 6.0 N range in 98 % of all trials. To prevent the digits from slipping when subjects applied tangential forces up to 3.5 N, the contact surfaces of the handles were covered with 100-grit sandpaper (static friction coefficient range: 1.4-1.5).

### *Experimental Procedures*

Subjects grasped the handle with the thumb and index finger of the right hand while sitting on an adjustable chair with both forearms resting on adjustable supports (Fig. 3.1C). The left hand rested on the table throughout the experiment with all digits straight, adducted, and in a pronated position. Vision of forearms, hands, and the handle was prevented by an opaque tabletop on which a computer monitor was placed at subjects' eye level (Fig. 3.1C). The positioning of the handle and platforms was adjusted for each subject so that subjects' digits could be placed on the handle in a comfortable posture. All subjects had similar postures of the wrist such that the wrist was semi-pronated and in a neutral posture ( $\sim 0^\circ$  flexion/extension and adduction/abduction). Motion of forearms and wrists was blocked by straps and rigid dowels anchored to the platform to minimize changes in posture across trials and throughout the experiment. The handle was anchored to the table to maintain a fixed position and distance relative to the hand. The experimental setup was the same across Experiments 1 and 2.

For both experiments, after subjects' digits were passively moved (*"passive  $d_y$  adjustment"* phase, Fig. 3.2A), we asked subjects to perceive and memorize the vertical distance ( $d_y$ ) between thumb and index CoP of the right hand (*"reference"* hand) (*"perceive and memorize"* phase, Fig. 3.2A), relax for 10 seconds, and match it using the same hand (*"test"* hand) (*"match"* phase, Fig. 3.2A). An important difference between the present study and our previous work (Shibata et al., 2013) is that subjects were asked to exert normal and tangential digit forces with different combinations of magnitude and direction during the *"perceive and memorize"* phase (see below).

*Reference hand.* As done in our previous study (Shibata et al., 2013), we measured three parameters of reference hand: (1) length, defined as the distance from the wrist crease to the tip of middle finger (mean  $\pm$  SD: Group 1:  $174.9 \pm 9.7$  mm; Group 2:  $181.4 \pm 8.1$  mm); (2) width, defined as the distance between the radial prominence of the second metacarpo-phalangeal (mcp) joint and the ulnar prominence of the fifth mcp joint (mean  $\pm$  SD:  $80.5 \pm 5.3$  mm; Group 2:  $84.2 \pm 6.0$  mm); and (3) thumb-index distance, defined as the distance between outstretched thumb and index fingertips (mean  $\pm$  SD:  $154 \pm 12.6$  mm; Group 2:  $160.7 \pm 14.3$  mm). No outliers were found for any of these three parameters across subjects.

Subjects' thumb and index fingertips of the reference hand were passively moved by an experimenter (*"passive  $d_y$  adjustment"* phase, Fig. 3.2A) such that the CoPs of both digits on the graspable surface were at the same vertical height relative to the base of the object. Throughout the manuscript, we will refer to this fingertip position as *'collinear'* ( $d_y = 0$  mm; Fig. 3.1B). During this procedure and while matching  $d_y$  with the test hand (see below for details), subjects were instructed to extend the middle, ring, and little

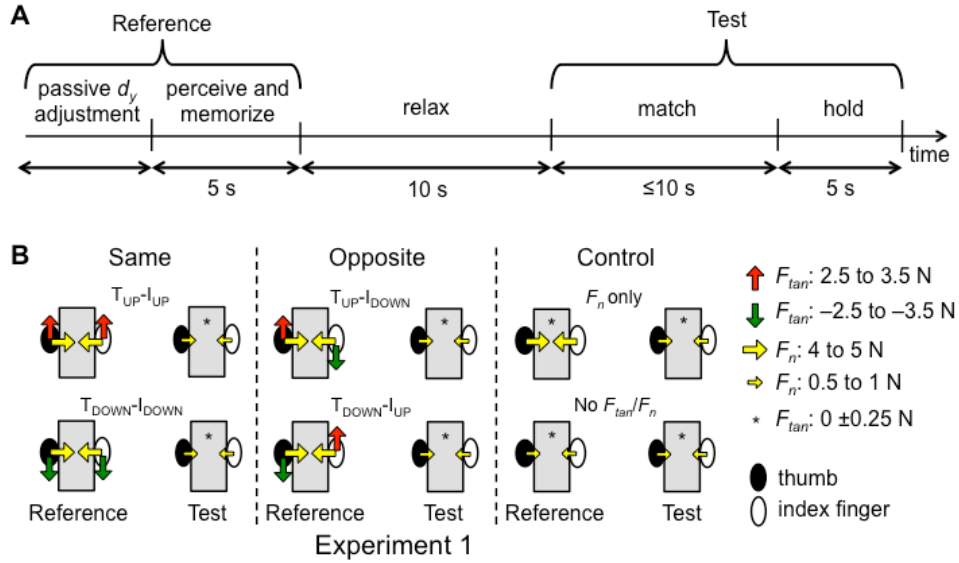


Figure 3.2. Experimental protocol and conditions (Experiment 1).

Panel A shows the time course of the experimental protocol. In the “*passive  $d_y$  adjustment*” phase, the subject’s thumb and index finger were passively placed by an experimenter to a collinear  $d_y$  (see Figure 1B). Once the desired  $d_y$  was reached and digit forces matched the desired target forces, recording of reference hand  $d_y$  started for 5 seconds while subjects were asked to perceive and memorize the reference hand  $d_y$  (“*perceive and memorize*” phase). During the “*relax*” phase, subjects were asked to relax their reference hand for 10 seconds, followed by the “*match*” phase in which they were asked to reproduce the remembered reference hand  $d_y$  using the (same) test hand within 10 seconds. The test hand  $d_y$  was then recorded for 5 seconds while subjects maintained the digit position and digit forces (“*hold*” phase). Panel B shows the experimental conditions for Experiment 1. The thumb and index finger (filled and open ellipse, respectively) of the reference hand exerted tangential forces either in the same or opposite directions (“Same” and “Opposite”, left and middle column, respectively). In the Same condition, thumb and index finger exerted tangential forces that were both upward or downward ( $T_{UP-I_{UP}}$  or  $T_{DOWN-I_{DOWN}}$ , respectively). In the Opposite condition, the tangential forces of the thumb and index finger were directed opposite to each other, i.e., either upward and downward ( $T_{UP-I_{DOWN}}$ ) or downward and upward ( $T_{DOWN-I_{UP}}$ ), respectively. In the Control condition (right column), subjects were asked to exert no tangential force while exerting large or negligible normal forces (“ $F_n$  only” or “No  $F_{tan}/F_n$ ”, respectively). The magnitude of tangential and normal forces was the same across these conditions ( $F_{tan}$ : 2.5-3.5 N,  $F_n$ : 4-5 N) with the exception of the ‘No  $F_{tan}/F_n$ ’ condition ( $F_{tan}$ :  $0 \pm 0.25$  N,  $F_n$ : 0.5-1 N). The test hand in Experiment 1 exerted only negligible tangential and normal forces ( $F_{tan}$ :  $0 \pm 0.25$  N,  $F_n$ : 0.5-1 N).



fingers to prevent them from contacting the handle (Fig. 3.1B). The CoP and forces for each digit and the resultant  $d_y$  of the reference hand was displayed on a second computer monitor that was not visible to the subject. Once an experimenter visually confirmed compliance of the desired hand posture and  $d_y$ , a verbal cue was given to generate forces in one of six combinations of direction and magnitude (Fig. 3.2B). Specifically, the reference hand exerted tangential force of thumb and index finger in either the same or opposite directions. When tangential forces were exerted in the same direction, both thumb and index finger exerted the tangential force upward ( $T_{UP-I_{UP}}$ ) or downward ( $T_{DOWN-I_{DOWN}}$ ) (“Same”; Fig. 3.2B and Fig. 3.3, left column). When tangential forces were exerted in opposite directions, the thumb and index finger exerted the tangential force either upward and downward ( $T_{UP-I_{DOWN}}$ ) or downward and upward, respectively ( $T_{DOWN-I_{UP}}$ ) (“Opposite”; Fig. 3.2B and Fig. 3.3, middle column). The range of the normal and tangential forces exerted by each digit of the reference hand was the same across these four experimental conditions (4-5 N and 2.5-3.5 N, respectively).

As these conditions always involve normal force of 4-5 N, subjects’ ability to match  $d_y$  may potentially be affected by the combined effect of exerting normal and tangential forces. To isolate the effect of tangential force, we asked subjects to exert different magnitudes of normal force in two additional conditions that served as controls for the above-mentioned four conditions (“Control”; Fig. 3.2B and Fig. 3.3, right column). In these control conditions, the tangential force was negligible ( $0 \pm 0.25$  N) and the normal force of the reference hand was either within the same range as for the above-mentioned conditions (4-5 N; ‘Fn only’ condition, Fig. 3.2B, right column), or negligible (0.5-1 N; ‘No Fn/Ftan’ condition, Fig. 3.2B, right column). The lower bound of the

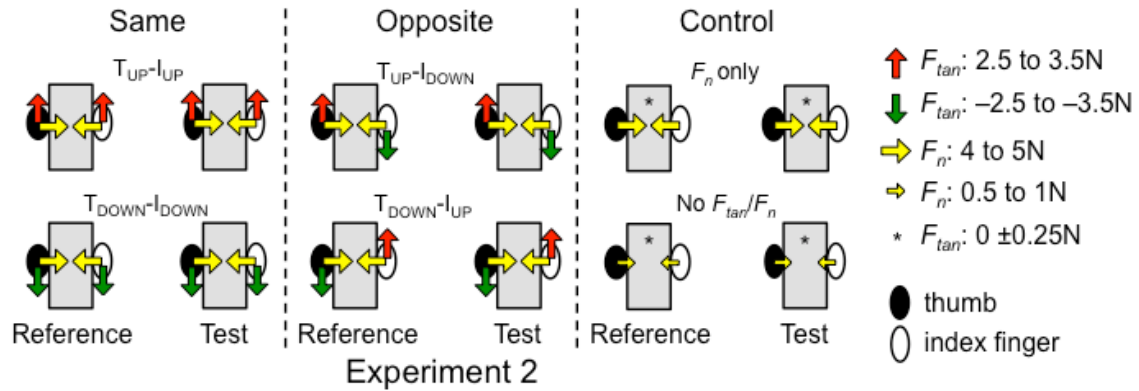


Figure 3.3. Experimental conditions (Experiment 2). The experimental conditions of Experiment 2 are shown in the same format as those shown in Figure 3.2 for Experiment 1. The only difference between Experiments 1 and 2 is that for the latter experiment, subjects were required to exert the same thumb and index fingertip normal and tangential forces across reference and test hands (see text for more details).

normal force was required for accurate computation of digit CoP using the force sensor (Fu et al., 2010). To facilitate control of digit forces, subjects received visual feedback of digit normal and tangential forces on a computer monitor placed on the tabletop throughout each trial. Note that subjects were not given visual feedback of digit CoP throughout the experiment.

Upon confirmation of both of the above-described force and collinear CoP criteria, an auditory cue was given to subjects to start perceiving and memorizing the  $d_y$  of the reference hand (“*perceive and memorize*”, Fig. 3.2A). During this phase, subjects were required to maintain a given combination of digit normal and tangential forces as well as initial  $d_y$  for 5 seconds within a tolerance window of  $\pm 3$  mm from the collinear  $d_y$ . If the digit CoPs shifted over the contact surface during the “*perceive and memorize*” phase and moved from their initial collinear placement ( $d_y \neq 0$  mm), subjects were asked to relax the digits while an experimenter adjusted the digit CoPs to their original placement and the trial was re-started. If this adjustment had to be performed more than three times within a given trial, subjects were asked to completely relax the digits, release them from the sensor, and place the hand flat on the table with all digits straight, adducted, and with the palm in a pronated position before the trial could be re-started. Throughout the experiment, subjects were able to maintain the collinear  $d_y$  within the  $\pm 3$  mm tolerance window in 98.3% of all trials and the target force with the reference hand within the prescribed range in 98.0% of all trials. This “*perceive and memorize*” phase was terminated by an auditory cue so that subjects released the digits of reference hand from the handle and placed the hand flat on the table (“*relax*” phase, 10 seconds; Fig. 3.2A). After this 10-second delay, another auditory cue was given to subjects to match

the remembered reference hand  $d_y$  using the same hand (“test hand”) within 10 seconds (see below for details). Note that the experimental setup, conditions, and procedures using the reference hand were identical for Experiments 1 and 2.

*Test hand.* Subjects were asked to actively place the thumb and index finger of the test hand to match the remembered  $d_y$  within 10 seconds after making contact with the same handle (“*match*”, Fig. 3.2A). During the “*match*” phase, subjects gave a verbal cue to the experimenter only when they could maintain digit forces within the target force range while matching the remembered  $d_y$  using the test hand. Note that digit forces exerted by the test hand differed across Experiments 1 and 2. Specifically, during the “*match*” phase of Experiment 1 subjects were asked to reproduce  $d_y$  while exerting negligible forces (0.5-1 N and  $0 \pm 0.25$  N, respectively; Fig. 3.2B). In contrast, for Experiment 2 subjects were asked to reproduce  $d_y$  while also matching the forces they had exerted with the “reference” hand during “*perceive and memorize*” phase (Fig. 3.3). Therefore, in Experiment 2, digit forces of the test hand were required to be the same as those exerted by the reference hand. Subjects controlled the digit forces using an online force gauge and values were shown separately for the tangential and normal forces of the thumb and index finger on a computer monitor. Throughout the experiment, subjects were able to maintain the target force with the test hand in 97.6% of all trials. The comparison between the Experiments 1 and 2 allowed us to study whether subjects’ ability to match the reference hand  $d_y$  would be sensitive to whether digit forces, contact area, and skin deformation of the finger pad differ (Experiment 1) or are identical (Experiment 2) across reference and test hands. Note that both Experiments 1 and 2 included the Same, Opposite, and Control conditions (Fig. 3.3).

After the subject's verbal cue and when the force criteria were met, the experimenter gave a verbal cue to hold the  $d_y$  and digit forces for 5 seconds during which CoPs of the test hand thumb and index finger were recorded (“*hold*”, Fig. 3.2A). The trial was repeated if subjects did not give the verbal cue signaling attainment of the remembered  $d_y$  or did not maintain digit forces within the target range during the “*match*” or “*hold*” phases. Finally, subjects were asked to release the test hand from the handle after another auditory cue was given.

Subjects practiced to control the required forces in all conditions for 10-20 minutes without being asked to match digit CoPs across reference and test hands. After the practice trials, at least 2 practice trials per condition (i.e., total of 12 practice trials) were given to subjects to familiarize themselves with the matching task. Note that subjects were not provided with feedback about matching performance during the practice or experimental trials. Subjects performed a total of 30 trials (5 trials  $\times$  6 experimental conditions). The order of presentation of experimental conditions was randomized across trials and subjects. Subjects were given rests every 10 trials or as appropriate to ensure that no fatigue occurred.

### *Data Processing*

Force and torque data were acquired, recorded, and stored in a computer with a 12-bit A/D converter board (PCI-6225, National Instruments, Austin, TX; sampling frequency: 1 kHz) through a custom data acquisition interface (LabVIEW version 8.0, National Instruments). During data collection, force data were filtered online using a moving average filter every 50 samples over the 5-second duration of data recording for both reference and test hands. The filtered force data were then used for computing and

displaying online normal and tangential force magnitudes and digit CoPs and  $d_y$  using LabVIEW.

After data collection, CoP data for each digit were averaged within each trial and used to compute  $d_y$  off-line with custom-written software (Matlab, The MathWorks, Natick, MA) for statistical analysis. The  $d_y$  was defined as the vertical coordinate of thumb CoP minus the vertical coordinate of index finger CoP. Thus, positive and negative  $d_y$  indicates that the thumb CoP is higher or lower relative to the index finger CoP, respectively. *Matching error* was defined as test hand  $d_y$  during the “*hold*” phase minus reference hand  $d_y$  during the “*perceive and memorize*” phase (Fig. 3.2A). Note that in the present study, the reference hand  $d_y$  was always  $0 \pm 3$  mm. Matching error can be positive or negative, and thus takes into consideration whether subjects made an error not only in reproducing the distance between fingertip CoPs but also in their relative position. Specifically, positive and negative matching errors indicate that the test hand  $d_y$  is positive and negative (i.e., the thumb CoP is higher and lower relative to the index finger CoP, respectively) compared to the reference hand  $d_y$ .

### *Statistical Analysis*

After computing matching errors and before performing statistical analyses, we determined whether there were outliers (data above or below three standard deviations of the mean) within each experimental condition per subject. As no outliers were found, all matching errors were included in statistical analyses.

We performed linear regression analysis on reference hand  $d_y$  versus test hand  $d_y$  on trials ( $n = 5$ ) from each experimental condition per subject. This analysis was performed to determine whether trial-to-trial deviations from the desired reference hand  $d_y$  within  $\pm 3$

mm tolerance window induced systematic changes in test hand  $d_y$ . Furthermore, to determine whether subjects' matching performance varied systematically throughout the duration of the experiment, we also performed linear regression analysis on the matching error over 30 consecutive trials within subjects.

A mixed-design analysis of variance (ANOVA) was performed on matching errors in the control conditions (right column, Figures 3.2B and 3.3) with within-subject factor *Digit normal force* (2 levels: large, negligible) and *Experiment* as between-group factor (2 levels: Experiment 1, Experiment 2). The within-subject factor was used to analyze the effect of digit normal force magnitude on  $d_y$  matching accuracy. The between-subject factor was used to test the effect of congruence of digit normal force between the reference and test hands on  $d_y$  matching accuracy.

Matching errors in the Same and Opposite conditions (Fig. 3.2B and Fig. 3.3, left and middle column) that were normalized to the errors in the 'Fn only' condition were analyzed using a mixed-design ANOVA with within-subject factors *Congruence of digit forces* (2 levels: Same, Opposite) and *Direction of tangential force* (2 levels: Up, Down), and *Experiment* as between-groups factor (Experiment 1, Experiment 2). The first within-subject factor was used to analyze the effect of all combinations of digit force direction on  $d_y$  matching accuracy (Same:  $T_{UP-I_{UP}}$  and  $T_{DOWN-I_{DOWN}}$  vs. Opposite:  $T_{UP-I_{DOWN}}$  and  $T_{DOWN-I_{UP}}$ ). The second within-subject factor was used to examine the effect of tangential force direction on  $d_y$  matching error. For this analysis, we used thumb tangential force direction to pool data in the "Up" and "Down" category (Up:  $T_{UP-I_{UP}}$  and  $T_{UP-I_{DOWN}}$  vs. Down:  $T_{DOWN-I_{DOWN}}$  and  $T_{DOWN-I_{UP}}$ ). For example, subjects might have made matching errors when thumb force was directed upward, but not downward. The between-subject

factor (*Experiment*) was used to test the effect of having equivalent versus different digit forces exerted by the reference and test hands on  $d_y$  matching accuracy. This mixed-design ANOVA was performed to test the hypotheses that (a) the ability to match  $d_y$  would be biased toward the direction of tangential force but only when the direction of tangential forces exerted by thumb and index finger was opposite, and (b)  $d_y$  matching error would be greater in the Experiment 1 than Experiment 2 because the digit forces and skin deformation of the test hand differed from those of the reference hand. A *post hoc* test was used to test the hypothesis that matching errors would be greater when the directions of tangential forces of the thumb and index finger were opposite than when they were the same. *Post hoc* tests were run using paired sample *t*-tests with Bonferroni corrections when appropriate. Additionally, matching error for each experimental condition was analyzed by two-tailed one-sample *t*-tests to determine whether the mean matching error was significantly different from zero.

Sphericity assumptions were tested for all analyses of matching error (Mauchly's sphericity test). When the sphericity assumptions were violated, we used Greenhouse-Geisser analysis ( $p < 0.01$ ). Box's test was used to test homogeneity of covariance ( $p > 0.05$ ). All tests were performed at the  $p \leq 0.05$  significance level. Values in the text are reported as means  $\pm$  standard error of the mean.

## **RESULTS**

### *Validation of Experimental Protocol*

*Effect of small trial-to-trial fluctuations on reference hand  $d_y$ .* Linear regression analysis on reference hand  $d_y$  versus test hand  $d_y$  revealed that 93% of linear fits were not statistically significant ( $p > 0.05$ ). The remaining 7% of linear fits that were statistically



significant ( $p < 0.05$ ) were characterized by inconsistent signs of regression coefficients. Therefore, the small trial-to-trial fluctuations in reference hand  $d_y$  did not elicit systematic changes in test hand  $d_y$ .

*Effect of experiment duration.* The linear regression analysis on the matching error over 30 trials within subjects revealed that all linear fits were not statistically significant ( $p > 0.05$ ). This indicates that matching error did not systematically vary throughout the experiment and was independent of potential effects of experiment duration that might have induced fatigue, decrease in attention, or increasing familiarization with the task.

#### *Matching error*

A mixed-design ANOVA on the matching errors in the two control conditions (Figs. 3.2B and 3.3, right column) revealed no significant difference between matching performance in Experiments 1 and 2 (no main effect of *Experiment*:  $F_{[1,28]} = 0.467$ ;  $p > 0.05$ ) and between the ‘*Fn* only’ and ‘No *Fn/Ftan*’ (no main effect of *Digit normal force*:  $F_{[1,28]} = 0.004$ ;  $p > 0.05$ ), and no significant interactions (*Digit normal force* × *Experiment*:  $F_{[1,28]} = 2.516$ ;  $p > 0.05$ ; Fig. 3.5A). These results indicate that subjects’ ability to reproduce the reference  $d_y$  with the test hand was not sensitive to whether reference and test hands exerted the same or different digit normal force. As matching error did not differ as a function of digit normal force in either experiment, the mean matching error from the ‘*Fn* only’ condition was used as a within-subject reference to normalize errors in the other experimental conditions characterized by the same normal force (4-5 N). The normalized matching error was defined as the mean matching error averaged within subjects in the Same and Opposite conditions minus the mean matching

error from the ‘ $F_n$  only’ condition. This resulted in a ‘normalized matching error’ denoting the effect of tangential force production only on  $d_y$  matching error.

Figure 3.4 shows the matching error from each subject and the mean matching error averaged across all subjects for Experiments 1 and 2 (top and bottom plots, respectively). Matching errors made by each subject are connected by color-coded lines whereas the mean matching error averaged across all subjects is denoted by the thick black line. Matching errors were very small and similar across conditions where both digits exerted tangential forces in the same direction, indicating that subjects could reproduce fairly accurately a collinear digit fingertip position. The same result was found for experimental conditions where subject exerted only normal force or no tangential and normal forces (Control, Fig. 3.4). However, matching error increased when digit tangential forces were exerted in opposite directions ( $T_{UP-I_{DOWN}}$ ,  $T_{DOWN-I_{UP}}$ , Fig. 3.6). For these experimental conditions, the direction of the error depended on whether a given digit exerted tangential force in the upward or downward direction. Specifically, for the  $T_{UP-I_{DOWN}}$  condition, subject placed the thumb higher than the index fingertip, whereas for the  $T_{DOWN-I_{UP}}$  subjects placed the index fingertip lower than the thumb. Overall, this trend of matching errors was similar across subjects and between experiments (top and bottom rows, Fig. 3.4).

The results of the mixed-design ANOVA revealed a statistically significant difference in the normalized matching errors when comparing the conditions where thumb force was directed upward ( $T_{UP-I_{UP}}$  and  $T_{UP-I_{DOWN}}$ ) and downward ( $T_{DOWN-I_{DOWN}}$  and  $T_{DOWN-I_{UP}}$ ) (main effect: *Direction of tangential force*:  $F_{[1,28]} = 143.428$ ;  $p < 0.001$ ), but no significant difference when force direction of the thumb and index finger was the

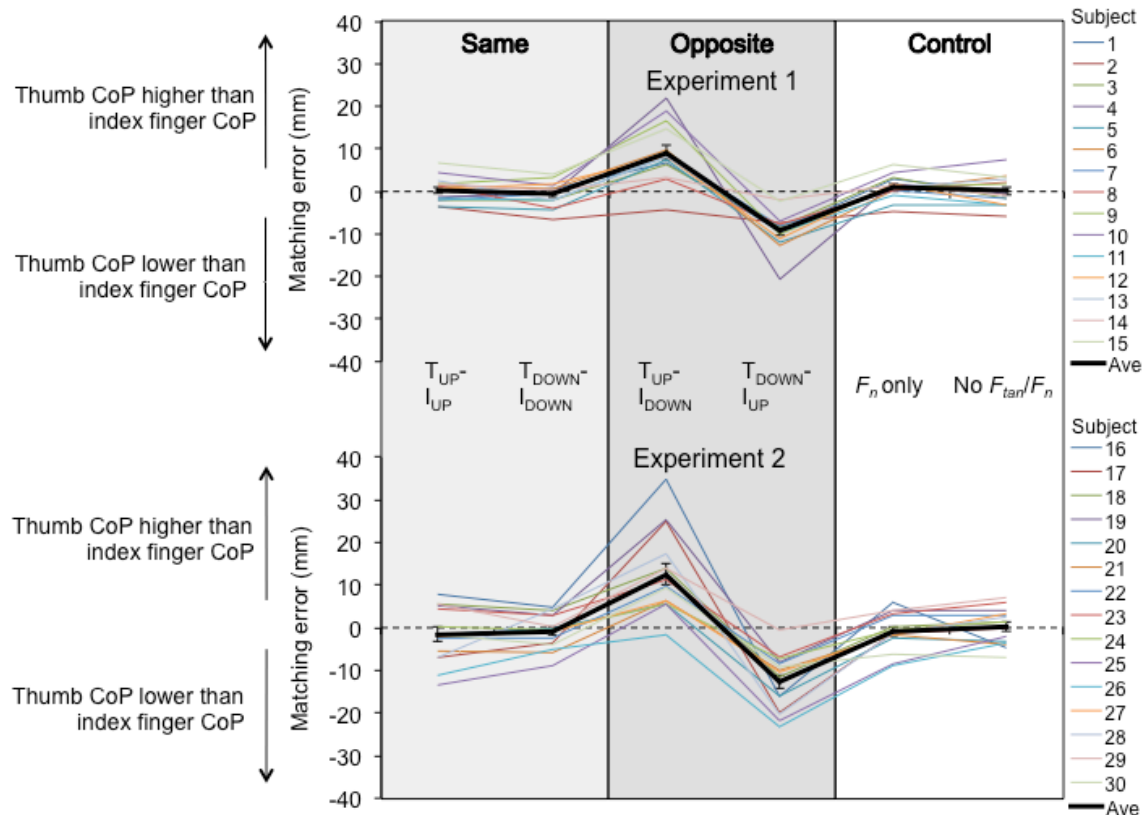


Figure 3.4. Fingertip vertical distance: Matching performance by individual subjects

Mean matching errors averaged across 5 trials from each subject are shown as a function of experimental condition from Experiments 1 and 2 (top and bottom plots, respectively). Each subject data is color coded whereas the thick black line denotes the mean matching error averaged across 15 subjects  $\pm$  standard error of the mean. For both experiments, positive and negative matching errors indicate that subjects reproduced remembered reference hand  $d_y$  by placing the thumb CoP higher and lower, respectively, than the index finger CoP.

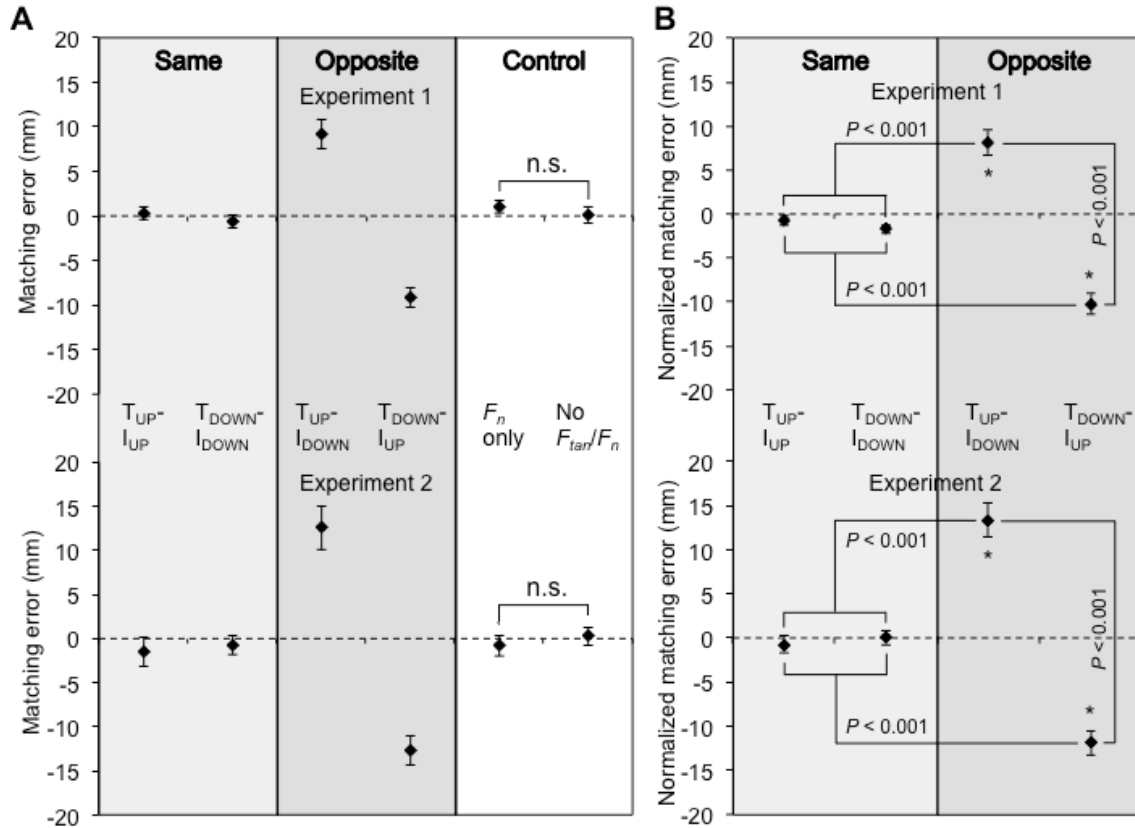
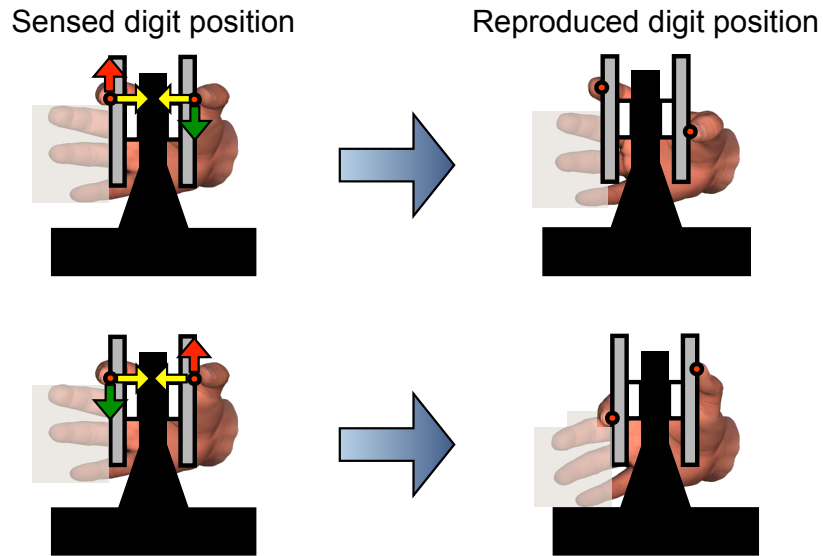


Figure 3.5. Fingertip vertical distance: Matching errors.

Matching errors were compared across experimental conditions and between experiments. Panel A shows average matching error for Experiments 1 and 2 (top and bottom plots, respectively) across matching conditions. The mean matching error in the ‘F<sub>n</sub> only’ condition was used as a reference to normalize the matching error in the Same and Opposite conditions (left and middle column, respectively; see text for more details). Panel B shows average normalized matching error for the Experiments 1 and 2 (top and bottom plots, respectively) across matching conditions. For all panels, matching and normalized errors were averaged across all subjects (vertical bars denote SE). Asterisks denote significant differences ( $p < 0.05$ ) from zero.



*Figure 3.6. Fingertip vertical distance: Matching errors in the Opposite conditions.*

Sensed (i.e., collinear) and reproduced digit position in the Experiment 1 are shown (left and right) when the thumb and index finger exerted downward and upward tangential forces, respectively (top) and the thumb and index finger exerted upward and downward tangential forces, respectively (bottom). Reproduced digit positions shifted toward the direction of the force production. This matching error was found in the Opposite conditions only.

same or opposite (no main effect of *Congruence of digit forces*:  $F_{[1,28]} = 1.47$ ;  $p > 0.05$ ; Fig. 3.5B). More importantly, we found a significant interaction between *Congruence of digit forces* and *Direction of tangential force* ( $F_{[1,28]} = 99.349$ ;  $p < 0.001$ ; Fig 3.5B). *Post hoc* paired *t*-tests with Bonferroni corrections found that subjects made significantly greater normalized matching errors when the force direction of the thumb and index finger was upward and downward (Opposite condition: T<sub>UP</sub>-I<sub>DOWN</sub>), respectively, than when it was the same (Same conditions: T<sub>UP</sub>-I<sub>UP</sub> and T<sub>DOWN</sub>-I<sub>DOWN</sub>;  $t_{[29]} = -8.290$ , and  $-9.335$ , respectively;  $p < 0.001$  for all conditions; adjusted  $\alpha = 0.008$ ; Fig. 3.5B).

Furthermore, subjects made greater absolute normalized matching errors when the force direction of the thumb and index finger was downward and upward (T<sub>DOWN</sub>-I<sub>UP</sub>) than when it was the same (T<sub>UP</sub>-I<sub>UP</sub> and T<sub>DOWN</sub>-I<sub>DOWN</sub>;  $t_{[29]} = -12.320$ , and  $-9.288$ , respectively;  $p < 0.001$  for all conditions; adjusted  $\alpha = 0.008$ ; Fig. 3.5B). Furthermore, the normalized matching error in the T<sub>UP</sub>-I<sub>DOWN</sub> condition was significantly different from that in the T<sub>DOWN</sub>-I<sub>UP</sub> condition ( $t_{[29]} = -10.978$ ;  $p < 0.001$ ; adjusted  $\alpha = 0.008$ ; Fig. 3.5B). No significant difference was found for pairwise comparison between the T<sub>UP</sub>-I<sub>UP</sub> and T<sub>DOWN</sub>-I<sub>DOWN</sub> conditions. These findings indicate that subjects' ability to match remembered reference hand  $d_y$  was sensitive to the congruence in the direction of tangential forces exerted by the thumb and index finger.

We also found a directional bias in  $d_y$  matching errors. Specifically, subjects tended to make positive and negative matching errors in the T<sub>UP</sub>-I<sub>DOWN</sub> and T<sub>DOWN</sub>-I<sub>UP</sub> conditions, respectively (Figs. 3.4, 3.5B, 3.6). The positive matching error denotes that subjects positioned the thumb CoP higher than index finger CoP when the tangential forces of thumb and index finger were directed upward and downward, respectively (T<sub>UP</sub>-

I<sub>DOWN</sub>; Fig 3.4, 3.5B, 3.6), and vice versa for the T<sub>DOWN</sub>-I<sub>UP</sub> condition. Two-tailed one sample *t*-tests revealed that normalized matching errors were significantly different from zero when the direction of tangential digit forces in the reference hand was opposite, but not when it was the same ( $p < 0.001$ ; Fig. 3.5B). This indicates that subjects' ability to match  $d_y$  was biased toward the direction of tangential force, as indicated by the congruence in the vertical placement of each fingertip and the direction of the tangential force exerted by the same fingertip, but only when the direction of tangential forces was opposite.

Lastly, a mixed-design ANOVA confirmed that there was no statistically significant difference in the normalized matching errors between Experiments 1 and 2 (no main effect of *Experiment*:  $F_{[1,28]} = 3.77$ ;  $p > 0.05$ ) and no significant interactions with *Experiment* (*Congruence of digit forces*  $\times$  *Experiment*:  $F_{[1,28]} = 0.803$ ; *Direction of tangential force*  $\times$  *Experiment*:  $F_{[1,28]} = 1.932$ ; *Congruence of digit forces*  $\times$  *Direction of tangential force*  $\times$  *Experiment*:  $F_{[1,28]} = 3.97$ ; all  $p > 0.05$ ). This indicates that subjects' ability to match the reference hand  $d_y$  was not dependent on equivalence in digit forces between reference and test hand.

## DISCUSSION

We quantified the effects of motor commands responsible for generating digit forces on accuracy of sensorimotor transformation of the relative vertical distance between digit contact points. The main findings of this study are that accuracy in the sensorimotor transformation of vertical fingertip distance (*1*) is sensitive to whether tangential, but not normal, forces of thumb and index finger are produced in the same or opposite direction, and (*2*) is not sensitive to whether the hand used for matching

fingertip distance exerts the same or different forces relative to those experienced during sensing. These results are discussed in the context of neural mechanisms underlying the sensorimotor transformation of digit position required for dexterous manipulation.

#### *Methodological considerations*

The extent to which digit normal forces might affect matching horizontal fingertip distance between the contacts was not the focus of the present study and therefore was not investigated. Nevertheless, our findings indicate that generating digit normal forces *per se* does not affect the reproduction of relative vertical contact points. Similarly, with regard to potential effects of tangential digit forces exerted in the same direction (Same condition:  $T_{UP-I_{UP}}$ ,  $T_{DOWN-I_{DOWN}}$ ), we did not require subjects to match the height at which both fingertips had to be positioned relative to the object. Thus, subjects might have placed both digits higher or lower relative to the object when the direction of digit tangential forces was the same. However, the rationale for these experimental conditions was to rule out the possibility that voluntary motor commands for tangential force production - even when exerted in the same direction – could affect subjects' ability to reproduce the relative vertical distance between contact points. As subjects could reproduce these points very accurately in the Same condition (Fig. 3.5B), we conclude that the reproduction of the relative vertical distance between contact points was interfered with only when tangential digit forces were exerted in opposite direction, rather than by tangential or normal force production *per se*.

#### *Effects of motor commands on sensorimotor transformations*

Biased matching errors found in the Opposite condition but not in the other conditions (see above) are accountable by the incongruent direction of digit tangential



forces. Specifically, neither the exertion of digit normal forces alone (i.e., ‘ $F_n$  only’) nor the congruent direction of digit tangential forces (i.e., Same condition:  $T_{UP-I_{UP}}$ ,  $T_{DOWN-I_{DOWN}}$ ) affected the reproduction of the remembered relative vertical distance between digit contact points. Consistent with our previous study (Shibata et al., 2013), we found that subjects can accurately reproduce relative vertical distance between contact points when the magnitude of neither tangential nor normal digit forces is significant (‘No  $F_{tan}/F_n$ ’, Fig. 3.5A) and when significant normal digit forces only were exerted (‘ $F_n$  only’, Fig. 3.5A).

This result supports our first hypothesis and confirmed such effects of voluntary motor commands on the sensorimotor transformations involved in matching fingertip distance as indicated by larger errors in the reproduced relative digit contact points when the tangential digit forces were exerted in opposite versus same directions (Fig. 3.5B). Importantly, the directionality of the matching errors in the present study was biased toward the direction of the voluntary motor commands, which is consistent with findings from previous studies (Gandevia et al., 2006; Smith et al., 2009; see below). Specifically, we found that subjects erroneously placed the thumb higher than the index finger (i.e., positive matching error) when the upward and downward tangential forces were exerted by the thumb and index finger, respective ( $T_{UP-I_{DOWN}}$ ), and vice versa for the  $T_{DOWN-I_{UP}}$  (Figs. 3.4, 3.5, 3.6). We also found that, contrary to our second hypothesis, the magnitude of the matching error was the same regardless of whether subjects were asked to exert negligible force or match digit force exerted with the Reference hand using the Test hand (Experiments 1 and 2, respectively). This result indicates that the mismatch in digit forces exerted by Reference and Test hands was not the primary cause of bias in matching error,

and further suggests that this might have been primarily driven by a conflict between motor commands and sensory feedback during the “*perceive and memorize*” phase (see below).

Note that matching tasks in previous studies (Gandevia, 1987; Gandevia et al., 2006; Smith et al., 2009) required subjects to indicate a joint angle using the contralateral limb relative to the one used as a ‘reference’, whereas our task required subjects to match the relative vertical digit contact points using the same hand. Thus, our task might be considered more complex due to the requirement of integrating the perceived spatial relation between two contact points to estimate their vertical distance. Moreover, subjects in the present study were required to perceive and memorize the contact points, retain the perceived fingertip distance for a short period of time, and then retrieve and use the memorized fingertip distance to place the digits at the remembered relative locations. In contrast, the above-cited previous work did not require subjects to memorize a given joint angle. Despite differences in matching task between previous work and the present study, we found a similar phenomenon: voluntary motor commands associated with force production affect the directionality of the matching error when the directions of digit forces were opposite (Opposite condition:  $T_{UP-I_{DOWN}}$ ,  $T_{DOWN-I_{UP}}$ ).

Centrally-generated voluntary motor commands for force production are thought to affect processing of somatosensory afferent signals to estimate limb joint angle (Gandevia, 1987; Gandevia et al., 2006; Smith et al., 2009; for review see Proske and Gandevia, 2012). This proposition is consistent with the framework of internal forward models in which a copy of motor commands is used to predict sensory consequences of motor commands, which are then compared with incoming sensory feedback to estimate

sensory state in the immediate future (Wolpert et al., 1995; Kawato, 1999). In the present study, voluntary motor commands responsible for digit tangential force production in opposite directions and in absence of friction would have resulted in increasing the relative vertical distance between the fingertips. It should also be noted that during digit force exertion, afferent discharge from skin, muscle, and tendon receptors should have accurately encoded the relative position of the finger pads. Therefore, the fact that matching error was highly sensitive to the pattern of digit tangential force direction implies that the prediction of sensory consequences of force generation overrode sensory feedback from the finger pads. Thus, fingertip distance reproduction was distorted in a way that resembled the relative fingertip position resulting from motor commands – had the fingertip being allowed to move – rather than the actual distance as encoded by somatosensory receptors.

*When did sensorimotor transformation errors occur?*

Throughout our matching task, errors in sensorimotor transformations might have been induced by four non-mutually exclusive factors: (1) inaccurate perception of the relative vertical contact points, (2) time-dependent decay of memory of perceived fingertip distance, (3) inaccurate memory retrieval, and/or (4) inaccurate motor commands for placing the digits to the remembered contact points. We propose that the last three factors did not play a significant role in causing the matching error. This interpretation is based on the similarity in the bias effect on matching error found by the above-cited psychophysical studies (Gandevia et al., 2006; Smith et al., 2009) despite major task differences. Specifically, this previous work did not incorporate a memory component or motor commands for reproducing joint angle. In contrast, our task required

subjects to store, retain, and retrieve memory of relative contact points, and send motor commands using the same hand for reproducing the remembered relative contact points. Therefore, we conclude that the sensorimotor transformation errors likely occurred when subjects perceived and memorized the relative vertical contact points.

*Dexterous manipulation: motor commands for positioning digits and generating forces*

Behavioral evidence indicates that subjects can accurately modulate digit forces as a function of variable digit placement while exerting a torque, thus indicating successful sensorimotor transformations (Fu et al. 2010). Importantly, such modulation is found following exertion of normal and tangential force up to the instant of object lift-off, as well as when digit tangential forces are exerted in opposite direction to generate a torque. In contrast, the present study shows that sensorimotor transformations are inaccurate when digit tangential forces are exerted in opposite directions. However, several factors might enable successful sensorimotor transformations in dexterous manipulation tasks while preventing them in our psychophysical task. First, visual feedback of contact points prior and following contact might wash out the bias induced by voluntary commands of digit forces, whereas visual feedback of the hand was prevented in our study. Second, manipulation tasks involve active digit placement on objects, whereas in our experiment subjects' fingertips were passively placed on the object.

Many studies have shown that an estimation of limb endpoint relative to the body after active reaching movements is more precise than after passive reaching movements (Adamovich et al., 1998; Gritsenko et al., 2007; Fuentes and Bastian, 2010; Bhanpuri et al., 2013). For the active movement case, subjects voluntarily moved their arm to a target,

whereas in the passive movement condition their arm was passively moved by a robot. In contrast, other studies have shown no difference in the estimation of limb endpoint between active and passive reaching movements (Jones et al., 2010; Capaday et al., 2013). Moreover, haptic sensitivity for discriminating between two curved paths of the arm movement was similar between the active and passive reaching movements (Sciutti et al., 2010). Furthermore, a difference in accuracy in the perception of the curved path (Sciutti et al., 2010) and joint angle during the reaching movement (Gritsenko et al., 2007) between the active and passive movements was most pronounced as the movement amplitude increased. These findings indicate that voluntary motor commands for force production and positioning the arm during the active movement might or might not facilitate the estimation of the limb endpoint. However, a recent study (Bhanpuri et al., 2013) has shown that estimation of hand endpoint after an active arm movement was more accurate when a physical contact of the hand to stop the arm movement could be predicted as a consequence of the movement. Hence, the estimation of the endpoint was likely facilitated by not only voluntary motor commands for the arm movement, but also by the expected sensory consequences, i.e., the predictable physical contact in the cited study. Further investigation, however, is needed to address potential effects of voluntary digit movement on sensing relative contact points for execution of dexterous manipulation.

### *Conclusions*

The present errors in somatosensory-motor transformations of relative vertical contact points indicate that voluntary commands responsible for generating digit forces in opposite direction affects the accuracy with which perceived fingertip distance can be

reproduced. We speculate that the CNS implements voluntary motor commands for position and force production as well as predictable sensory consequences for successful sensorimotor transformations required for object manipulation. The extent to which predictable sensory consequences from motor commands for digit position and force underlie accurate force modulation during a dexterous manipulation is the subject of ongoing investigation.

## CHAPTER 4

### PERCEPTION-ACTION COUPLING UNDERLYING CONTROL OF RELATIVE FINGERTIP POSITION

#### INTRODUCTION

Dexterous object manipulation requires fine coordination of digit forces (Johansson and Westling, 1988; Johansson and Flanagan, 2009) and position on an object (Lukos et al., 2007, 2008; Fu et al., 2010, 2011; Zhang et al., 2010; Crajé et al., 2011). It has been documented that when subjects are asked to grasp and lift objects that allow choice of digit placement, they modulate digit forces on trial-to-trial basis to compensate for digit placement variability. It should be noted that digit placement in precision grips often requires placement of the fingertips that are vertically separated, e.g., when the task requires subjects to generate a torque at the onset of manipulation (Fu et al., 2010). This behavior is thought to be critically important for performing dexterous manipulation in a consistent fashion (Fu et al., 2010, 2011). The phenomenon of digit force-position coordination suggests that the central nervous system (CNS) integrates the sense of relative location of digit contact points with motor commands responsible for distributing forces among the digits. However, the mechanisms underlying digit position-force coordination for dexterous manipulation remain unclear.

To investigate the sensorimotor transformations of digit position required for dexterous manipulation, our previous studies examined how accurately subjects could reproduce the sensed and remembered relative vertical distance between the center of pressure (CoP) of thumb and index finger pads with a negligible digit force production (Shibata et al., 2013). It was found that the reproduced relative digit position was

accurate when sensorimotor transformations occurred with larger vertical fingertip separations, within the same hand, and at the same hand posture. A follow-up study examined the sensorimotor transformations using the same digit position-matching task while generating forces in different directions (Shibata et al., in review). This study revealed that subjects reproduced the thumb CoP higher than the index finger CoP when vertical digit forces were directed upward and downward, respectively, and vice versa. Thus, the motor commands responsible for vertical digit forces produced in the opposite direction may bias the sensed relative digit position toward the direction of force production. Overall, these studies were instrumental in identifying factors that influence the accuracy of sensorimotor transformations responsible for digit position control.

However, the matching task protocols used in the previous psychophysics studies did not involve actions that are normally required in dexterous manipulation, i.e., static force application onto an object followed by a dynamic phase, e.g., object translation or rotation. Furthermore, there were distinct sensing and matching phases separated by a 10-second resting phase in our previous matching tasks. Thus, subjects were required to sense and retain memory of digit position during the sensing phase, and retrieving remembered digit placement to reproduce it during the matching phase. Object manipulation, however, involves a transition characterized by a short delay of few hundred milliseconds from initial object contact to vertical force production for object lifting (for review see Johansson and Flanagan, 2009). Therefore, tasks such as object lifting can be performed through concatenated sequential actions, i.e., contact, static force production, estimation of relative digit position, and modulation of forces to lift. Thus, for the task to be performed successfully, within a single object lift these actions require



integrating sensed relative digit position for digit force production without having to recall remembered digit position. When digit placement is not constrained by the task or experimenter, trial-to-trial variability of digit placement requires accurate sensing of digit position for appropriate force modulation (Fu et al., 2010, 2011). Therefore, to further understand the sensorimotor integration mechanisms underlying this phenomenon of digit force-position coordination, it is important to examine subjects' ability to sense the relative digit position within a single object lift without memory recall, and their ability to modulate forces in the context of a grasp-lift task performed at different digit relative positions.

Another major difference between the previous psychophysics and object manipulation studies is whether a limb is moved voluntarily or passively to a target location. Psychophysics studies generally require subjects to indicate the sensed limb position after their limb was *passively* placed to a given position by an experimenter or an apparatus. However, in object manipulation subjects *actively* place their digits on the object for its manipulation. The effects of execution of voluntary movement to the sense of limb position have been studied using reaching movements. It has been shown that estimation of limb endpoint after active reaching movements is more accurate than after passive reaching movements (Adamovich et al., 1998; Gritsenko et al., 2007; Bhanpuri et al., 2013). Furthermore, predictable sensory consequence of active movements appears to benefit limb position sensing. Specifically, a recent study has shown that a predictable physical contact of the hand after an active arm movement results in an accurate estimation of hand endpoint (Bhanpuri et al., 2013). Conversely, the estimation of limb endpoint was less accurate when contact could not be predicted due to passive arm

movement or a perturbation during the active movement. Hence, not only the active arm movement, but also the corresponding sensory consequences (i.e., the predictable physical contact in the cited study) may facilitate subjects' ability to estimate limb endpoint.

It has been proposed that a copy of motor commands for active movement is used to predict sensory consequences of motor actions through internal forward models, which are then compared with incoming sensory afferent signals to estimate sensory state in the immediate future (Wolpert et al., 1995; Kawato, 1999). In object manipulation, active digit positioning and sensory consequence of digit contact with the object surface can be predicted. This phenomenon may facilitate sensing a relative digit position and subsequent manipulative actions. However, the extent to which voluntary motor commands for active digit placement influences perception-action coupling, i.e., the relation between sensing relative digit position and force modulation, remains to be investigated.

The present study was designed to address the above gaps between psychophysical and object manipulation studies by quantifying subjects' ability to estimate index fingertip position relative to the thumb while grasping an object to lift it while minimizing its object roll. We designed two experiments to isolate the perceptual component from the perception-to-action continuum (Perception and Action tests). Furthermore, for each study we addressed the question of whether active digit placement improves accuracy of perception of digit placement as well as force modulation as a function of digit placement. This question was addressed by having subjects' digits placed on the object either actively or passively by an experimenter. We hypothesized

that 1) subjects would discriminate the relative digit position more accurately after active than passive digit placement, and 2) digit forces would be more accurately modulated as a function of the digit position in the active than passive condition. The hypotheses are based on the above studies of reaching movements that showed more precise estimation of arm endpoint after active than passive arm movement (Adamovich et al., 1998; Gritsenko et al., 2007; Bhanpuri et al., 2013).

## **MATERIAL AND METHODS**

### *Subjects*

Fifteen right-handed healthy volunteers (10 males and 5 females, mean  $\pm$  SD:  $23.4 \pm 5.8$  yrs.) participated in this study. All subjects were classified as right-handed based on the mean Laterality Quotient and standard deviation ( $80.8 \pm 14.1$ ) based on the 10-item Edinburgh Handedness Inventory (Oldfield, 1971). All subjects were naïve to the purpose of the study. Subjects gave their written 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.

### *Apparatus*

A custom-made grip object was used to measure digit forces and center of pressure (CoP) of the thumb and index finger pad (Fig. 4.1B). The sensorized object has been described in detail elsewhere (Fu et al., 2010; Shibata et al., 2013). Briefly, two six-component force/torques sensors were mounted on each side of the object (ATI Nano-25 SI-125-3, ATI Industrial Automation, Garner, NC; force range: 125, 125, and 500 N for  $x$ -,  $y$ - and  $z$ -axes, respectively; force resolution: 0.06 N; torque range: 3000 N•mm; torque resolution: 0.378 N•mm; Fig. 4.1B). The vertical coordinate ( $y$ ) of the CoP of each digit

on the contact surface was computed from the force-torque sensor output. To prevent the digits from slipping when subjects applied tangential forces, the contact surfaces of the handles were covered with 100-grit sandpaper (static friction coefficient range: 1.4-1.5). The location of center of mass of the object was adjusted by adding a mass (400 g) in the slot at the base of the object on the index finger side (Fig. 4.1B). The total mass of the object was 915 g. This additional mass created an asymmetrical mass distribution and introduced a torque on the frontal plane of 230 N·mm towards the index finger. This sensorized object was used for all experiments described in the present study. Object position was recorded using an active marker 3D motion capture system (PhaseSpace: frame rate 480 Hz; spatial accuracy: ~1mm; spatial resolution: 0.1 mm) with eight cameras. Two markers were placed on the lateral extremities of the object (green dots, Fig. 4.1B).

### *Experimental Procedures*

*Perception test.* Subjects grasped the object with the thumb and index fingertip of the right hand while sitting an adjustable chair with both forearms resting on a table or foam cushion (Fig. 4.1A). The left hand rested on the table throughout the experiment with all digits straight, adducted, and in a pronated position. Vision of the right forearm, hand, and object was prevented by a board placed between the right arm and a computer monitor (Fig. 4.1A). The positioning of the object, monitor, and board was adjusted for each subject so that subjects' digits could be placed on the object in a comfortable posture.

We used a two-alternative force-choice paradigm. Subjects had to report whether the index finger CoP was higher or lower than the thumb CoP. Four relative vertical

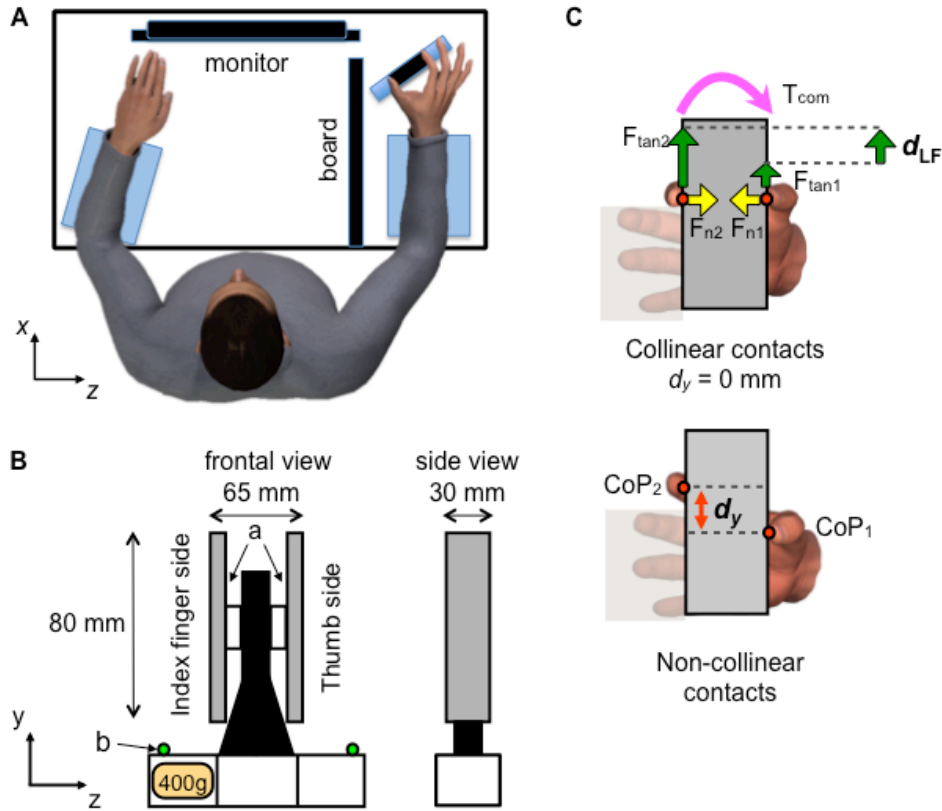


Figure 4.1. Experimental setup.

A: Top view of the experimental setup. The subject is shown contacting the handle with the right thumb and index fingertip, while the left hand is kept flat on the table. When relaxing in between trials, both hands were kept flat and relaxed. Note that the board was placed such as to prevent subjects from seeing their right forearm and hand. Foam cushions were placed underneath the forearms and wrist for subjects' comfort. B: Frontal and side views of the grip device; "a" and "b" denote force/torque sensors and active markers for motion tracking, respectively. A mass (400 g) was added to the slot at the bottom of the device on the index finger side. C: Frontal views of the object. The top and bottom figures show thumb and index fingertip center of pressure (CoP; red circles) of the reference hand located at the same or different  $y$ -coordinates (collinear and non-collinear contacts), respectively. The vertical distance between thumb and index fingertip CoP is denoted by  $d_y$ . The top figure also shows normal and tangential forces generated by the digits ( $F_n$  and  $F_{tan}$ ) and the torque generated by the digits ( $T_{com}$ ) to compensate the torque caused by the object's asymmetrical mass distribution.

distances between the digits were used (blue box, Fig. 4.2A). When subjects actively placed their digits on the object, feedback of the relative fingertip position (vertical distance between fingertips,  $d_y$ ) was shown as a dot on the computer monitor. Subjects were required to move the dot to the target area by adjusting digit position (“*active  $d_y$  adjustment*” phase; Fig. 4.2B). Specifically, we adjusted the gain used to display the cursor movement for each target  $d_y$  such that the excursion of the cursor was always the same regardless of the actual  $d_y$ . Thus, subjects could not extract information about the relative digit position from visual feedback of the cursor. This visual feedback of digit position was removed when subjects’ digits were passively placed on the grasped object by an experimenter at the designated target digit positions (“*passive  $d_y$  adjustment*” phase, Fig. 4.2B). After the active or passive digit placement, we asked subjects to sense the  $d_y$  while making a slight contact with the vertical surfaces of the grip device (“*contact and sense*” phase; Fig. 4.2B). The same monitor that provided feedback of the digit position was used to provide feedback of digit forces. Once an experimenter visually confirmed compliance of the desired hand posture and  $d_y$ , subjects were given a verbal cue to generate digit forces. Specifically, subjects were asked to exert negligible normal and tangential forces with each digit (0.5-1 N and  $0 \pm 0.25$  N, respectively; Fig. 4.2A). After sensing the  $d_y$  for 2 seconds, subjects were asked to verbally report whether the index finger CoP was higher or lower than the thumb CoP (“*verbal response*” phase; Fig. 4.2B). Subjects released their digits after providing an answer, and then rested and prepared for the following trial.

*Action test.* For this test we asked subjects to grasp and lift the same sensorized object used for the Perception test with the thumb and index finger. Similar to the

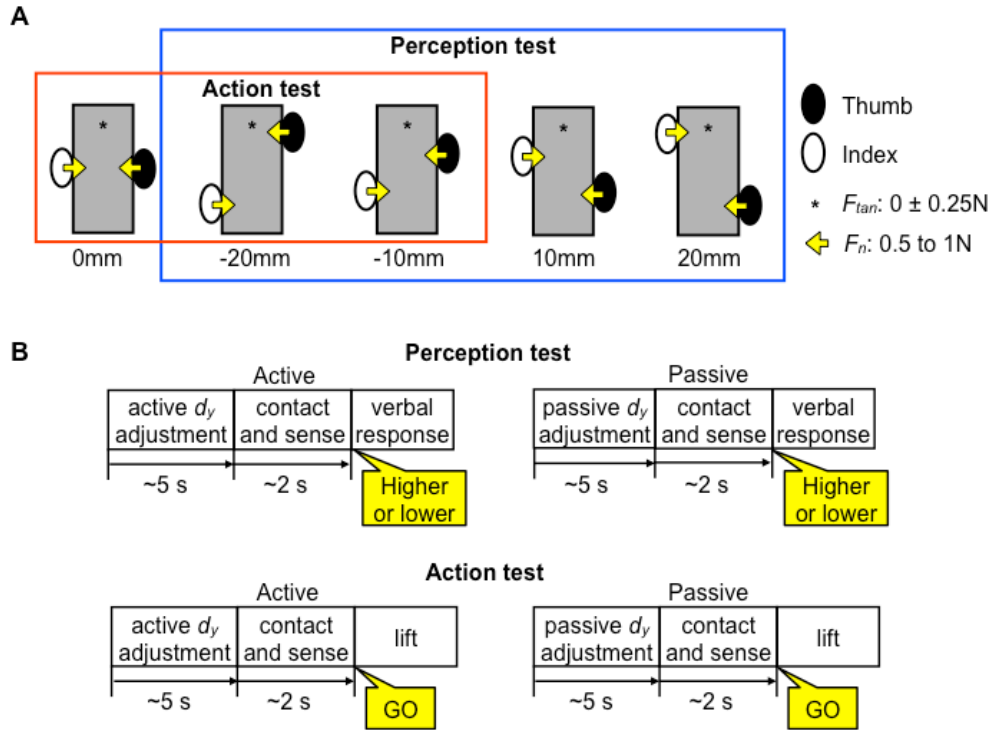


Figure 4.2. Experimental conditions and protocol.

A: Relative digit positions and force requirements for Perception and Action tests. We tested four relative digit positions ( $d_y = -20, -10, 10, \text{ and } 20 \text{ mm}$ ) for the Perception test (blue box), and three positions ( $d_y = 0, -10, -20 \text{ mm}$ ) for the Action test (red box). Subjects were asked to exert negligible tangential and normal digit forces. B: Time course of the experimental protocols. In the “*passive  $d_y$  adjustment*” phase of the Perception and Action tests, the subject’s thumb and index fingertip were passively placed by an experimenter to a given digit position. In contrast, subjects actively placed their digits to a given digit position in the “*active  $d_y$  adjustment*” phase of the Perception and Action tests. Once the desired  $d_y$  and target digit forces were reached, subjects were asked to sense  $d_y$  while maintaining the digit contacts and forces for about 2 seconds (“*contact and sense*” phase). In the Perception test, subjects were cued too verbally report whether the index finger CoP was higher or lower than thumb CoP (“*verbal response*” phase). In the Action test, a “GO” signal was given to subjects to lift the object while preventing it from tilting (“*lift*” phase).

Perception test, vision of the right forearm, hand, and object was prevented by a board placed between the right arm and a computer monitor (Fig. 4.1A). Each trial started with active or passive  $d_y$  adjustment (“*active  $d_y$  adjustment*” or “*passive  $d_y$  adjustment*” phase, Fig. 4.2B; three  $d_y$ s, red box Fig. 4.2A). We then asked subjects to sense the  $d_y$  while maintaining the given  $d_y$  with negligible forces (Fig. 4.2A) for about 2 seconds (“*contact and sense*” phase, Fig. 4.2B). The same feedback of digit forces and position as described for the Perception test was provided on the computer monitor for the Action test. Once the experimenter visually confirmed compliance of the desired hand posture and  $d_y$ , a visual ‘GO’ signal was displayed on the monitor to cue subjects to lift the grasped object. We instructed subjects to lift the object vertically to a comfortable height at a natural speed while trying to maintain its vertical alignment, hold it for  $\sim 1$  s, and replace it on the table.

Prior to the Perception and Action tests, all subjects practiced controlling the required digit forces and position, sequence of the Perception and Action tests, and lifting the object while minimizing the object roll at all  $d_y$ . Only in this familiarization phase, visual feedback of object tilt minimization (task performance) in the Action test was given to subjects in order to facilitate learning of the torque to generate at object lift onset necessary to compensate the external torque. After this familiarization phase, the board (Fig. 4.1A) was placed to block vision of hand and object so that subjects needed to perform the lifting task using the haptic feedback only. Feedback of task performance in the Perception test was never given to subjects throughout the experiment including this familiarization phase. This familiarization phase lasted about 30 minutes. For each experimental condition, the order of presentation of  $d_y$  (Perception test:  $-20$ ,  $-10$ ,  $10$ ,  $20$



mm; Action test: -20, -10, 0 mm) was randomized across trials and subjects. Each experimental condition (Active, Passive) in the Perception and Action tests consisted of 24 and 18 trials (6 trials per  $d_y$ ), respectively. The entire experimental session consisted of 84 trials (48 + 36 trials per test) and lasted about 1.5 hr. The presentation of the two tests was counterbalanced across subjects. Within each test, the presentation of experimental conditions was counterbalanced across subjects.

### *Data Processing*

Force and torque data were acquired with a 12-bit A/D converter board (PCI-6225, National Instruments, Austin, TX; sampling frequency: 1 kHz) through a custom data acquisition interface (LabVIEW version 8.0, National Instruments) and stored in a computer for offline analysis. During data collection, force data were filtered online using a moving average filter every 50 samples over the 5-second duration of data recording. The filtered force data were then used for computing and displaying online normal and tangential digit forces and  $d_y$  using LabVIEW.

After data collection, force and position data were temporally aligned off-line with custom-written software (Matlab, The MathWorks, Natick, MA). Analyses focused on the following variables: (1) digit center of pressure (CoP), the vertical coordinates of the CoP of the contact between each finger pad and the graspable surface relative to the center of the sensor (Fig. 4.1C); (2) digit force normal (grip force, GF) and tangential (load force, LF) to the grip surface (Fig. 4.1C); (3) object lift onset, defined as the time at which the vertical position of one of the active marker on the object exceeded the threshold of 2 mm for 5 ms (red dashed line, Fig. 4.3); and (4) object roll, defined as the angle between the gravitational vector and the vertical axis of the grip device, and peak

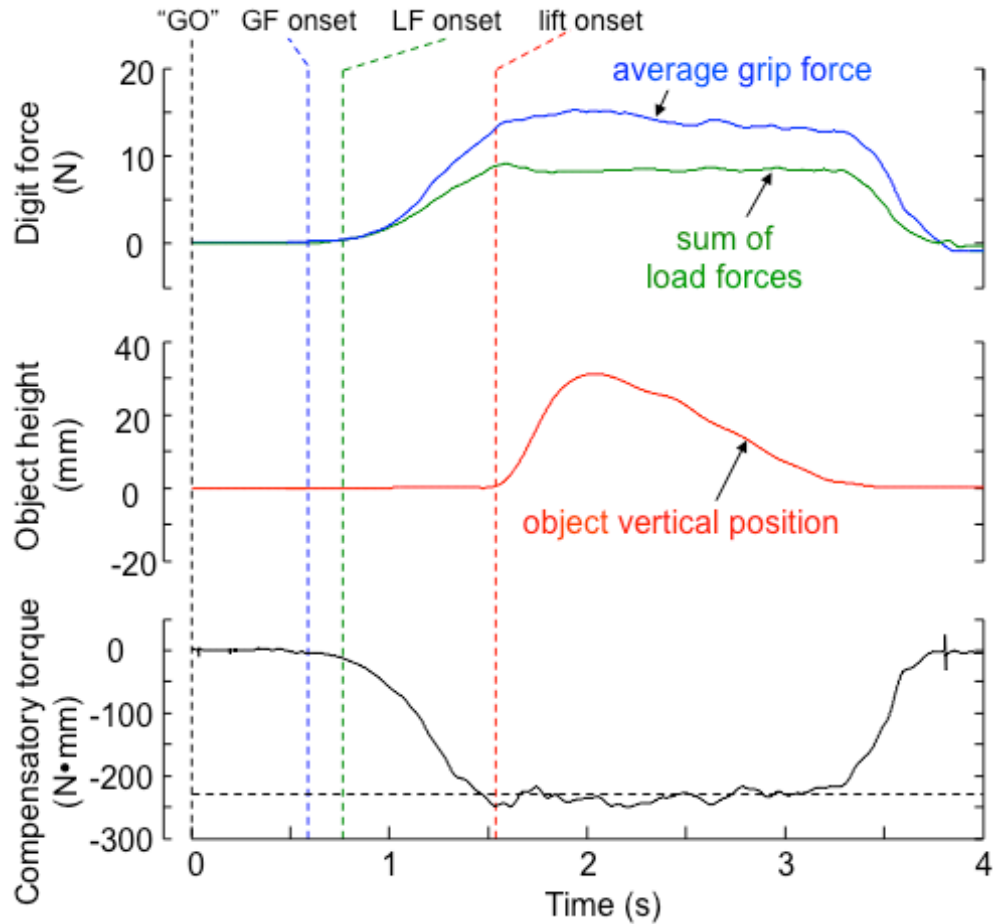


Figure 4.3. Experimental variables and grasp phases.

The time course of the experimental variables and grasp phases are shown for one representative trial. From top to bottom: the blue and green traces denote the grip force averaged across thumb and index fingers and the sum of load forces exerted by the thumb and index finger, respectively; the red trace denotes the vertical height of the object; the black trace denotes the compensatory torque, whereas the dashed horizontal line denotes the target torque subjects had to exert to counter the external torque caused by the added mass at the bottom of the object. The “GO” signal (black dash line) was given to subjects 2 s after the “*contact and sense*” phase (see Fig. 2B) to cue the subject to initiate object lift. The blue, green, and red vertical dashed lines denote the onset of grip and load force, and object lift, respectively (see text for details).

object roll, defined as the peak of object roll occurring shortly (~500 ms) after object lift onset.

Digit forces and CoP were used to compute the following variables: (1)  $d_y$ , defined as the vertical coordinate of thumb CoP minus the vertical coordinate of index finger CoP (Fig. 4.1C); (2) the average of the normal forces of the thumb and index finger ( $F_{GF}$ ) (Fig. 4.1C); and (3) the difference between the tangential forces of the thumb and index finger ( $d_{LF}$ ) (Fig. 4.1C). The combination of these three variables result in compensatory torque ( $T_{com}$ ) generated at object lift onset to counter the external torque caused by the added mass to maintain the object's vertical alignment during the lift (bottom trace, Fig. 4.3; for details see Fu et al., 2010).

GF, LF, and lift onset were used to determine grasp phases (Fig. 4.3). The time at which the GF and LF exceeded the threshold of 0.4 N for 50 ms was defined as GF and LF onset, respectively (blue and green dashed lines, Fig. 4.3). The time between GF onset and LF onset was defined as 'preloading phase', and the phase between the LF onset and lift onset was defined as 'loading phase'.

### *Statistical analysis*

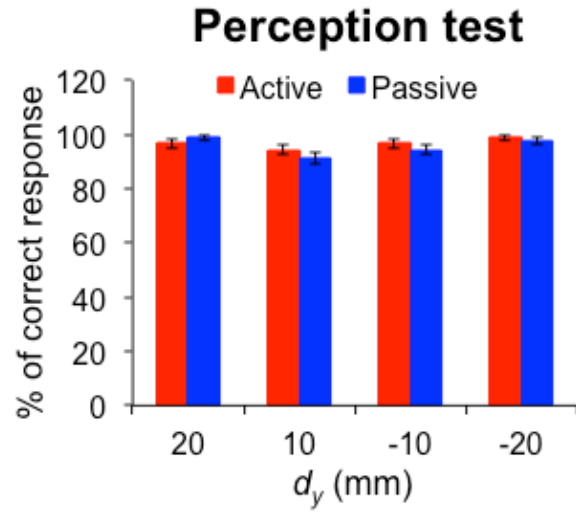
For the Perception test, mean percentages of correct response across subjects per  $d_y$  were analyzed using analysis of variance (ANOVA) with repeated measures within *Condition* (2 levels: Active, Passive) and *Digit position* (4 levels: -20, -10, 10, 20). For the Action test, we performed repeated-measures ANOVA to assess the effects of *Condition* (2 levels: Active, Passive) and *Digit position* (3 levels: -20, -10, 0) on load phase duration across subjects per  $d_y$ . Linear regression analyses were performed to quantify the relation between load force difference ( $d_{LF}$ ) and  $d_y$ , and the average normal

force of the thumb and index finger and  $d_y$  at lift onset over all trials from all subjects. To compute the coefficient of determination ( $R^2$ ), each data point was normalized for each subject by removing the mean of all trials from the value of each trial and dividing the result by the standard deviation of the mean. *Post hoc* tests were run using paired sample *t*-tests with Bonferroni corrections when appropriate. Sphericity assumptions were tested for all analyses (Mauchly's sphericity test). When the sphericity assumptions were violated, we used Greenhouse-Geisser analysis ( $p < 0.01$ ). All tests were performed at the  $p \leq 0.05$  significance level. Values in the text are reported as means  $\pm$  standard error of the mean.

## RESULTS

*Perception test.* A repeated-measures ANOVA on the mean percentages of correct responses across subjects per  $d_y$  revealed no significant difference between the Active and Passive digit placement conditions (no main effect of *Condition*:  $F_{[1,14]} = 52.910$ ,  $p > 0.05$ ; Fig. 4.4). The ability to discriminate relative digit position was high (range: 91-99%, across all the digit position and experimental conditions). Therefore, neither voluntary digit placement nor vertical fingertip distance drastically affected the accuracy with which subjects could perceive relative digit position.

*Action test.* We first examined whether subjects could appropriately modulate digit forces as a function of position at object lift onset as found for self-paced dexterous manipulation tasks (e.g., Fu et al., 2010). There was no difference in variables at lift onset including LF, GF, Tcom, and peak roll between the active and passive conditions (Table 1). Moreover, digit load force difference ( $d_{LF}$ ) and relative digit position ( $d_y$ ) negatively covaried in a similar fashion for the Active and Passive conditions, as indicated by



*Figure 4.4. Perception test: accuracy of correct responses.*

Mean percentages of correct verbal response across all subjects in the Perception test are plotted per vertical center of pressure (CoP) distance ( $d_y$ ). Data are mean values averaged across all subjects (vertical lines denote S.E.).

Table 4.1. Summary of lifting performance variable in the Action test across all subjects

	$F_{GF}$ (N)	$d_{LF}$ (N)	$T_{com}$ (N•mm)	Peak roll (deg)
$dy = 0$				
Active	12.2 ( $\pm 1.2$ )	-5.0 ( $\pm 0.2$ )	-227.7 ( $\pm 4.5$ )	2.0 ( $\pm 0.3$ )
Passive	13.3 ( $\pm 1.4$ )	-5.0 ( $\pm 0.3$ )	-225.8 ( $\pm 3.0$ )	1.5 ( $\pm 0.3$ )
$dy = -10$				
Active	11.3 ( $\pm 1.2$ )	-2.6 ( $\pm 0.3$ )	-222.7 ( $\pm 4.1$ )	1.6 ( $\pm 0.2$ )
Passive	12.2 ( $\pm 1.3$ )	-2.1 ( $\pm 0.3$ )	-223.2 ( $\pm 3.2$ )	1.3 ( $\pm 0.2$ )
$dy = -20$				
Active	10.4 ( $\pm 1.1$ )	-0.1 ( $\pm 0.5$ )	-219.9 ( $\pm 5.7$ )	1.8 ( $\pm 0.2$ )
Passive	11.1 ( $\pm 1.2$ )	0.4 ( $\pm 0.5$ )	-225.0 ( $\pm 4.0$ )	1.3 ( $\pm 0.3$ )

Data are mean values ( $\pm$  S.E.) of average grip force ( $F_{GF}$ ), load force difference ( $d_{LF}$ ), compensatory torque ( $T_{com}$ ), and peak roll of object in degree per vertical distance between digit center of pressure ( $d_y$ ) averaged across all subjects for the Active and Passive conditions.

similar coefficients of determination ( $R^2 = 0.89, p < 0.001$ ; and  $0.88, p < 0.001$ , Active and Passive, respectively, Fig. 4.5A-B). A similar positive correlation between the average grip force ( $F_{GF}$ ) and  $d_y$  was also found for both conditions ( $R^2 = 0.27, p < 0.001$ ; and  $0.37, p < 0.001$ , Active and Passive, respectively; Fig. 4.5C-D). These findings indicate that the accuracy of sensorimotor transformations responsible for modulating digit forces as a function of position was not affected by whether digit placement occurred in an active or passive fashion.

However, the time from the GO signal to object lift onset was longer in the Passive than Active condition. To determine the task phase underlying this result, we examined the duration of preloading phase (from GF onset to LF onset) and loading phase (from LF onset to object lift onset) (Fig. 4.3). We found no significant difference in the preloading phase duration (9 ms on average across subjects;  $t_{[14]} = -0.792; p > 0.05$ ). In contrast, the loading phase duration was consistently longer in the Passive condition by 136 ms and across all digit positions (Fig. 4.6A). A repeated-measures ANOVA on average load phase duration across subjects per  $d_y$  revealed significant difference between the active and passive digit placement (main effect of *Condition*:  $F_{[1,14]} = 12.005, p < 0.01$ ; Fig. 6A), but no significant difference across  $d_y$ s (no main effect of *Digit position*:  $F_{[2,28]} = 0.991, p > 0.05$ ; Fig. 4.6A). A repeated-measures ANOVA on peak grip force rate revealed a significant difference across  $d_y$ s (main effect of *Digit position*:  $F_{[2,28]} = 11.910, p < 0.01$ ), but not between Active and Passive digit placement (no significant effect of *Condition*:  $F_{[1,14]} = 40.723, p > 0.05$ ; Fig. 4.6B). Therefore, the longer load phase duration could not be accounted for by difference in grip force rates. However, we found that subjects develop load force faster in the Active than Passive condition (main

## Action test

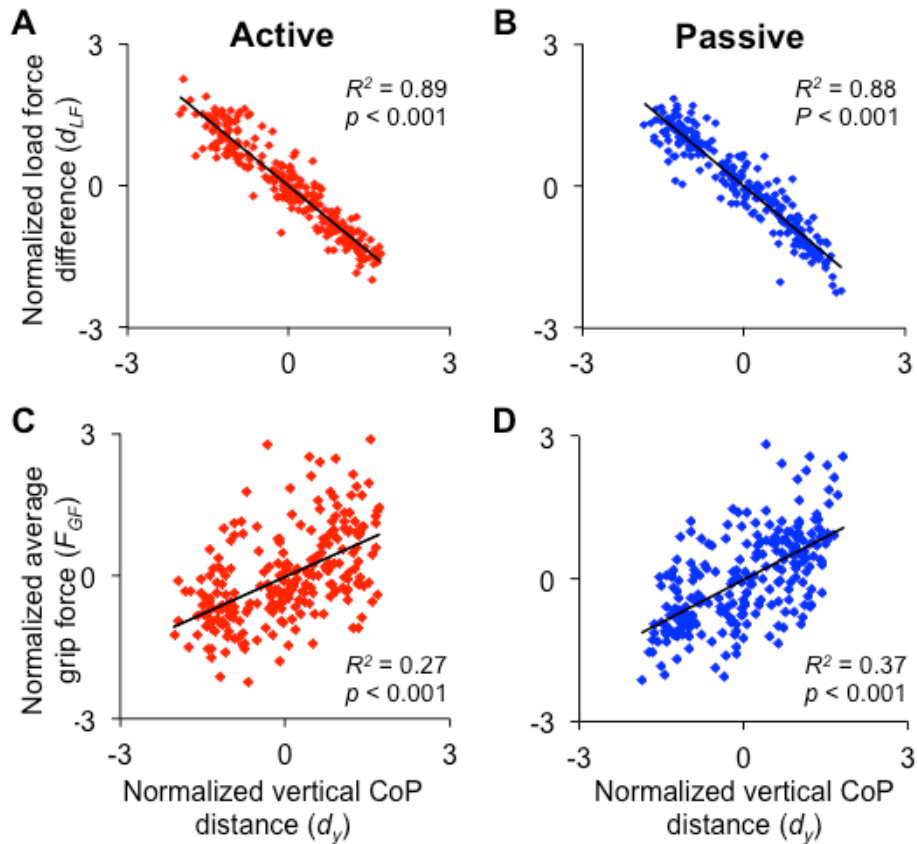


Figure 4.5. Action test: relations between digit forces and center of pressure.

A and B: Correlations between the difference in digit load force ( $d_{LF}$ ) and relative digit positions ( $d_y$ ) for Active and Passive conditions, respectively. C and D: Correlations between average grip force ( $F_{GF}$ ) and  $d_y$  for Active and Passive conditions, respectively. Data from all trials and subjects are plotted for each condition (18 trials  $\times$  15 subjects = 270) and expressed in normalized form (see text for details). Coefficient of determination ( $R^2$ ) and corresponding  $p$  value are shown in each plot.



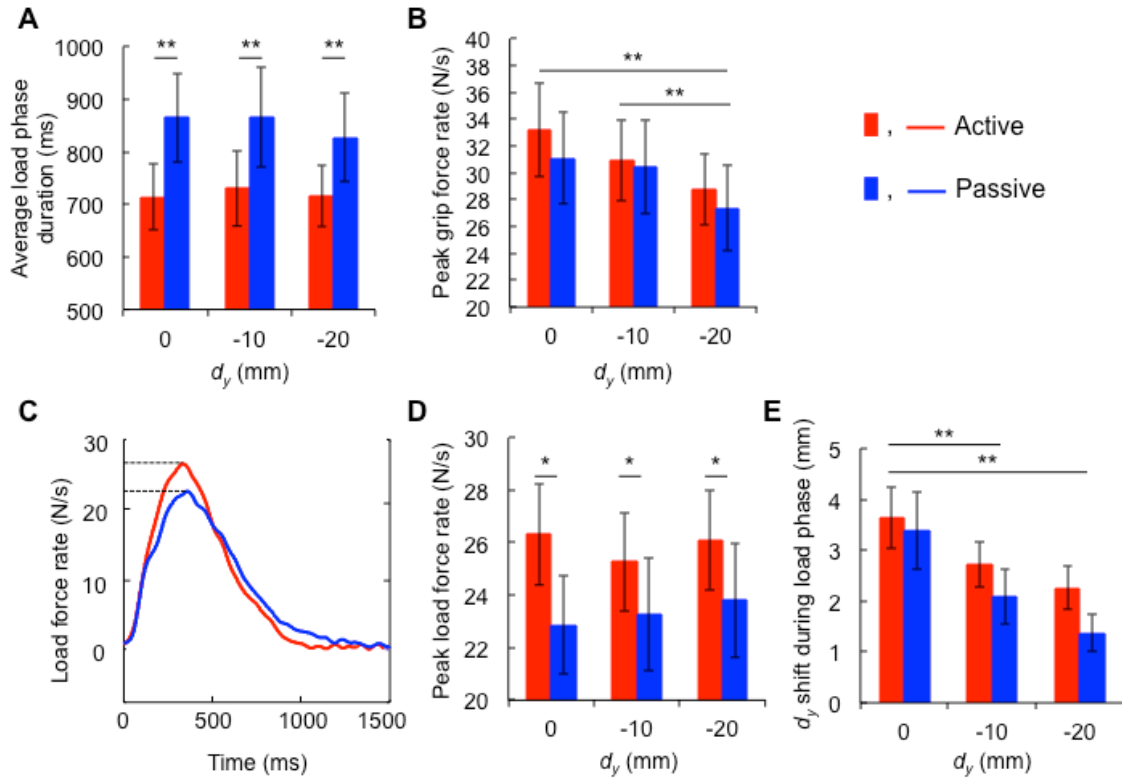


Figure 4.6. Load phase duration, load and grip force rate, and shift in digit center of pressure during load phase.

A: Average load phase duration as a function of initial vertical distance between digits center of pressure ( $d_y$ ). C: Load force rate from a representative trial. The horizontal dashed lines denote peak load force rates. B, D: Average peak load and grip force rate, respectively, as a function of  $d_y$ . E: Shift of  $d_y$  during the load phase as a function of  $d_y$ . Data are mean values averaged across all subjects (vertical lines denote S.E.). Asterisks denote a statistically significant difference (\* and \*\*:  $p < 0.05$  and  $0.01$ , respectively).

effect of *Condition*:  $F_{[1,14]} = 6.568, p < 0.05$ ), but no significant difference across  $d_y$ s (no main effect of *Digit position*:  $F_{[2,28]} = 0.833, p > 0.05$ ; Fig. 4.6C,D).

Lastly, we examined the magnitude of  $d_y$  changes during the load phase to quantify a possible contribution of different amount of skin deformation of the finger pads to the longer load phase duration in the Passive condition. A repeated-measures ANOVA on shift of  $d_y$  during the load phase revealed a significant difference as a function of  $d_y$  (main effect of *Digit position*:  $F_{[2,28]} = 16.587, p < 0.01$ ), but not between the Active and Passive condition (main effect of *Condition*:  $F_{[1,14]} = 1.470, p > 0.05$ ; Fig. 4.6E). Thus, the longer loading phase duration in the Passive condition can be accounted for a lower rate of load force development relative to the Active condition.

## DISCUSSION

The present study was designed to quantify the effects of voluntary motor commands responsible for digit placement on sensing relative digit position and subsequent modulation of digit forces. We found that subjects could accurately discriminate the index fingertip position relative to thumb and modulate fingertip forces to variable digit position regardless of whether they actively positioned their fingertips or had their fingertips passively moved by an experimenter. However, in the passive condition subjects took longer in developing manipulative digit forces as a function of digit placement during the loading phase. Therefore, voluntary digit placement in grasping only affected one component of the perception-action coupling, i.e., the duration of force development, but not the perception of digit position or the subsequent fingertip force scaling. We discuss these results in the context of the role of voluntary motor

commands for digit placement and perception-action coupling required in dexterous manipulation and underlying neural mechanisms.

*Role of active digit movement on estimation of digit relative position and digit force-position coordination*

Active digit placement did not improve accuracy of digit position estimation relative to passive digit placement (Fig. 4.4). This finding does not support our first hypothesis and is not consistent with previous observations that limb endpoint estimation is more accurate after active than passive reaching movements (Adamovich et al., 1998; Gritsenko et al., 2007; Bhanpuri et al., 2013). This finding might suggest task- or effector-specific differences in the extent to which the CNS can estimate the position of the fingertip through voluntary motor commands. Specifically, a major difference between reaching movements and our task is that the proximal component (shoulder and elbow joint rotation) are negligible in our task, thus motor commands are mostly limited to small digit movements at a static hand position (Fig. 4.1A). Therefore, one may speculate that the discrepancy between our result and previous findings from reaching movements may be due to a higher ‘signal-to-noise’ ratio in motor commands involved for large upper limb joint excursion and trajectory control for reaching than small digit movements. However, further work is needed to test this interpretation.

We also found that, contrary to our second hypothesis, the accuracy of digit force modulation to position was the same regardless of whether subjects actively positioned their fingertips or had them passively moved by the experimenter. However, the development of digit forces between contact and object onset occurred over a longer period for the active digit placement condition (Fig. 4.6). Thus, whether digit placement

is actively or passively implemented appears to affect only the time it takes to transform sensory feedback of digit placement into motor commands for scaling fingertip forces to position, but not the accuracy with which digit force is modulated to position. The longer duration of the loading phase in the passive condition could be interpreted as resulting from slower processing of somatosensory feedback in the absence of the contribution of the efference copy of motor commands for digit placement.

A previous study also found that subjects took longer to modulate digit force to position after object contact by ~150 ms when vision of object width was eliminated (Fu and Santello, 2014). In that study, subjects had to exert a torque in response to spatial and temporal accuracy constraints, and visual feedback of object width allowed subjects to anticipate the digit forces necessary to manipulate the object. Similarly to the present study, subjects were able to accurately modulate digit force to position also when object width had to be perceived through somatosensory feedback alone than with visual feedback. The findings from this previous work and the current study point to the CNS' ability to compensate for lack of visually-based control of digit forces through haptic feedback, but also indicate that the former mechanisms allows for the implementation of faster sensorimotor transformations.

*Role of active vs. passive movement for motor control: neural mechanisms*

Whereas the Perception test found no effect of active vs. passive digit placement on fingertip position estimation, the Action test revealed faster sensorimotor transformations for the active digit placement. It has been suggested that sensory processing for perception and action is functionally and anatomically separate. Milner and Goodale (1995) originally proposed two broad streams of projections from the visual

cortex: a ventral stream projecting to the infero-temporal cortex and a dorsal stream projecting to the posterior parietal cortex. Visual information processed through the ventral stream would be used to recognize and discriminate a stimulus as well as preparing an appropriate action, thus called 'vision for perception'. However, the subsequent implementation of that action would be processed in the dorsal stream, thus called 'vision for action'. The dorsal stream would therefore play a significant role in programming and controlling skilled movements needed to carry out the action based on visual information. Dijkerman and de Haan (2007) proposed this scenario of separate visual processing streams for somatosensory processing. A neuroimaging study using functional magnetic resonance imaging has shown that cortical regions of somatosensory processing associated with perception *per se* are different from those associated with action (Reed et al., 2005). Specifically, when subjects were asked to localize the stimulus by moving the hand, bilateral superior parietal areas were activated. In contrast, when subjects were asked to recognize a stimulus presented on their hand without a movement, frontal and inferior parietal areas were activated. Furthermore, it has been suggested that the latter processing for perception *per se* may involve in the insula, an area involved with tactile object recognition (Olausson et al., 2002; Craig, 2003; Reed et al., 2005; Dijkerman and de Haan, 2007). Therefore, the differential effects of active versus passive digit placement on perception and action may be accounted for by a parallel processing of haptic feedback: one mostly involved with perception, e.g., estimation of relative digit position, and another for action, e.g., integration of haptic feedback for force modulation to sensed digit position.

When proprioception is selectively engaged in estimating finger position, active finger movements were associated with greater activation of contralateral primary sensorimotor cortex (SI), premotor cortex, bilateral secondary somatosensory cortex (SII), basal ganglia, and ipsilateral cerebellum compared with passive finger movements (Mima et al., 1999). Thus, proprioceptive feedback together with voluntary motor commands appears engage cortical and subcortical activity to a greater extent than proprioceptive feedback alone. Note that our experimental task involved active or passive touch with the object. It has been proposed that tactile feedback elicited by touch is integrated with proprioceptive feedback for accurate estimation of fingertip position relative to the body during a reaching task (Rincon-Gonzalez et al., 2011). Although our task did not require estimation of fingertip position in a body-frame of reference, it is conceivable that grasp-to-lift task might have benefited from the integration of proprioceptive and tactile feedback. A brain mapping study (Simões-Franklin et al., 2011) reported that when subjects were asked to discriminate the roughness of a surface through active touch, this exploratory movement elicited greater activity in SI, basal ganglia, and cerebellum than when the finger was passively moved across the surface. Therefore, in our study active digit placement prior to lifting an object might have engaged these brain areas to a greater extent than during passive digit placement.

It has been suggested that the cerebellum is involved in an active movement to predict sensory consequences using an efferent copy of motor commands for the movement (Wolpert et al., 1998). Recent behavioral evidence from Bhanpuri and colleagues (2013) is consistent with this theoretical framework. Specifically, subjects could accurately estimate the end point of active limb movement when a physical contact

with the limb was predictable, whereas cerebellar patients did not benefit from active movement to the same extent as healthy controls (Bhanpuri et al., 2013). Moreover, the accuracy of limb endpoint estimation for unpredictable movement outcomes was similar across the two groups. These findings suggest that the cerebellum uses predictive sensory feedback through internal forward models by comparing the proprioceptive feedback during voluntary movement. A major difference with this study is that proprioceptive and tactile feedbacks are present in our active and passive conditions. Furthermore, both conditions resulted in similar digit positions and fingerpad deformation, thus eliciting similar proprioceptive and tactile inputs, respectively, as suggested by similar estimation errors in the active and passive condition (Figs. 4.4, 4.6E). Therefore, we speculate that subjects could predict the relative digit position through internal forward models in the cerebellum following active but not passive digit placement. This predicted digit position might be readily available to be integrated for appropriate digit force production as a function of the digit position in order to lift an object. As noted above, removal of this predictive component would be detrimental only to the time it takes to process somatosensory feedback of digit placement, but not fingertip force scaling to position.

### *Conclusions*

The present study revealed that, regardless of whether digit placement on an object is actively or passively implemented, subjects can successfully discriminate relative fingertip position and modulate manipulative forces accordingly using somatosensory feedback only. However, force development from contact to the onset of manipulation took longer in the absence of voluntary motor commands for digit placement. We speculate that passive and active digit placement engage different neural

mechanisms and brain areas. Prediction of sensory consequences associated with active digit placement might account for faster sensorimotor transformations of haptic feedback into fingertip force modulation to position.



## CHAPTER 5

### SUMMARY AND CONCLUSIONS

#### GENERAL FINDINGS

Humans are able to modulate digit forces as a function of position for object manipulation despite digit placement variability that might occur from trial to trial or when changing grip type. Although this phenomenon suggests that the CNS relies on the integrations of sensing relative digit position with motor commands responsible for active digit placement and force production, we have a limited understanding of the underlying mechanisms. The purposes of this dissertation were to provide behavioral data for understanding humans' ability to sense digit position and integrate it with motor commands for digit force modulation for dexterous manipulation.

#### *Haptic-motor transformations for the control of vertical fingertips distance*

To understand the extent to which humans can sense the distance between fingertips in contact with an object, we quantified subjects' ability to match perceived vertical distance between the thumb and index finger pads ( $d_y$ ) of the right hand ("reference" hand) using the same or opposite hand ("test" hand) after a 10-second delay without vision of the hands in Study #1 (Chapter 2). The reference hand digits were passively placed non-collinearly so that the thumb was higher or lower than the index finger ( $d_y = 30$  or  $-30$  mm, respectively) or collinearly ( $d_y = 0$  mm). Subjects reproduced the reference hand  $d_y$  by using a congruent or inverse test hand posture while exerting negligible digit forces onto an object. We found that matching error (reference hand  $d_y$  minus test hand  $d_y$ ) would be greater (a) for collinear than non-collinear  $d_y$ s (Fig. 2.4A), (b) when reference and test hand postures were not congruent (Fig. 2.4B), and (c) when

subjects reproduced  $d_y$  using the opposite hand (Fig. 2.4B). The  $d_y$ s were underestimated when the postures of reference and test hand were not congruent, and when the opposite hand was used as test hand (Fig. 2.6A, 2.6B). These findings indicate that sensed finger pad distance is reproduced less accurately (1) when sensorimotor transformations involve transferring memorized feedback of fingertip distance to the contralateral cerebral hemisphere, and (2) when higher-level processing of the somatosensory feedback might be required to transform sensory feedback obtained at a given posture into motor commands to the hand in a different posture. We propose that erroneous sensing of finger pad distance, if not compensated for during contact and onset of manipulation, might lead to manipulation performance errors as digit forces have to be modulated to sensed digit placement.

#### *Biased sensorimotor transformations for the control of fingertip position*

To further understand the extent to which voluntary motor commands responsible for digit force production influence sensorimotor transformations for the control of relative digit position, for Study #2 (Chapter #3) we used a similar protocol used for Study #1. Briefly, we asked subjects to match sensed  $d_y$  of the right hand (“reference” hand) using the same hand (“test” hand) after the digits were passively placed collinearly. Subjects were then asked to exert different combinations of normal and tangential digit forces ( $F_n$  and  $F_{tan}$ , respectively) using the reference hand and then match the memorized  $d_y$  using the test hand. Thumb and index finger of the reference hand exerted  $F_{tan}$  in the same or opposite directions. For the test hand, digit forces were either negligible ( $0.5-1$  N,  $0 \pm 0.25$  N) or the same as those exerted by the reference hand. We found that matching error was biased towards the direction of digit tangential forces:

thumb CoP was placed higher than the index finger CoP when thumb and index finger  $F_{tan}$  were directed upward and downward, respectively, and vice versa (Fig. 3.5).

However, matching error was not dependent on whether the reference and test hand exerted similar or different forces. We propose that the expected sensory consequences derived from a copy of voluntary motor commands for tangential digit forces in opposite directions overrides estimation of fingertip position through haptic sensory feedback.

#### *Differential effects of voluntary digit placement on perception vs. action*

In Study #2 and #3, subjects' digits were passively placed to control for possible contributions of voluntary movement to the digit position sensing. Moreover, the remembered digit position was reproduced after a 10-s resting phase between sensing and matching phases. This delay between sensing and using memorized feedback of digit placement requires subjects to store and later retrieve sensed digit position. However, dexterous manipulation normally involves a very short delay (a few hundred milliseconds) from initial object contact to vertical force production for object lifting. Therefore, in Study #3 (Chapter 4) we investigated the extent to which motor commands responsible for active digit placement may affect estimation of relative digit placement and sensorimotor transformations underlying digit force-position coordination. In two different experiments, we asked subjects to estimate the index fingertip position relative to the thumb (Perception test) or grasp and lift an object with an asymmetrical mass distribution while preventing object roll (Action test) without visual feedback of the hand and object. Both Perception and Action tests were performed after subjects' digits were placed actively at different relative distances by the subjects (Active condition) or passively by an experimenter (Passive condition). We found that subjects could

discriminate the relative digit position equally well in the Active and Passive conditions (correct response: > 90%; Fig. 4.4). Furthermore, subjects could minimize object roll by modulating digit forces as a function of digit position in both Active and Passive conditions ( $r^2 = 0.89$  and  $0.88$ , respectively; Fig. 4.5). However, the time between load force onset and object lift-off was longer in the Passive than Active condition (Fig. 4.6A). We conclude that estimation of fingertip relative position and force-position coordination can still be accomplished in the absence of voluntary commands for positioning the digits on the object. Therefore, we speculate that sensory feedback and voluntary commands associated with force production from contact to onset of manipulation might play a greater role in enabling force-position coordination.

#### **FUTURE WORK**

The findings of Study #2, where the matched digit position was biased toward the direction of tangential digit forces when exerted in opposite directions, revealed a strong contribution of motor commands associated with force production to the accuracy of sensorimotor transformations. However, it is unclear yet to what extent skin deformation of the finger pads may contribute to biasing sensorimotor transformations since digit force production and skin deformation were coupled. Specifically, when tangential digit forces were exerted in the opposite direction, the finger pads were also deformed in opposite directions, thus tactile afferent signals might have contributed to bias the perception of fingertip distance. Thus, we could not rule out potential contributions of the skin deformations to the biased digit position.

It has been documented that the combination of tactile and proprioceptive feedback provides an accurate estimation of the fingertip relative to the body during a

reaching task (Rincon-Gonzalez et al., 2011). Furthermore, perceptual bias of a joint angle is greater when only motor commands are available following anesthesia and paralysis (Gandevia et al., 2006) than when motor commands and afferent signals are available while muscles are paralyzed (Smith et al., 2009). These findings suggest that voluntary motor commands and tactile feedback may interact each other to estimate relative digit position.

This possible contribution of tactile feedback through skin deformation may be tested using a haptic device that generates compressive and shear forces onto the finger pad. With this device, skin deformation of the finger pad only could be induced without digit force application onto an object surface. Thus, skin deformation can be decoupled from voluntary motor commands. As shown in the previous studies, tactile feedback through skin deformation may affect subjects' ability to sense and match relative digit position. By using such a haptic device, one would verify the contributions of motor commands to the biased digit position found in Study #2.

This dissertation focused on and provided human behavioral data for understanding humans' ability to sense digit position and integrate it with motor commands for digit force modulation. However, neural circuits underlying the sensorimotor transformations for dexterous manipulation remain unclear. Functional magnetic resonance imaging (fMRI) could be used to provide anatomical evidence what brain regions are involved in our matching (Chapter 2 and 3) and lifting tasks (Chapter 4). One advantage of using fMRI over other techniques such as transcranial magnetic stimulations is the ability to access structures such as basal ganglia and cerebellum. In Study #3 (Chapter 4), we speculate that the active digit placement may elicit distinct

activation of these subcortical regions to process somatosensory feedback for digit force modulation as a function of digit position, resulting in a quicker force development compared to the passive digit placement. This speculation could be verified using fMRI to provide physiological data for further understanding the mechanisms underlying digit position-force coordination.

Lastly, it may be possible to extend findings of the sensorimotor integration of two contacts of the digits on an object to that of two contacts of two feet on the ground for maintaining balance. To maintain balance, the center of gravity of the body needs to be located over the base of support, both of which should be accurately sensed through multi sensory feedback. Somatosensory feedback through the lower extremities is crucial to sense mass distribution over the base of support and integrate it with visual and vestibular feedbacks to maintain balance. Without an accurate estimation of the relative location of the center of pressure of the feet, the projection of the center of gravity of the body on the base of support may not be appropriately adjusted to a given task e.g., postural adjustments during standing or gait. Further experiments are needed to address the extent to which the findings from our findings about the ability to integrate the sensed relative digit position for the force modulation in object manipulation may generalize to other sensorimotor effectors.

## **CONCLUSIONS**

This dissertation extends previous knowledge about humans' ability to sense joint and limb position by provides new insights about sensorimotor transformations underlying sensing and reproducing relative digit position for grasping and manipulation.

Skin stretch of the dorsal area of the hand induced by vertical digit separation in the non-collinear digit position might produce higher signal-to-noise ratio of afferent signals compared to a collinear digit position. However, high-level processing of digit position feedback appears to affect sensorimotor transformations' accuracy, e.g., when sensory feedback has to be transferred across cerebral hemispheres and using a hand posture that differs from that used to sense fingertip distance.

After making contact with an object, digit forces must be produced to manipulate it. Voluntary motor commands responsible for digit force production appears to play a critical role in biasing sensorimotor transformations in a directional manner. The data presented here suggest that a copy of voluntary motor commands might be used for predicting sensory consequences associated with digit forces that would increase fingertip vertical distance and override the estimation of digit position based on haptic feedback.

Furthermore, voluntary motor commands responsible for placing the digits on an object seem to facilitate sensory transformations of haptic feedback through object contact into digit force modulation for dexterous manipulation. Conversely, in absence of voluntary motor commands for positioning the digits, subjects exert digit forces accurately but such forces develop over a longer time period. Therefore, active digit placement appears to facilitate the time required by sensorimotor transformations responsible for modulating digit forces to position in reach, grasp, and lift tasks.

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APPENDIX A

IRB APPROVALS AND HUMAN SUBJECTS CONSENT FORMS

## SUBJECT CONSENT FORM

### Collaborative Research: Sensory Integration and Sensorimotor Transformations for Dexterous Manipulation

*SCHOOL OF BIOLOGICAL AND HEALTH SYSTEMS ENGINEERING,  
ARIZONA STATE UNIVERSITY*

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#### **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<sup>1</sup>), Dr. Veronica Santos, Ph.D. (Assistant Professor<sup>2</sup>), Dr. Pranav Parikh, Ph.D. (Postdoctoral Research Associate<sup>1</sup>), Qiushi Fu, Ph.D. (Postdoctoral Research Associate<sup>1</sup>), Dr. Alycia Gailey Ph.D. (Postdoctoral Research Associate<sup>1</sup>), Daisuke Shibata, M.S. (Graduate Student<sup>3</sup>), Dr. Michael De Gregorio, Ph.D. (Research Assistant<sup>2</sup>), Keivan Mojtahedi (Graduate Student<sup>1</sup>), Juan Laitano (Graduate Student<sup>1</sup>), Nathan Gaw (Graduate Student<sup>1</sup>), Saba Rezvani (Graduate Student<sup>1</sup>), Edoardo Battaglia (Graduate Student<sup>1</sup>), Juan Soto (Undergraduate Student<sup>1</sup>), Chris Zeigler (Undergraduate Student<sup>1</sup>), and Katie Hemphill (Undergraduate Student<sup>1</sup>) have invited your participation in a research study.

<sup>1</sup>School of Biological and Health Systems Engineering, <sup>2</sup>Department of Mechanical and Aerospace Engineering, <sup>3</sup>Kinesiology program

#### **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 one or multiple experimental conditions described below:

(1) You may be asked to grasp a light-weight object (less than 2 pounds) with one or two hands 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 fingers are placed over target areas. You may be asked to come back for the second session with similar task requirements. The time between two sessions varies from several minutes to days.

(2) You may be asked to cooperate with another subject or experimenter to lift objects (less than 5 pounds) up from the table. The two of you will then make simple actions when holding the object together (5-80 seconds), such as keeping balance, translation, and rotation, etc. You may be asked to come back for the second session with similar task requirements. The time between two sessions varies from several minutes to days.

(3) You may 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.

(4) You may be asked to attach your fingers to the ends of one, two, or three-hinge linkage system to control virtual objects displayed on a computer monitor. The linkage system can exert a movement on the object in any direction (up/down, forward/backward, and side-to-side). 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.

(5) You may be asked to wear multiple wearable devices 'ThimbleSense' on your fingers while performing the aforementioned object grasping tasks. The device consists of a pair of thin metal shells that are assembled around a small force sensor. You will be wearing latex finger gloves covered with Velcro, which are then attached to the inside Velcro surface of the inner shell which allows a stable fixation on fingertips. The outer shell of the device allows contact with grasped objects, with an external coating improving friction and making the contact compliant.

(6) Certain properties of the object may be changed (such as center of mass, weight, or texture).

(7) You may be asked to close your eyes during portions of the experiment, including times in which you reach to and grasp the objects. 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.

(8) For some of the experiments, surface electromyography (EMG) will be used to measure the muscle activity from four hand muscles. This will allow investigation of muscle coordination patterns during manipulation tasks. For EMG, you will be prepped for the application of surface EMG electrodes. This process begins by cleaning the areas that the electrodes will cover using an alcohol pad. Once the target regions are clean, the electrodes will be applied. During application, you may be asked to flex their hand in various ways to help in the identification of the appropriate muscles.

(9) For some instances, the grip strength will be measured using a pinch meter. You will be instructed to squeeze this meter with maximum strength.

(10) Your hand and arm movements during each experimental session might be videotaped for the purpose of data and movement analysis.

Experiments will be performed at the PEBE building in room 171 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 300 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. The potential risks are highlighted below. However, as with any research, there is some possibility that you may be subject to risks that have not yet been identified.

(1) 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 in some cases your fingers 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 to protect yourself from potential discomfort, pain, or injury.

(2) Removal of surface EMG electrodes at the end of the experiment may cause some discomfort, which will not last more than a few min.

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(3) The metal cylindrical object you will be lifting 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.

(4) When you are wearing the 'ThimbleSense' on your fingers for long experiment sessions, you may experience some minor numbing on fingertips or fatigue with your fingers. The numbness is caused by the tight finger gloves you wear on the fingertips. You are free to take them off to protect yourself from potential discomfort, pain, or injury. The numbness should not last more than 10 minutes after you take off the finger gloves.

#### **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 you will be paid based on total time of participation (see payment). Furthermore, 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.

#### **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**

If you are not considering getting extra credits for your participation in the research, you will be eligible for monetary compensation. You will be paid \$5 for every 30 minutes spend in the laboratory.

#### **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, Arizona State University, (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 \_\_\_\_\_

APPENDIX B

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## **PERMISSIONS FROM MANUSCRIPT COAUTHORS**

Mr. Jason Choi and Juan Laitano, coauthors of “Haptic-motor transformations for the control of finger position” published in *Public Library of Science ONE* in June 2013, has given permission to Daisuke Shibata for use of this manuscript in his dissertation.

Dr. Marco Santello, coauthors of the above manuscript has given permission to Daisuke Shibata for use of this manuscript in this dissertation.