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Effect of Terminal Haptic Feedback on the Sensorimotor Control of Visually and Tactile-Guided Grasping

Shirin Davarpanah Jazi
The University of Western Ontario

Supervisor
DR MATTHEW HEATH
The University of Western Ontario

Graduate Program in Kinesiology
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Abstract

When grasping a physical object, the sensorimotor system is able to specify grip aperture via absolute sensory information. In contrast, grasping to a location previously occupied by (no-target pantomime-grasp) or adjacent to (spatially dissociated pantomime-grasp) an object results in the specification of grip aperture via relative sensory information. It is important to recognize that grasping a physical object and pantomime-grasping differ not only in terms of their spatial properties but also with respect to the availability of haptic feedback. Thus, the objective of this dissertation was to investigate how terminal haptic feedback influences the underlying mechanisms that support goal-directed grasping in visual- and tactile-based settings.

In Chapter Two I sought to determine whether absolute haptic feedback influences tactile-based cues supporting grasps performed to the location previously occupied by an object. Results demonstrated that when haptic feedback was presented at the end of the response absolute haptic signals were incorporated in grasp production. Such a finding indicates that haptic feedback supports the absolute calibration between a tactile defined object and the required motor output. In Chapter Three I examined whether haptic feedback influences the information supporting visually guided no-target pantomime-grasps in a manner similar to tactile-guided grasping. Results showed that haptic sensory signals support no-target pantomime-grasping when provided at the end of the response. Accordingly, my findings demonstrated that a visuo-haptic calibration supports the absolute specification of object size and highlights the role of multisensory integration in no-target pantomime-grasping. Importantly, however, Chapter Four demonstrated that *a priori* knowledge of haptic feedback is necessary to support the aforementioned calibration process. In Chapter Five I demonstrated that, unlike no-target pantomime-grasps, spatially dissociated pantomime-grasps precluded a visuo-haptic calibration. Accordingly, I propose that the top-down demands of decoupling stimulus-response relations in spatially dissociated pantomime-grasping renders aperture shaping via a visual percept that is immutable to the integration of haptic feedback. In turn, the

decreased top-down demands of no-target pantomime-grasps allows haptic feedback to serve as a reliable sensory resource supporting an absolute visuo-haptic calibration.

Keywords

Action, Allocentric, Egocentric, Feedback, Grasping, Haptic, Just Noticeable Difference, Manual Estimation, Memory Delay, Pantomime, Perception, Tactile, Vision, Visually Guided, Weber's Law

Co-Authorship Statement

The current dissertation was completed under the guidance and supervision of Dr. Matthew Heath. Specifically, I designed, collected and analyzed human data, interpreted results, and finally prepared the manuscripts. Further, For Chapter 2 Stephanie Hosang (undergraduate scholars elective student) assisted with data collection and she has been included as a co-author in the published version of this chapter. For Chapter 3 Michelle Yau (undergraduate volunteer research assistant) was involved in data collection and Dr. David Westwood provided intellectual input. Both these individuals have been credited as co-authors of the published version of Chapter 3. Chapters 2 through 4 contain material that have been already published and work presented in Chapter 5 is currently under review. On all stated manuscripts I am the first author and Dr. Heath is a co-author.

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Now that I have completed writing my dissertation I can clearly understand how this period of intense learning has affected me, not only in the science arena, but also on a personal level. Moving to Canada to pursue my PhD studies has had a big impact on me and thus I would like to thank people who have supported and helped me get through this period.

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List of Abbreviations

2D: two-dimensional

3D: three-dimensional

ANOVA: analysis of variance

AIP: anterior intraparietal area

APC: anterior parietal cortex

BPH-: blocked pantomime-grasping without haptic feedback

BPH+: blocked pantomime-grasping with haptic feedback

CL: closed-loop

CH-: closed-loop without haptic feedback

CH+: closed-loop with haptic feedback

ERP: event-related brain potential

fMRI: functional magnetic resonance imaging

GA: grip aperture

GT: grasping time

H-: without haptic feedback

H+: with haptic feedback

Hz: hertz

IREM: infrared emitting diode

JND: just-noticeable-difference

LOC: lateral occipital cortex

MG: memory-guided

MH-: memory-guided without haptic feedback

MH+: memory-guided with haptic feedback

MLE: maximum-likelihood-estimation

MS: milliseconds

PAM: perception-action model

PGA: peak grip aperture

PH-: no-target pantomime-grasp, without haptic feedback

PH+: no-target pantomime-grasp, with haptic feedback

P_DH-: spatially dissociated pantomime-grasp, without haptic feedback

P_DH+: spatially dissociated pantomime-grasp, with haptic feedback

P_{DM}H+: spatially dissociated pantomime, memory-guided, with haptic feedback

P_{DO}H+: spatially dissociated pantomime, open-loop, with haptic feedback

P_{DT} H-: spatially dissociated pantomime-grasp, no target, without haptic feedback

P_{DT} H+: spatially dissociated pantomime-grasp, no target, with haptic feedback

PPC: posterior parietal cortex

RPH-: randomized pantomime-grasping without haptic feedback

RPH+: randomized pantomime-grasping with haptic feedback

SD: standard deviation

SII: secondary somatosensory cortex

SPM: somatosensory processing model

SR: stimulus and response

TGA: terminal grip aperture

TPGA: time to peak grip aperture

V1: primary visual cortex

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Chapter 1

1 General Introduction

1.1 Precision grasp

In order to manipulate, transport, or touch a static object, one has to perform a goal-directed grasping movement. Despite different action goals (e.g., grasp to lift, throw or place) (see Marteniuk et al., 1987), a fundamental characteristic of all grasping movements is the establishment of a stable grip that prevents perturbations of the target object (Napier, 1956). In particular, the fingers have to apply opposing force vectors against the object's surface to permit a stable grasp. Although the hand has the ability to securely grasp objects in a variety of ways, the functional and physical constraints of object and hand interactions limit the number of appropriate grasp types. For example, functional constraints often depend on how the object will be used for the task goal, whereas physical constraints are related to the target object's *intrinsic* (e.g., size, shape, texture) and *extrinsic* (e.g., location, orientation) characteristics as well as postural properties of the acting limb (MacKenzie & Iberall, 1994). For example, there is limited surface for finger placement when lifting a small rectangular block. Thus, and as demonstrated in Figure 1-1, a precision grasp is one type of human grasping motion that allows a successful grip of small objects between the forefinger and thumb (Napier, 1956; for review see MacKenzie & Iberall, 1994). According to the double-pointing hypothesis (Smeets & Brenner, 1999), the opposite force vectors of the forefinger and thumb should create a connecting line that runs through the target's center of gravity and is perpendicular to the forefinger and thumb's contact surface at each side. Indeed, approaching the target with such perpendicular directional forces minimizes the risk of missing or colliding with the target. Further, the amount of force necessary for a precision grasp depends on additional parameters such as the target's weight, shape and surface friction (Johansson & Cole, 1994). Notably, throughout the current dissertation individuals adopted a precision grasp in order to hold target objects between their forefinger and thumb.

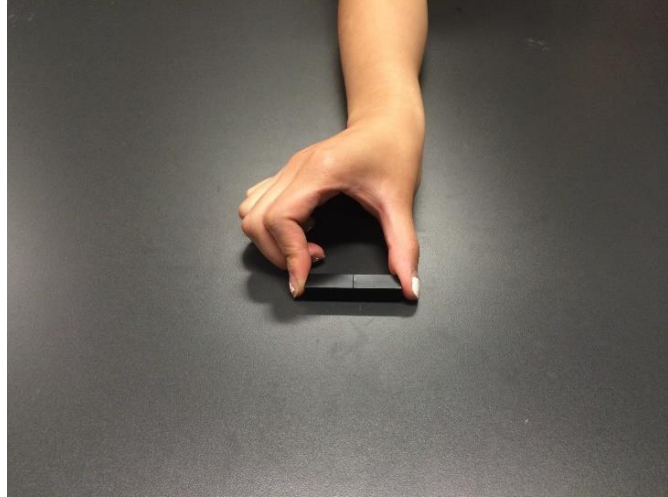


Figure 1-1: Image of an individual performing a precision grasp to firmly hold a small rectangular block between their right forefinger and thumb. As demonstrated, precision grasps provide a stable and comfortable grip on small objects with a limited grasping surface. Further, and as depicted here, for all grasps evaluated in the present dissertation participants were instructed to grasp the target object's long axis.

1.2 Kinematics of grasping

The seminal work by Jeannerod (1981,1984) first characterized the kinematics of human grasping via examining grip (i.e., peak grip aperture: PGA) and transport (e.g., wrist velocity) components separately. Jeannerod reported that participants achieved their peak grip aperture (i.e., PGA) at a relatively fixed time (~ 75% of total grasping time) and that the peak velocity associated with their transport component followed a general bell shaped pattern (see Figure 1-2 for a schematic wrist and grip aperture trajectory profile). Further, with an increase in the size of target objects positioned at a fixed location, PGAs systematically increased while wrist velocities remained unchanged. In contrast, grasping to more distant targets of equal size did not affect PGAs but resulted in higher peak velocities (Jeannerod, 1981;1984;1986). Jeannerod also reported that movement times did not reliably vary with target size or distance which was due to increase in movement velocity. However, the number of participants in Jeannerod's experiments were limited and thus similar pattern of results might not be observed with a larger sample size. Based on his findings, Jeannerod concluded that the grip and transport components of a grasp operate via independent visuomotor channels that are temporally synchronized (dual-channel hypothesis: Jeannerod, 1999). Since Jeannerod's work, a wealth of studies have been dedicated to examining how the extrinsic (Paulignan et al., 1991a) and intrinsic (Castiello, 1996; Johansson & Westling, 1988; Paulignan et al., 1991b) properties of a target object influence grasping. For example, Jakobson and Goodale (1991) examined the effect of target size and distance on grip and transport components of a precision grasp. Results showed that increasing target object size while keeping reaching distance constant resulted in larger and later occurring PGAs with overall increase in movement time. Further, peak wrist velocities increased with increasing object size or distance. Thus, and contrary to the dual-channel hypothesis, results showed that varying target object size or distance have mutual effects on grip and transport components of grasping actions (for review see Jones & Lederman, 2006). These findings indicate that a higher-order central mechanism controls the two grasping components (i.e., grip and transport) that operate independently at a lower level (Jakobson & Goodale, 1991).

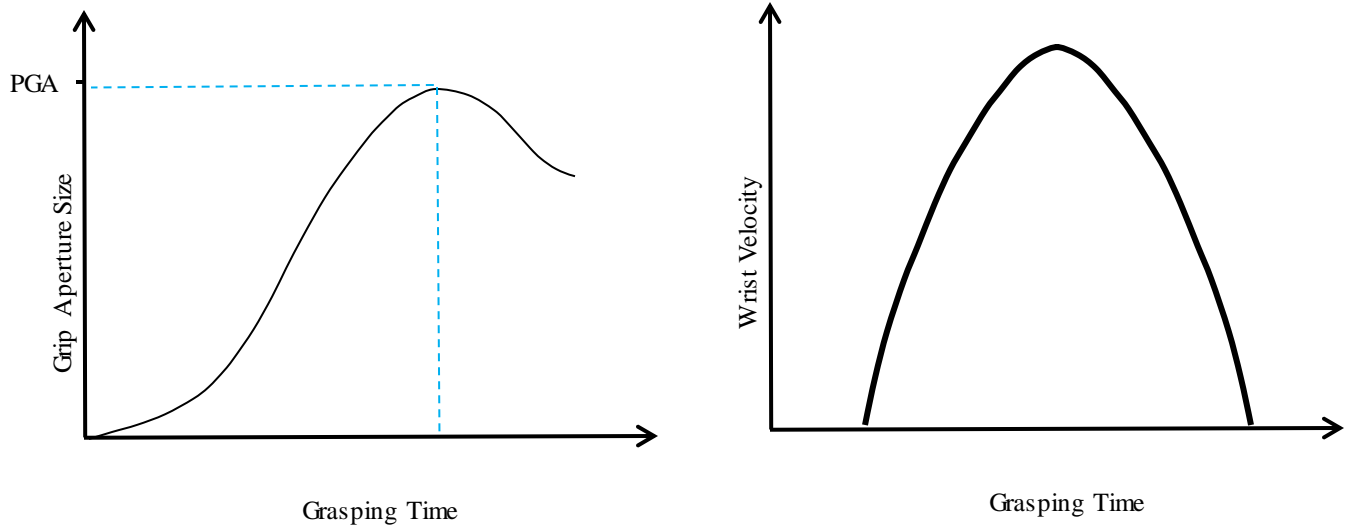


Figure 1-2: Schematic of grip aperture size (left panel) and wrist velocity (right panel) as a function of grasping time. The figure shows that peak grip aperture (PGA) is reached at approximately 75% of the grasping time after which the value decreases to veridical target object size. Moreover, the wrist velocity profile demonstrates a rise towards maximum velocity followed by a deceleration towards grasp end point.

1.3 Sensory contribution to grasping

1.3.1 Visual feedback

In addition to studies investigating the effect of varying target object properties, researchers have examined how manipulating visual information influences grasp control. Visual feedback provides crucial information about the target object's intrinsic (via past experiences with the target object) and extrinsic properties as well as information about the position of the acting limb. More specifically, in a *closed-loop* (CL) visual condition – also referred to as naturalistic grasping – vision of the grasping environment is presented during the planning and execution of the grasping response. Notably, the availability of vision during both planning and execution phases permits: (1) response programming via veridical target properties, and (2) movement execution mediated via egocentric-based comparisons between the acting limb and target to permit trajectory amendments as the movement unfolds (i.e., online mode of control). In contrast, withdrawing vision at (*open-loop* (OL) visual condition) or some time prior to movement onset (*memory-guided* (MG) visual condition) results in responses that are completed while visual feedback is unavailable during movement planning (as in MG condition) and/or execution (as in OL and MG conditions). Therefore, individuals structure their response entirely based on central planning mechanisms with minimal modifications applied to their unfolding grasping motion (i.e., offline mode of control) (Heath, 2005). A large number of studies have compared grasp kinematics under CL, OL and MG visual conditions to investigate the manner a response is structured (i.e., online vs. offline mode of control). In particular, Jeannerod (1984) reported that removing target and limb vision does not affect the PGA or wrist velocity but leads to shorter grasping times. It was concluded that grasping actions are controlled via mechanisms that operate independent of incoming visual feedback and that visual information require additional processing time (Jeannerod, 1984;1986a,b). Later studies however, showed that OL and MG reaches produced more variable PGAs (Berthier et al., 1996; Chieffi & Gentilucci, 1993; Hu et al., 1999; Wing et al., 1986) as well as lower peak wrist velocities that had a more asymmetrical pattern than their CL counterparts (Berthier et al., 1996; Churchill et al., 2000; Winges et al., 2003). Interestingly, however, PGAs continued to scale to target

object size regardless of visual feedback manipulations – a result indicating that across visual conditions individuals were able to distinguish between the differently sized target objects (Berthier et al., 1996; Chieffi & Gentilucci, 1993; Hu et al., 1999; Jakobson & Goodale, 1991; Wing et al., 1986). Such findings as well as results from more recent work (Fukui et al., 2006; Hesse & Franz, 2009; 2010) emphasize the importance of online vision during grasping. More specifically, results indicate that online vision serves as an important sensory source in supporting the efficiency and effectiveness of precision grasps.

1.3.2 A model of visual processing

The perception-action model (PAM) asserts that functionally and anatomically distinct visual pathways support “vision-for-perception” and “vision-for-action” (Goodale & Milner, 1992). The PAM contends that a dorsal stream extending from the primary visual cortex (V1) to the posterior parietal cortex (PPC) subserves motor actions (e.g., goal-directed grasping) and processes absolute visual information in egocentric frames of reference. The term ‘absolute’ describes those metrical characteristics that are specific to the target itself and do not relate to the surrounding objects (Hu & Goodale, 2000). Further, egocentric frames of reference refer to calculating target object properties (e.g., size, position) with respect to the observer’s body (e.g., head, shoulder, trunk). Accordingly, visuomotor transformations code actions with regard to the state of the acting limb, independent of scene-based visual cues (Goodale & Haffenden, 1998). During an action task the position and orientation of the target object with respect to the observer changes on a moment-to-moment basis and thus the dorsal stream is optimized to compute and update the egocentric-based specifications of the target in real-time (Westwood & Goodale, 2003). In contrast, the PAM contends that a ventral stream extending from V1 to the inferotemporal cortex mediates the perceptual identification of objects (i.e., shape, size, color) via computing relative visual information in allocentric reference frames. ‘Relative’ target attributes are concerned with identifying the target’s features with respect to its surrounding objects/scene. Moreover, allocentric frames of reference are computed based on how the target is placed within a visual context so that with change in the viewer’s perspective the target preserves its relation to other objects in

the environment (Goodale, 2011). Notably, a perceptual understanding of the surrounding world requires the ventral stream to rely on memory-based visual representations (Figure 1-3 presents a schematic of the ventral and dorsal visual streams at the level of the human cerebral cortex).

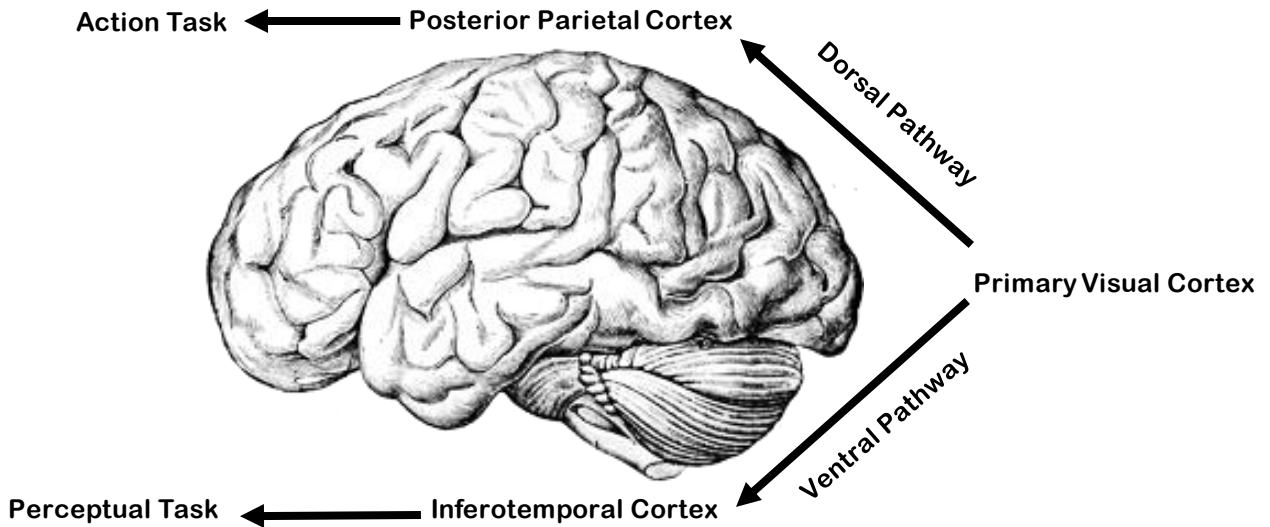


Figure 1-3: Schematic organization of the two visual streams of information processing proposed by the perception-action model (PAM: Milner & Goodale, 1992). The ventral stream mediates explicit visual judgments, whereas goal-directed actions are supported via the dorsal stream's dedicated visuomotor mechanisms.

1.3.2.1 Clinical findings

Support for the PAM is derived from a broad range of clinical, behavioral and neuroimaging studies. In particular, evidence stems from individuals with visual agnosia. For example, patient DF who has been studied extensively during the past twenty-five years has bilateral lesions to the lateral occipital cortex (LOC) of her ventral visual pathway that impairs her perceptual recognition of visual forms (James et al., 2003). In a seminal study, Goodale et al. (1991) instructed DF to match the orientation of a hand-held card with that of a slot presented at different angles (i.e., perceptual task) or manually post the card into the slot (i.e., action task) oriented at different angles. Results showed that while DF was unable to accurately perceive the orientation of the slot she nonetheless demonstrated performance on par to healthy controls during the “posting” component of the task. Goodale et al.’s (1991) findings suggest that the neural substrates subserving visual perceptions are distinct from those mediating motor actions. In turn, persons with lesions to the posterior parietal regions of the dorsal visual stream exhibit impaired visuomotor performance in the absence of visuoperceptual deficits (i.e., optic ataxia). Perenin and Vighetto (1988) studied ten optic ataxic patients with unilateral lesions to their posterior parietal brain areas. Patients had to verbally identify the spatial location of dots presented at different eccentricities (i.e., perceptual task), whereas goal-directed grasping was used to observe patients’ motor abilities. Results for the perceptual task indicated that persons with PPC lesions exhibited comparable performance to aged-matched controls, whereas they demonstrated impaired performance in the grasping task. Therefore, despite patients’ accurate perceptual knowledge about the target’s spatial location, they were unsuccessful at visually guiding their motor actions. Taken together then, observations from individuals with visual agnosia and optic ataxia provide a double dissociation (see also Damasio & Benton, 1979; Karnath et al., 2009; Rondot et al., 1977) that support the theoretical tenets of the PAM.

1.3.2.2 Neuroimaging findings

Evidence from neuroimaging studies support the PAM’s contention that distinct neural substrates underlie visual perceptions and actions. In particular, fMRI findings have

revealed activation of the LOC when neurologically intact individuals were passively presented with pictures of familiar or novel objects (i.e., line drawings or photographs) as compared to scrambled and unrecognizable textures (Kanwisher et al., 1996; Malach et al., 1995). These data revealed that the LOC is linked to extracting shape features as well as recognizing faces and objects; all of which are categorized as perception-based tasks (for review see Grill-Spector et al., 2001). Interestingly, however, the LOC does not show activation when individuals grasp toward visually presented objects (Cavina-Pratesi et al., 2007; Culham et al., 2003; see also Culham et al., 2008). Moreover, Cavina-Pratesi et al. (2007) showed that the anterior intraparietal (AIP) area was activated when participants performed grasping actions on 3D target objects but not during perceptual identification of target size. The aforementioned neuroimaging findings are indicative of separate neural pathways subserving object recognition and goal-directed action.

1.3.2.3 Behavioral findings: visual illusions

Another area of inquiry supporting the PAM is the degree to which pictorial illusions influence perceptions vs. actions. In particular, studies have shown that while motor actions are mostly immune to the effects of pictorial illusions, perception-based responses are influenced by illusory contexts. These studies have explained their findings based on the theoretical tenets of the PAM; that is, motor actions are mediated by absolute metrical information of the dorsal processing stream, whereas perceptual tasks are supported by the relative and context-dependent visual properties projecting to the ventral stream. For example, Aglioti et al. (1995) had healthy participants manually estimate (via separating the distance between their thumb and forefinger) or grasp target objects embedded within the Ebbinghaus illusion. The Ebbinghaus illusion is constructed of a central (i.e., “target”) circle surrounded by non-target annuli that are smaller or larger than the target. Individuals typically perceive the size of the circle as smaller or larger when respectively surrounded by the ‘small’ or ‘large’ non-target annuli. As expected, Aglioti et al. showed that participants’ perceptual judgments were “tricked” by the illusion, whereas grasping responses to the target circle were (mostly) refractory to the illusion. Thus, and in line with the PAM, results indicated that perceptual responses were influenced by the relative and allocentric properties of the illusion, whereas grasping responses were supported via

absolute visual information computed in an egocentric space. In another size-contrast illusion study the effect of visual delay on grasping responses in neurological intact individuals was investigated (Hu et al., 1999). In particular, manual estimations and grasping responses of target objects that were accompanied by a smaller/larger object under CL and MG visual conditions were performed. Hu et al. showed that individuals' performance was influenced by the presence of the second object in the MG grasping and manual estimation but not the CL grasping condition. The findings were interpreted as evidence that grasps performed in the absence of continuous vision are perception-based and supported by relative and allocentric computations between the target object and its surrounding (Hu et al., 1999; for more examples see Hughes et al., 2004; Servos et al., 2000).

1.3.2.4 Behavioral findings: pantomime-grasping

The spatial relation between a visual target and the location of a grasp response (stimulus and response: SR) can also influence the nature of the information supporting motor output. More specifically, in pantomime-grasping the spatial location of the target object with respect to the grasping endpoint is dissociated (i.e., spatially dissociated pantomime-grasp) or the response is performed towards the location of a previously presented target object (i.e., no-target pantomime-grasp). Such manipulation can uncover the cognitive processes that influence visual information mediating grasping responses. For example, Goodale et al. (1994a) had participants perform spatially dissociated and no-target pantomime-grasps of differently sized target objects. The researchers showed that pantomime-grasps were associated with lower peak velocities and had smaller PGAs than CL grasps. Goodale et al. concluded that visuomotor control mechanisms underlying CL grasping actions are distinct from the cognitive strategies mediating spatially dissociated and no-target pantomime-grasping. More specifically, pantomime actions are driven by relative and allocentric-based comparisons between the SR and/or perceptual representations that are stored in memory (see also Cavina-Pratesi et al., 2011; Fukui & Inui, 2013; Westwood et al., 2000). In other words, the top-down demands of dissociating SR relations or maintaining a target object in memory is thought to be a perception-based task mediated via relative visual information.

1.3.2.5 Evidence opposing the PAM

Researchers have attempted to propose alternative explanations for the findings that support the PAM's contention of dissociated ventral and dorsal streams of visual processing. Nevertheless, most studies have been unsuccessful at rejecting the PAM as a whole but rather they have asserted that independent but interacting visual pathways support perceptions and actions (see also Goodale & Westwood, 2004). In this section I will provide a selection of evidence from pictorial illusions, behavioral studies and clinical findings of patient DF that challenge a clear segregation between perceptions and actions and will emphasize the communication between the two streams of visual processing.

Studies involving pictorial illusions have been a significant source for advocating perception and action dissociations, but this same area of research has become disadvantageous to the tenets of the PAM (for review see Schenk & McIntosh, 2010; Smeets & Brenner, 2006). According to the PAM, information traveling through the ventral and dorsal streams use allo- and egocentric spatial representations, respectively, to process visual cues. Thus, perceptions are 'tricked' by the context-based effects of visual illusions whereas motor actions are refractory to those same illusions. In contrast to the PAM's contention, studies have shown that pictorial illusions can influence motor actions to various degrees (Daprati & Gentilucci, 1997; Dyde & Milner, 2002). The degree to which visual illusions effect motor responses are explained in terms of the level at which it influences visual processing (i.e., before or after the two streams diverge). Even though the strength of the illusion on perceptions and actions depends on whether it acts on early visual areas like V1 (e.g., Ponzo and simultaneous tilt illusions) or areas of the ventral stream (e.g., rod and frame illusion), the underlying reason for the null effect of the Ponzo illusion on action tasks remains unexplained (Dyde & Milner, 2002; Murray et al., 2006; but see also Brenner & Smeets, 1996; Stöttinger & Perner, 2006). Further, researchers have shown that if the experimental methods used to study illusions are manipulated then the effect of illusions on motor actions becomes evident. For example, in the case of the Ebbinghaus illusion, during each trial both sets of circles are presented. However, it has been shown that if each set of circles is presented only one at a time then

grasping responses are also tricked by the illusory effects (see Figure 1 of Pavani et al., 1999; see also Franz et al., 2000). Moreover, in some instances of the Ebbinghaus illusion the annuli surrounding the target object are treated as obstacles that the grasping limb tries to avoid and thereby leads to a response that is immune to the illusion (Biegstraaten et al., 2003; Smeets & Brenner, 2006). The kinematic measures used to report the distinct effect of visual illusions on perceptions is another source of disagreement. For example, Jackson and Shaw (2000) demonstrated that kinematic variables (i.e., grip force) other than PGAs reveal the induced effect of illusions on grasping (see also Brenner & Smeets, 1996). These findings suggest that PGAs might not be the best index for measuring the degree to which illusions influence actions. Taken together and as suggested by Schenk and McIntosh (2010), differences in methodological factors (and not spatial attributes of the two visual streams) best serve to explain how pictorial illusions influence perceptual and motor responses.

Other challenges against the functional dissociation of perceptions and actions come from behavioral findings of reaching and grasping experiments. Grasping studies have indicated that specific target properties, such as target weight, cannot be calculated on the basis of real-time information that are available to the dorsal stream. This means that in order to lift a target object, the required finger forces are predetermined according to previous encounters with similar objects (Gordon et al., 1991; Johansson & Westling, 1988). These findings point out to the involvement of the ventral stream in determining grip aperture properties of grasping actions. Further and as described earlier, one core characteristic of the PAM is that allo- and egocentric visual information are respectively involved in ventral and dorsal stream processing. However, studies have demonstrated that the availability of non-illusory visual structure helps reduce endpoint variability of reaching responses (Krigolson & Heath, 2004; Krigolson et al., 2007). Such findings can be taken as evidence that action tasks, mediated by the visuomotor networks of the dorsal stream, not only process the egocentric target cues but also the scene-based visual information (Krigolson & Heath, 2004; Krigolson et al., 2007; see also Obhi & Goodale, 2005).

Finally, studies examining patient DF have demonstrated that when methodological factors (i.e., experimental tasks or instructions) are manipulated her motor performance mirrors that of her perceptual deficit. In an early study DF was instructed to either recognize a series of letters including the letter T (i.e., perceptual task) or manually insert a T-shaped block into a slot that had the same cut out shape (i.e., motor task). As expected, her perceptual identification of the letters was impaired. Interestingly, however, DF's performance in posting T-shaped blocks into a slot (Goodale et al., 1994b) was also degraded as compared to her posting performance using simple square-shaped blocks (Goodale et al., 1991). Thus, DF's damaged ventral stream was unsuccessful in providing her information about more complex geometric shapes to guide her visuomotor performance. These findings suggest that the dorsal and ventral visual streams do not operate independently; rather, convergent evidence suggests that dorsal and ventral streams communicate to successfully complete higher-order computations in motor processing. In another study Schenk (2006) showed that when DF was asked to identify the distance between two points (allocentric-based computation) her performance was impaired. However, when DF had to report the distance from her limb to a target point (egocentric-based computation) she performed comparable to healthy individuals. In other words, the nature of the spatial computations (allocentric vs. egocentric) and not the task itself (perception vs. action) determine DF's success in visually guided responses (see also Schenk & Milner, 2006).

1.3.3 Tactile and haptic feedback

When an external stimulus (e.g., differently shaped objects, sharp tips, hot or cold surfaces, material with different textures) touches the skin while the body is in a passive state the mechanoreceptors of the skin are activated. This type of somatosensory information is regarded as tactile feedback. Mechanoreceptive signals are acquired through cutaneous receptors located in the superficial layers of the skin across the body. Depending on their size, approximate location, and adaptation characteristics, different cutaneous receptors respond to a variety of stimuli. Another source of somatosensory information is haptic feedback obtained through physically manipulating a target object and is derived from: 1) mechanoreceptive feedback from the fingertips while touching

the surface of a target object and 2) proprioceptive cues from finger position that deliver absolute size information. Unlike tactile feedback that informs the body about the physical nature of its environment, haptic feedback provides information about the state of the limb itself (for review see Lederman & Klatzky, 2009). Although haptic feedback is an important source of sensory information it has received insufficient attention in the grasping literature. In order to study the effect of haptic feedback on visually guided grasping one has to spatially decouple or remove the target object from the grasping endpoint. Accordingly, the pantomime-grasps mentioned in section 1.3.2.4 not only have distinct visual attributes as compared to CL grasping but also preclude haptic feedback. Indeed, studies examining pantomime-grasping have not disentangled the role of SR spatial relations from terminal haptic feedback in grasp control (e.g., Cavina-Pratesi et al., 2011; Goodale et al., 1994a; Westwood et al., 2000). Bingham et al., (2007) however, examined grasp kinematics of healthy individuals while completing pantomime-grasps and CL grasps in separate blocks of trials as well as a third block wherein CL and pantomime-grasps were presented in a randomized order. For the pantomime-grasp condition participants viewed – but could not feel – the target object when reaching out to grasp. Results demonstrated that when haptic feedback was unavailable (i.e., blocked pantomime-grasp) grasping accuracy (i.e., reach distance), PGA, and terminal grip aperture (TGA) decreased. Interestingly however, when terminal haptic feedback was presented in a randomized order participants' grasp accuracy, PGA and TGA did not reliably differ from that of the CL condition. Bingham et al.'s results suggest that individuals produce pantomime-grasps comparable to CL grasps only when their responses are calibrated according to absolute haptic feedback signals. In a later study Schenk (2012) employed Bingham et al.'s experimental paradigm to investigate how haptic feedback influences patient DF's grasping performance. As expected, DF showed metrical aperture shaping in the blocked CL – but not pantomime-grasp – condition. More notably, when CL and pantomime-grasping trials were performed in a randomized order DF's grip aperture for the pantomime responses scaled to absolute target size. In line with Bingham et al., Schenk highlighted the role of terminal haptic feedback in grasp control and also identified the multisensory integration/calibration

processes that occur when visual and haptic feedback cues are available (see also Whitwell et al., 2014).

1.3.4 A model of somatosensory processing

Dijkerman and deHaan (2007) introduced the somatosensory processing model (SPM) with distinct anatomical and functional pathways for tactile-guided perceptions and actions. The model is largely driven as a haptic analogue to the PAM and provides a basis for the dissociable nature of the tactile information mediating perceptions and actions. In particular, the model states that a ventral stream extending from the anterior parietal cortex and the secondary somatosensory cortex to the posterior insula supports tactile-based perceptual identifications. In turn, a dorsal stream that supports tactile-based actions projects from the anterior parietal cortex and the secondary somatosensory cortex to the PPC. Tactile-based perceptions use *relative* computations to compare the target with other objects in the tactile surrounding (i.e., *allocentric* frame of reference) or employ memory-based representations of target objects from past experiences. In contrast, tactile-based actions compute the target's *absolute* properties in relation to the observer (i.e., *egocentric* frame of reference). Clinical and behavioral evidence support the theoretical tenets of the SPM. For example, Paillard et al. (1983) examined an individual with lesions to her ventral somatosensory pathway. The researchers stimulated specific points on the patient's contralesional (i.e., affected) hand and asked her to locate the stimulation via verbal report (i.e., perception task) or point to the stimulated location using her unaffected limb (i.e., motor task). Paillard et al.'s findings indicated that while the patient failed to perceptually identify the stimulus location, she was successful in pointing to that same location. In a more recent study two brain-damaged individuals (JO and KE) with lesions that were mostly associated with putative dorsal and ventral streams were examined. The patients were stimulated on different areas of their affected hand and were asked to point to the stimulus location as presented in a picture (i.e., perceptual task) or localize with their unaffected limb to the stimulus point (i.e., action task). Patient KE showed accurate localization in the perceptual task but not the action task, whereas the converse findings were observed in patient JO (Anema et al., 2009). Overall, lesion

studies suggest that tactile-based perceptual identifications and motor actions operate through distinct neural pathways.

Moreover, in a behavioral study involving neurologically healthy individuals I provided support for perception and action dissociations in somatosensory processing (Davaranah Jazi & Heath, 2014). In particular, in Experiment 1 participants manually estimated (via separating the distance between their thumb and forefinger) (i.e., perceptual task) or grasped (i.e., motor task) differently sized objects placed on their opposite forearm or palm. In order to equate for haptic feedback availability at the end of grasping responses, participants had to grasp the target object following each manual estimation trial. Across experimental tasks vision was removed and participants had to exclusively rely on the touch (i.e., tactile) information they received from the target object. To examine the extent to which different tasks adhered to, or violated, the psychophysical principles of Weber's law just-noticeable-difference scores (JNDs) were computed. Weber's law asserts that the ability to discriminate between an original (e.g., the target stimulus) and a comparator (e.g., grip aperture size) stimulus is proportional to the magnitude of the original stimulus and that the sensitivity of detecting a change in any physical continuum is *relative* as opposed to *absolute*. Thus, a linear increase in JNDs with increasing object size indicates adherence to Weber's law and therefore provides a law-based demonstration of the processing of relative – but not absolute – object properties (i.e., size). Results for the grasping task elicited JNDs that violated Weber's law. However, results for the manual estimation task demonstrated that JNDs for the palm – but not the forearm – condition adhered to Weber's law. Subsequently, in Experiment 2 manual estimations of targets positioned on the palm or forearm were performed while terminal haptic feedback was removed. Results showed that responses adhered to Weber's law irrespective of target location (palm vs. forearm). Findings from Experiments 1 and 2 provide location-dependent support for the SPM's contention that grasping and manual estimations are mediated via absolute and relative tactile information, respectively. Further, results indicated that this dissociation is influenced by the absolute haptic feedback introduced following response completions.

1.4 Dissertation objectives

The primary goal of my dissertation was to investigate the role of haptic feedback on the sensorimotor control of goal-directed grasping. The basis for my research was rooted in the findings from Schenk's (2012) work with DF as well as my earlier research (Davarpanah Jazi & Heath, 2014). According to Schenk (2012), DF's intact grasping performance stems from a multisensory (i.e., vision and haptic) integration process. In addition, findings from my previous work are indicative of a within-sensory (i.e., tactile and haptic feedback) integration during tactile-guided manual estimations. Therefore, I sought to further investigate the effect of terminal haptic feedback on tactile-based manual estimation and grasping. More specifically, the first goal of Chapter 2 was to determine the temporal properties by which absolute tactile cues mediate responses. To accomplish that objective, manual estimation and grasping trials were performed while tactile feedback was available throughout the response (i.e., CL trials) and while a memory delay was presented prior to movement onset (i.e., MG trials). More importantly, the main goal of this chapter was to examine the effect of haptic feedback on tactile processes that mediate manual estimation and grasping responses under CL and MG conditions. The results of Chapter 2 demonstrated that: (1) manual estimations are supported via relative and perceptual-based tactile information regardless of the temporal delay or terminal haptic feedback, and (2) the availability of haptic touch information following grasp completion supports an absolute calibration process that serves future trial performance.

The findings from Chapter 2 led me to examine how introducing terminal haptic feedback information influences visually guided no-target pantomime-grasps. More specifically, in Chapter 3 participants grasped to an area once occupied by a target while a memory delay was introduced (i.e., MG response). Results showed that if terminal haptic feedback was presented at the end of a no-target pantomime-grasp then absolute – as opposed to relative – sensory information mediated aperture shaping. Accordingly, I proposed that the provision of haptic feedback in a pantomime-grasping task supports an absolute visuo-haptic calibration process (Ernst & Banks, 2002). Notably, however, a

potential shortcoming of Chapter 3 was that participants were provided advanced knowledge related to the availability of haptic feedback in a pantomime-grasping task. Indeed, it might be the case that the advance knowledge of haptic feedback accounts for the visuo-haptic calibration supporting pantomime responses. To address this issue, Chapter 4 examined no-target pantomime-grasps performed in two types of haptic feedback schedules. In the blocked feedback schedule participants were informed that they would (or would not) receive haptic feedback related to the absolute size of a target object at the end of a trial, whereas in the random feedback schedule no prior information about the availability of terminal haptic feedback signals was presented. The results of Chapter 4 showed that knowledge about haptic feedback availability is necessary in order to support an absolute visuo-haptic calibration. According to these findings, an internal forward model based on “expected” sensory (i.e., haptic feedback) signals is formed. Following response completion an error signal is calculated by comparing the “expected” and “actual” haptic feedback cues. Importantly, however, knowledge of haptic feedback availability is required in order for such visuo-haptic calibration mechanism to occur. Finally, the goal of Chapter 5 was to examine whether the absolute visuo-haptic calibration associated with the no-target pantomime-grasps performed in Chapters 3 and 4 extends to spatially dissociated pantomime-grasps. More specifically, individuals performed spatially dissociated pantomime-grasps under different visual (i.e., CL, OL and MG) conditions while haptic feedback was introduced at the end of the response. The results of Chapter 5 showed that an absolute calibration process does not underlie spatially dissociated pantomime-grasps. To address the findings of Chapter 5, I have relied on the maximum-likelihood-estimation model (MLE) proposed by Ernst and Banks (2002). According to the MLE, response production is based on the integration of all incoming sensory signals with weighting placed on the more reliable sense. As such, I proposed that the top-down perceptual (and allocentric-based) demands of dissociating SR spatial relations is more reliable, and preferentially weighted, and therefore precludes an absolute visuo-haptic calibration.

1.5 References

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Chapter 2

2 Memory delay and haptic feedback influence the dissociation of tactile cues for perception and action

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2.1 Introduction

Vision predominates many of the goal-directed activities that we perform on a day-to-day basis. It is, however, important to recognize that tactile cues play a pivotal role in object identification and movement control. For example, a coin placed on the palm of the left hand mechanically deforms the skin and leads to mechanoreceptor-derived (i.e., tactile) feedback supporting perceptual identification of the object (Lederman & Klatzky, 2009). Moreover, in executing a motor response tactile feedback provides the information necessary to allow the right limb to effectively reach-to-grasp the coin resting in the left palm. Interestingly, Dijkerman and deHaan's (2007) somatosensory processing model (SPM) asserts that tactile perceptions and actions are mediated via functionally and anatomically distinct cortical pathways. In particular, the SPM contends that a ventral pathway extending from the anterior parietal cortex (APC) and the secondary somatosensory cortex (SII) to the posterior insula mediates perceptions. In turn, a dorsal pathway originating from the APC and the SII and extending to the posterior parietal cortex (PPC) is proposed to support goal-directed actions. Moreover, the SPM asserts that the ventral pathway mediates perceptions via relative cues wherein the properties of an object (e.g., size) are compared to other objects and/or by accessing memory-based information (i.e., allocentric frame of reference). Thus, a coin on the palm of one's hand can be identified via: (1) concurrent tactile feedback, and/or (2) temporally persistent knowledge from previous tactile experiences. In contrast, the spatial and temporal demands associated with goal-directed actions require that the dorsal stream regulate motor output via absolute information related to the size and position of the to-be-grasped object (i.e., egocentric frame of reference) (for review of tactile frames of reference see Lederman & Klatzky, 2009).

Initial support for the SPM was derived from the clinical neuropsychology literature and the report of a double dissociation for tactile perceptions and actions in persons recovering from unilateral stroke (Anema et al., 2009; see also Paillard et al., 1983). Moreover, recent work by my group (Davaranah Jazi & Heath, 2014) demonstrated a perception/action dissociation in neurologically intact individuals. In that study,

participants used their right hand to manually estimate (i.e., perceptual task) or grasp (i.e., motor task) differently sized objects (20, 30, 40 and 50 mm) placed on the forearm or palm of their left limb, with all responses being completed in the absence of vision¹. Importantly, just-noticeable-difference scores (JNDs) were computed to examine the extent to which the different tasks adhered to, or violated, the psychophysical principles of Weber's law. Indeed, Weber's law asserts that the ability to discriminate between an original (e.g., the target stimulus) and a comparator (e.g., grip aperture size) stimulus is proportional to the magnitude of the original stimulus and that the sensitivity of detecting a change in any physical continuum is *relative* as opposed to *absolute*. Thus, a linear increase in JNDs with increasing object size indicates adherence to Weber's law and therefore provides a rule-based demonstration of the processing of relative – but not absolute – object properties (i.e., size). Results for the manual estimation task showed that JNDs increased linearly with increasing object size, whereas JNDs for the grasping task were refractory to object size. In other words, tactile perceptions but not actions adhered to Weber's law – a finding supporting the theoretical tenets of the SPM.

The first goal of the present investigation was to determine the temporal properties by which absolute tactile cues are available to support grasping. The basis for this question stems from Goodale and Milner's (1992) influential duplex model of visual processing (i.e., the perception-action model: PAM). In particular, the PAM asserts that absolute visual information mediated by dedicated visuomotor networks residing in the PPC (i.e., the dorsal *visual* pathway) support goal-directed actions. Moreover, the PAM contends that absolute visual information is available to the motor system only on a moment-to-moment basis (for review see Goodale, 2011). In support of this view, Goodale et al. (1994) reported that an individual with a visual form agnosia (DF) was able to scale her grip aperture to a target object when it was visible at the time of response cuing; however, that ability was lost when the target object was occluded 2000 ms prior to response cuing². As well, extensive work has shown that reaching and grasping efficiency and effectiveness in neurologically intact individuals is diminished following a period of visual delay (e.g., Bridgeman et al., 1997; Elliott & Madalena, 1987; Elliott et al., 1999; Heath, 2005; Heath et al., 2004; Hu et al., 1999; Westwood et al., 2000; for

review see Heath et al., 2010). For example, Westwood and Goodale (2003) found that grasping responses were refractory to the relative properties of a pictorial illusion “...*only* after the response is cued, and *only* if the target is visible” (p. 243) (i.e., real-time control hypothesis). According to the PAM, the absence of real-time control results in actions mediated via a temporally stable and relative target percept maintained by visuoperceptual networks in the inferotemporal cortex (i.e., the ventral *visual* pathway).

Based on the findings from the visual domain, I modified the tactile manual estimation and grasping tasks used in my group's previous work (Davarpanah Jazi & Heath, 2014) to include a memory delay. Participants used their right hand to manually estimate or grasp differently sized target objects placed on the palm of their left hand. Importantly, responses were completed in: (1) a closed-loop (CL) condition wherein the target object remained on the left palm throughout the response (see also Davarpanah Jazi & Heath, 2014) and, (2) a memory-guided (MG) condition wherein the target object was removed from the left palm 2000 ms prior to response cuing and was unavailable throughout the response. Thus, real-time tactile feedback was unavailable in the MG condition. In terms of research outcomes, if manual estimations are supported via a relative – and temporally stable – tactile percept then JNDs in CL and MG conditions should adhere to Weber's law. In other words, it is predicted that a memory-delay will not influence the nature of the tactile cues supporting perceptions. In terms of the grasping tasks, if absolute tactile cues are available to the motor system only on a moment-to-moment basis then JNDs for the CL and MG conditions should respectively violate and adhere to Weber's law. In particular, it is predicted that the absence of real-time tactile feedback will render the processing of object size via the same relative percept as supporting manual estimations.

The second objective of my study was to determine whether *terminal haptic feedback* derived from physically grasping (i.e., touching) an object influences the nature of the tactile information supporting grasping. In this context I emphasize that haptic feedback is different from tactile feedback because the former stems from physically grasping a target object. Notably, haptic feedback is derived from proprioceptive information

related to finger and thumb orientation and therefore provides absolute cues related to object size. In the context of the present investigation then, haptic feedback offers an additional source of information than the static tactile cues related to the object resting on the palm of the non-grasping limb. Thus, the CL and MG grasping conditions described in the preceding paragraph differ not only in terms of the availability of tactile feedback at the time of response cuing but also with regard to the availability of terminal haptic feedback. To my knowledge, the issue of haptic feedback has not been previously explored in a non-visual grasping experiment. Notably, however, work from the visual domain (Schenk, 2012a; Schenk, 2012b) reported that DF's visual grasping in the absence of haptic feedback was no better than her well-documented visuoperceptual deficits. Accordingly, Schenk proposed that haptic feedback provides a visuo-haptic calibration that can be applied in a predictive fashion to support absolute aperture shaping on future trials (Schenk, 2012a). Although Schenk's findings have received a number of serious challenges (Milner et al., 2012; Whitwell & Buckingham, 2013; Whitwell et al., 2014), his contention represents a salient consideration for tactile-based CL and MG grasping. Thus, I sought to disentangle the putative influence of a memory delay from haptic feedback. To that end, in addition to the MG grasping condition described previously (henceforth referred to as *memory-guided without haptic feedback*: MH-) I included a MG grasping (and manual estimation) condition wherein the experimenter placed the target object between participants' thumb and forefinger once they completed their response to the remembered target location (i.e., *memory-guided with haptic feedback*: MH+). Thus, if haptic feedback engenders a forward calibration based on absolute object information then JNDs in the MH+ grasping condition should be comparable to the CL grasping condition. In other words, the provision of haptic feedback may result in MG grasping responses that violate Weber's law.

2.2 Methods

2.2.1 Participants

Fifteen individuals (2 males and 13 females: age range = 19-31 years) from the University of Western Ontario community volunteered to participate in this study.

Participants self-declared that they were right hand dominant with normal or corrected-to-normal vision. Participants signed consent forms approved by the Office of Research Ethics, University of Western Ontario, and this work was completed according to the Declaration of Helsinki.

2.2.2 Apparatus and procedures

Participants sat for the duration of the experiment in front of a table-top (height = 780 mm, depth = 760 mm, width = 1060 mm) and manually estimated or grasped with their right hand (i.e., thumb and forefinger precision grip) target objects located on the palm of their left hand. Target objects were acrylic blocks painted flat black and were 20, 30 and 40 mm in width and 10 mm in height and depth. Further, target objects were weight-matched (7 g) to preclude size information from being derived from weight cues. In advance of each trial, participants placed the medial surface of their right wrist on a pressure sensitive switch (henceforth referred to as start location) located 200 mm to the right of their midline and 100 mm from the front edge of the table-top. The configuration of the right arm at the start location was such that the shoulder was abducted approximately 40° with elbow and wrist flexed approximately 90° and 45° , respectively. As well, prior to each trial participants were instructed to keep their thumb and forefinger lightly pinched together. In turn, participants positioned their left supinated palm 200 mm to the left of their midline and in the same transverse plane as the right limb's start location. In particular, the left shoulder was at a neutral angle with the elbow flexed at approximately 90° . Computer and auditory events were controlled via MATLAB (7.9.0: The MathWorks, Natick, MA, USA) and the Psychophysics toolbox extensions (ver 3.0) (Brainard, 1997). Moreover, I emphasize that participants wore translucent goggles (PLATO Translucent Technologies, Toronto, ON, Canada) throughout data collection to preclude visual information regarding target objects.

2.2.3 Manual estimation tasks

For all manual estimation trials a target object was placed on the center of the left palm (denoted via a 10 mm by 10 mm cross) with the target's long-axis oriented in the anteroposterior plane. Subsequently, the experimenter initiated a 4000 ms tactile preview

phase after which time participants completed manual estimations in each of four conditions. In the closed-loop with haptic feedback condition (CH+), a high-frequency tone (2900 Hz for 1000 ms) presented after the preview phase signaled participants to manually estimate the width of the target object by separating the distance between the thumb and forefinger of their right hand. Importantly, the response was completed while participants maintained contact with the start location. Once participants indicated that they had appropriately estimated the size of the target object (via verbal prompt), they were instructed to close the separation between their thumb and forefinger and subsequently reach to grasp – but not lift – the target object. At the end of the grasping response participants thumb and forefinger were therefore in contact with the target object and the palm of their non-grasping limb. Participants held the target object for approximately 2000 ms before returning to the start location in preparation for a subsequent trial. For the closed-loop without haptic feedback condition (CH-) participants completed the same experimental procedures as described above with the only exception that a grasping response was not initiated following the manual estimation. Thus, the CH+ but not the CH- condition provided terminal haptic feedback related to object size.

In the memory-guided with haptic feedback condition (MH+) the experimenter removed the target object from the left palm following the preview period and initiated a 2000 ms delay. Following the delay, a tone (see above) signaled participants to complete their manual estimation. Once participants were confident that they had accurately estimated the target object size they were instructed to close the separation between their thumb and forefinger and subsequently reach to “grasp” the remembered target object. At the end of the grasping response participants’ thumb and forefinger were in contact with the palm of their left hand; however, the absence of the physical target object precluded immediate haptic feedback related to the size of the target object. Thus, to provide terminal haptic feedback the experimenter placed the target object between participants’ right thumb and forefinger following movement offset (see definition in Section 2.2.5). In particular, at movement offset a computer-generated cue signaled the experimenter to place the target object on the lateral surface of participants’ left palm and the experimenter subsequently

slid the object until it first contacted the thumb of the grasping hand and then positioned the opposite side until it contacted the forefinger of the grasping hand. Participants were then instructed to adjust the target object between their thumb and forefinger to produce a stable grasp (i.e., a grasp that would allow for lifting of the target object). As in the CH+ condition, the target object was then held (but not lifted) for 2000 ms before the participant returned to the start location. In turn, in the memory-guided without haptic feedback condition (MH-) participants remained at the start location following their manual estimation; that is, the response was completed without terminal haptic feedback.

2.2.4 Grasping tasks

In line with the manual estimation tasks, grasping trials began with the experimenter placing a target object on the palm of participants' left hand after which time a 4000 ms tactile preview was provided. Following the preview, grasping responses were completed in each of three conditions. In the closed-loop with haptic feedback condition (CH+) participants reached to grasp – but not lift – the target object in response to the imperative tone. Following contact, participants held the object for approximately 2000 ms before returning to the start location. In the memory-guided with haptic feedback (MH+) condition the target object was removed from participants' palm following the preview phase and the imperative tone was provided after a 2000 ms delay. In response to the tone participants completed a grasp to the remembered target location and after achieving their goal location the experimenter positioned the physical target object between participants' right thumb and forefinger as per the description outlined for the MH+ condition in the manual estimation task. For the memory-guided without haptic feedback (MH-) condition participants completed the same procedures as described for the MH+ condition with the only exception being that the experimenter did not position the target object between participants' thumb and forefinger at movement offset. In other words, at the end of the response participants contacted the palm of their non-grasping limb but did not received haptic feedback related to object size. The grasping tasks did not entail the same fully factorial combinations as the manual estimation tasks because it was not possible to structure a CL grasp without terminal haptic feedback (see Figure 2-1 for a schematic of the timeline of tactile, auditory and haptic events).






















	Task	4000 ms Tactile Preview	Response	Movement Offset
Manual Estimation	CH+		 	
	CH-		 	-
	MH+		2000 ms 	
	MH-		2000 ms 	-
Grasping	CH+		 	
	MH+		2000 ms 	
	MH-		2000 ms 	-

Figure 2-1: Schematic representation of the timeline of tactile, auditory and haptic events across manual estimation (CH+ and CH- refer to closed-loop with and without haptic feedback, respectively; MH+ and MH- refer to memory-guided with and without haptic feedback, respectively) and grasping (CH+ refers to closed-loop with haptic-feedback, MH+ and MH- refer to memory-guided with and without haptic feedback, respectively) conditions. For all tasks, participants were provided a 4000 ms tactile preview of the target object. For CL manual estimation and grasping tasks, responses were cued immediately following the preview phase and the schematic's transparent depiction of the target object during the 'Response' phase indicates that it remained on the palm of participants' non-grasping limb throughout the response. In the MG tasks, the target object was removed from the palm following the preview phase and a 2000 ms delay was then introduced – removal of the target object precluded real-time tactile feedback at movement cuing and during the 'Response' phase. As well, the depiction of a target object at 'Movement Offset' indicates those conditions wherein terminal haptic feedback was available either immediately after the response (i.e., CH+ tasks) or when provided by the experimenter (i.e., MH+ tasks).

Manual estimation and grasping tasks were performed in separate sessions conducted at least 24 h apart with tasks being counterbalanced in a sequential order. Within each session, the different manual estimation and grasping conditions were completed in separate and randomly ordered blocks that entailed 15 trials (ordered randomly) to each object size. Thus, 180 and 135 trials were performed for the manual estimation and grasping tasks, respectively. Further, the manual estimation and grasping tasks required approximately 65 and 50 min, respectively to complete. Thus, it was imperative that the different tasks were performed in separate sessions (see above) to reduce participants' physical and mental fatigue.

2.2.5 Data analysis

The position of the right limb was measured via infrared emitting diodes (IREDs) placed on the lateral surface of the distal phalanx of the forefinger, the medial surface of the distal phalanx of the thumb, and the styloid process of the wrist. IRED position data were sampled at 400 Hz via an OPTOTRAK Certus for 1500 ms following response cuing. IRED position data were filtered offline via a second-order dual-pass Butterworth filter employing a low-pass cutoff frequency of 15 Hz. Subsequently, instantaneous velocities were computed from the position (i.e., displacement) data via five-point central finite difference algorithm. For the manual estimation task, grip aperture (GA) was measured after participants confirmed (via oral response) that they had produced an appropriate size judgment and when offline analysis showed that they had achieved a stable aperture. For the grasping conditions, movement onset was marked when participants released pressure from the start location switch and movement offset was determined when wrist velocity fell below a value of 50 mm/s for 20 consecutive frames (i.e., 50 ms).

2.2.6 Dependent variables and statistical analyses

For the manual estimation tasks, I examined grip aperture (GA: resultant distance between thumb and index finger) and associated JNDs via 2 (delay condition: CL and MG) by 2 (haptic feedback condition: H+ and H-) by 3 (object size: 20, 30 and 40 mm) repeated measures ANOVA. For the grasping tasks, I examined grasping time (GT: time

from movement onset to movement offset), peak grip aperture (PGA: maximum resultant distance between thumb and forefinger) and associated JNDs via 3 (condition: CH+, MH+, MH-) by 3 (object size: 20, 30 and 40 mm) repeated measures ANOVA. Main effects and interactions were considered significant at an alpha level of 0.05 or less. Post-hoc contrasts of within-condition effects of object size were examined via power-polynomials (i.e., trend analysis: see Pedhazur 1997), whereas between-condition effects were decomposed via paired samples *t*-tests.

2.2.7 Just-noticeable-difference scores (JNDs)

Weber's law states that the smallest detectable difference (i.e., the JND) between an original and a comparator stimulus is proportional to the magnitude of the original stimulus. In the majority of the literature, JNDs are determined via an arbitrary statistical criterion wherein participants reliably discriminate (via oral report or other perceptual judgment) between the original and comparator stimulus (e.g., 75% of trials). Of course, for a grasping task a statistical criterion is not available for JND computation; rather, the JNDs computed here and elsewhere (Davarpanah Jazi & Heath, 2014; Davarpanah Jazi et al., 2014; Ganel et al., 2008a; Ganel et al., 2008b; Heath et al., 2012; Holmes & Heath, 2013; Holmes et al., 2013; Holmes et al., 2011; Pettypiece et al., 2009) represent the within-participants standard deviation of grip aperture. According to Ganel et al. (2008a) the basis for this JND computation is drawn from the classic method of adjustment wherein variance provides a measure of visuomotor uncertainty "...for which the observer is unable to tell the difference between the size of the comparison and the target object" (p. 600) (see also Marks & Algorn, 1998). In demonstration of this approach, Figure 2-2 shows manual estimation and grasping task results of an exemplar participant in the CH+ condition. The figure demonstrates that trial-to-trial grip aperture variability (i.e., the JNDs) in the manual estimation task increased linearly as a function of increasing object size, whereas JNDs for the grasping task (computed at PGA) did not vary systematically with object size. Thus, I interpret a linear increase in JNDs with increasing object size as adherence to Weber's law.

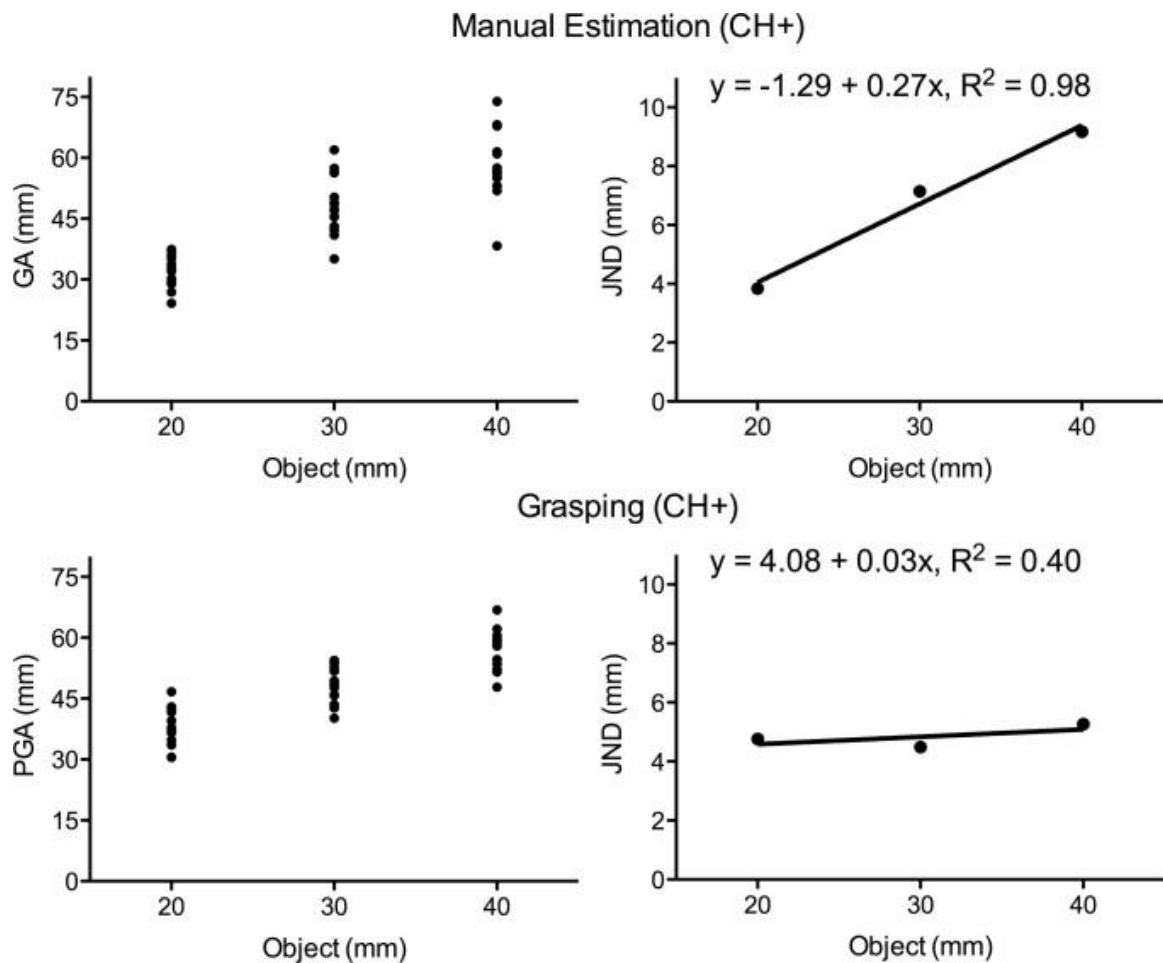


Figure 2-2: Exemplar data from a participant in the current study performing CH+ manual estimation and grasping tasks. The upper left panel shows trial-to-trial grip aperture (GA: mm) for manual estimations of differently sized objects and the upper right panel shows the just-noticeable-difference scores (JNDs) associated with the trial-to-trial GA values. The lower left panel shows trial-to-trial peak grip aperture (PGA: mm) values associated with grasping differently sized objects and the lower right panel shows the computed JNDs associated with the trial-to-trial PGA values. Notably, JNDs for the manual estimation task increased with increasing object size, whereas JNDs for the grasping task did not systematically vary as a function of object size. In other words, CH+ manual estimation and grasping tasks adhered to and violated, respectively, the psychophysical principles of Weber's law.

2.3 Results

2.3.1 Manual estimation

Results for GA produced main effects of haptic feedback, $F(1,14) = 11.52$, $p < 0.01$, and object size, $F(2,28) = 149.39$, $p < 0.001$. In particular, H+ trials (39 mm, SD = 8) produced larger GAs than their H- trial counterparts (35 mm, SD = 9), and Figure 2-3 demonstrates that GAs (for all conditions) increased linearly with increasing object size (linear effect: $F(1,14) = 178.17$, $p < 0.001$). Results for JNDs revealed a main effect of object size, $F(2,28) = 48.92$, $p < 0.001$, indicating that values (for all conditions) increased linearly with increasing object size (linear effect: $F(1,14) = 93.43$, $p < 0.001$). Further, I note that JNDs for delay and feedback conditions did not produce main effects ($F_s(1,14) = 0.16$ and 1.34 for delay and feedback manipulations, respectively, $p_s > 0.26$) or higher-order interactions involving object size ($F_s(2,28) = 2.44$, 0.43 and 0.35 for delay by object size, feedback by object size and delay by feedback by object size interactions, respectively, $p_s > 0.10$) (see also Figure 2-3). I highlight these null findings because they demonstrate that manual estimations adhered to Weber's law independent of the availability of real-time tactile feedback and terminal haptic feedback.

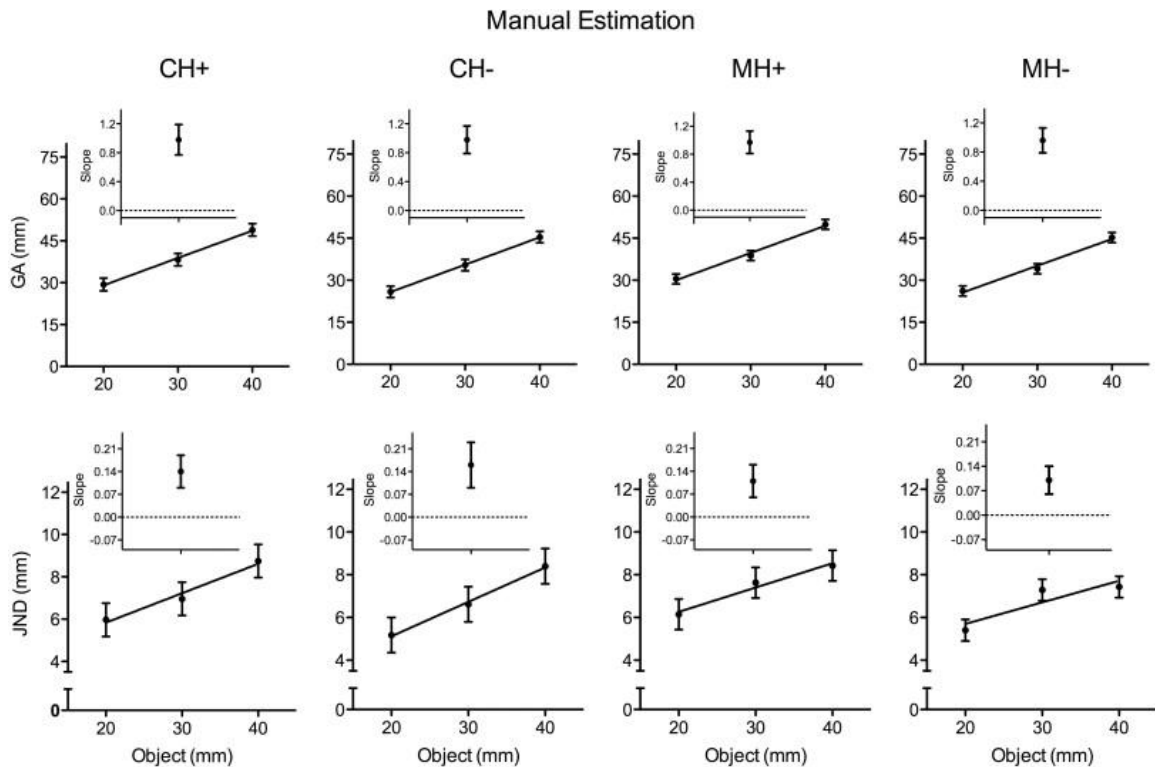


Figure 2-3: Manual estimation tasks: mean grip aperture (GA) (upper panels) and just-noticeable-difference scores (JNDs) (lower panels) for the different target objects across closed-loop and memory-guided conditions performed with (i.e., CH+ and MH+, respectively) and without (i.e., CH- and MH-, respectively) terminal haptic feedback. The solid line in each panel represents the regression line and error bars represent 95% within-participants confidence intervals computed as a function of the mean-squared error term for object size (Loftus & Masson, 1994). The inset figure for each panel represents the mean participant-specific slope representing GA and JND scores to object size and the error bar in each panel represents the 95% between-participant confidence intervals. The absence of overlap between the error bar and zero represents a slope value that differs from zero (Cumming & Finch, 2005).

2.3.2 Grasping

GT elicited a main effect of condition, $F(2,28) = 5.10$, $p < 0.05$, such that the CH+ condition (600 ms, $SD = 25$) produced shorter movement durations than MH+ (620 ms, $SD = 30$) and MH- (613 ms, $SD = 28$) conditions ($t_s(14) = -2.88$ and -2.26 for CH+ vs. MH+ and CH+ vs. MH-, respectively, $p_s < 0.05$), and the latter conditions did not reliably differ ($t(14) = 1.09$, $p = 0.29$). Results for PGA revealed main effects of condition, $F(2,28) = 23.24$, $p < 0.001$, object size, $F(2,28) = 72.62$, $p < 0.001$, and their interaction, $F(4,56) = 4.46$, $p < 0.01$. Figure 2-4 shows that PGAs for all conditions increased linearly as a function of increasing object size (linear effect: $F_s(1,14) = 64.89$, 86.03 and 59.89 for CH+, MH+ and MH-, respectively, $p_s < 0.001$); however, PGAs in the CH+ and MH- conditions were respectively larger ($t(14) = 4.63$, $p < 0.001$) and smaller ($t(14) = 3.43$, $p < 0.01$) than their MH+ condition counterpart.

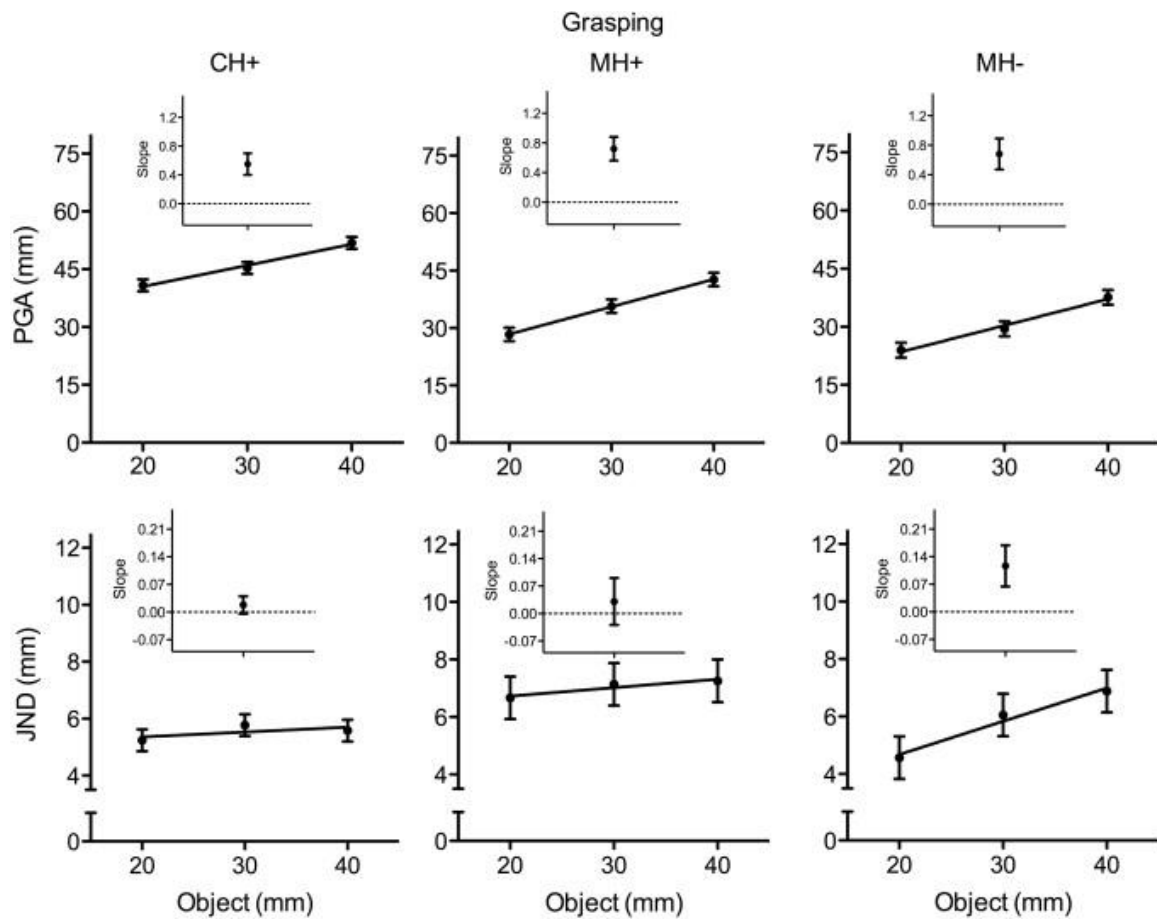


Figure 2-4: Grasping tasks: mean peak grip aperture (PGA) (upper panels) and just-noticeable-difference scores (JNDs) (lower panels) for the different target objects in closed-loop (CH+) and memory-guided conditions performed with (MH+) and without (MH-) terminal haptic feedback. The solid line in each panel represents the regression line and error bars represent 95% within-participants confidence intervals computed as a function of the mean-squared error term for object size (Loftus & Masson, 1994). The inset figure for each panel represents the mean participant-specific slope representing PGA and JND scores to object size and the error bar in each panel represents the 95% between-participant confidence intervals. The absence of overlap between the error bar and zero represents a slope value that differs from zero (Cumming & Finch, 2005).

Results for JNDs revealed main effects of condition, $F(2,28) = 5.63$, $p < 0.01$, object size, $F(2,28) = 6.71$, $p < 0.01$, and their interaction, $F(4,56) = 4.82$, $p < 0.01$. JNDs for the MH- condition produced an effect for object size, $F(2,28) = 10.56$, $p < 0.001$), such that values increased linearly with increasing object size (linear effect: $F(1,14) = 23.09$, $p < 0.001$). In contrast, JNDs for CH+ and MH+ conditions did not reliably differ with object size ($F_s(2,28) = 2.05$ and 0.74 for CH+ and MH+, respectively, $p_s > 0.15$). More directly, JNDs for the CH+ and MH+ conditions did not increase linearly with increasing object size (linear effects: $F_s(1,14) = 1.96$ and 1.15 , for CH+ and MH+, respectively, $p_s > 0.18$).

2.3.3 Participant-specific slopes relating GA/PGA and JNDs to object size

I computed participant-specific slopes relating GA/PGA and JND values to object size. For the manual estimation tasks, slopes were examined via 2 (delay condition: CL and MG) by 2 (haptic feedback condition: H+ and H-) repeated measures ANOVAs, whereas the slopes for the grasping tasks were examined via one-way repeated measures ANOVAs. Manual estimations did not elicit main effects or interactions for GA ($F_s(1,14) = 0.06$, 0.03 and 0.04 for main effects of delay and feedback and their interaction, respectively, $p_s > 0.81$) or JND ($F_s(1,14) = 2.74$, 0.04 and 0.56 for main effects of delay and feedback and their interaction, respectively, $p_s > 0.12$) slopes (see Table 1 and Table 2 for GA and JND slopes and associated regression equations). For the grasping tasks, PGA slopes for the CH+ condition (0.55 , $SD = 0.26$) were shallower than the MH- (0.68 , $SD = 0.34$) and MH+ (0.72 , $SD = 0.30$) conditions ($t_s(14) = -3.75$ and -2.81 for CH+ vs. MH+ and CH+ vs. MH-, respectively, $p_s < 0.02$), and the latter tasks did not reliably differ ($t(14) = 0.62$, $p = 0.54$). In terms of JND slopes, the CH+ (0.02 , $SD = 0.04$) and MH+ (0.03 , $SD = 0.11$) conditions did not reliably differ ($t(14) = -0.44$, $p = 0.67$), and were less than the MH- (0.12 , $SD = 0.09$) condition ($t_s(14) = -5.38$ and -2.48 for CH+ vs. MH- and MH+ vs. MH-, respectively, $p_s < 0.03$) (see also Table 2-1 and Table 2-2).

Table 2-1: Linear regression equations and proportion of explained variance (R^2 values) relating grip aperture (i.e., manual estimation tasks) and peak grip aperture (i.e., grasping tasks) to object size for each experimental condition.

	Feedback Condition	Delay Condition			
		CL	R^2	MG	R^2
Manual Estimation	H+	$y = 9.53 + 0.98x$	(0.99)	$y = 10.55 + 0.97x$	(0.99)
	H-	$y = 6.26 + 0.98x$	(0.99)	$y = 6.54 + 0.95x$	(0.99)
Grasping	H+	$y = 29.52 + 0.55x$	(0.99)	$y = 14.04 + 0.72x$	(0.99)
	H-	-	-	$y = 9.90 + 0.68x$	(0.99)

Note: CL = closed-loop; MG = memory-guided; H+ = with haptic feedback; H- = without haptic feedback

Table 2-1: Linear regression equations and proportion of explained variance (R^2 values) relating just-noticeable-difference scores for grip aperture (i.e., manual estimation tasks) and peak grip aperture (i.e., grasping tasks) to object size for each experimental condition.

	Feedback Condition	Delay Condition			
		CL	R^2	MG	R^2
Manual Estimation	H+	$y = 3.06 + 0.14x$	(0.97)	$y = 3.98 + 0.11x$	(0.97)
	H-	$y = 1.89 + 0.16x$	(0.99)	$y = 3.68 + 0.10x$	(0.80)
Grasping	H+	$y = 5.02 + 0.02x$	(0.41)	$y = 6.14 + 0.03x$	(0.90)
	H-	-	-	$y = 2.37 + 0.12x$	(0.97)

Note: CL = closed-loop; MG = memory-guided; H+ = with haptic feedback; H- = without haptic feedback

The inset panels of Figure 2-3 and Figure 2-4 present the mean participant-specific GA/object size, PGA/object size, and JND/object size slopes and their associated 95% between-participant confidence interval for all manual estimation (Figure 2-3) and grasping (Figure 2-4) tasks. Notably, the absence of overlap between the error bar and zero represents a slope that reliably differs from zero (Cumming & Finch, 2005). As such, the inset panels of Figure 2-3 graphically demonstrate that GA/object size and JND/object size slopes for each manual estimation task differed from zero. In turn, the inset panels of Figure 2-4 demonstrate that PGA/object size slopes for each grasping task differed from zero and that the JND/object size slope for the MH- condition differed from zero. In turn, JND/object size slopes for the CH+ and MH+ conditions did not reliably differ from zero. Thus, my graphical analyses demonstrate that: (1) manual estimations adhere to Weber's law independent of delay and haptic feedback, and (2) grasping responses performed with (CH+ and MH+) and without (MH-) haptic feedback respectively violate and adhere to Weber's law.

2.4 Discussion

Previous work has shown that tactile-based manual estimations adhere to Weber's law, whereas grasping violates the law (Davaranah Jazi & Heath, 2014) – a result consistent within the SPM's assertion that tactile perceptions and actions are mediated via relative and absolute cues, respectively (Dijkerman & deHaan, 2007). In the present investigation, I sought to determine whether the introduction of a memory-delay and/or the availability of terminal haptic feedback influence the nature of the information supporting tactile-based manual estimations and grasping. In the below, I first discuss results for my manual estimation tasks prior to outlining the findings for the different grasping conditions.

2.4.1 Manual estimation: a relative percept supports obligatory judgments of size

GAs for the different manual estimation conditions increased linearly with increasing object size. As such, participants discriminated between the different objects regardless of the memory delay and terminal haptic feedback manipulations used here. It is,

however, important to note that the H+ trials produced larger GAs than their H- counterparts. In accounting for this finding, I note that H+ trials involved physically grasping the target object following the manual estimation response. Indeed, grasping a physical object results in the adoption of orthogonal thumb and forefinger approach vectors to avoid an early collision (i.e., safety margin strategy) and to ensure that the forces applied by effectors are parallel to one another at the time of contact (i.e., prevents slipping) (Smeets & Brenner, 1999). Thus, obligatory knowledge that a manual estimation would be followed by a grasping response may have resulted in the adoption of a ‘safety margin’ task-set similar to that used for grasping. Furthermore, I note that the proposed safety margin task-set did not influence the representation of object size as the slopes relating GA to object size were consistent across H+ and H- trials.

Results showed that JNDs for the different manual estimation conditions increased linearly with increasing object size; that is, results adhered to Weber's law. Of course, that CH+ and CH- trials adhered to Weber's law supports earlier work by my group (Davarpanah Jazi & Heath, 2014) and provides direct evidence for the SPM's contention that tactile-based perceptions are mediated via relative information. Moreover, the observation that the memory delay in combination with terminal haptic feedback manipulation (i.e., MH+, MH-) also showed adherence to Weber's law – and produced equivalent JND/object size slopes - demonstrates that tactile-based perceptions are supported via an immutable percept. This result is analogous to the properties of the visual system (Goodale & Milner, 2013) and the notion that obligatory judgments are supported via a top-down and experiential-dependent representation of the physical environment.

2.4.2 Grasping: memory delay and the provision of terminal haptic feedback influence PGA

PGAs across all conditions increased linearly with object size; however, values for the CH+ condition were larger than the MH+ condition, which in turn were larger than the MH- condition. That the memory conditions yielded smaller PGAs is consistent with work from the visual domain showing that responses directed to an area once occupied

by, or adjacent to, a target object (so-called pantomime-grasping) results in smaller PGAs than grasping a physical target object (Cavina-Pratesi et al., 2011; Davarpanah Jazi et al., 2014; Goodale et al., 1994; Holmes & Heath, 2013; Holmes et al., 2013; Westwood et al., 2000). After all, grasping to an area once occupied by an object obviates the need for orthogonal effector approach vectors because the participant and not the physical properties of the ‘remembered’ object determine the aperture size necessary for a successful response. In addition, that PGAs for the MH+ condition were intermediary to the CH+ and MH- conditions suggests that the terminal haptic feedback used here (i.e., the feedback that was provided following the end of the grasping response) allowed for improved – albeit incomplete – calibration of the aperture necessary to grasp a physical target object (see also Bingham et al., 2007). It is, however, less clear why PGA/object size slopes for MH+ and MH- conditions were equivalent and were steeper than the CH+ condition. One account for such a finding is that both MH+ and MH- conditions were associated with an obligatory and perception-based representation of object size. In other words, the PGA/object size slopes can be interpreted to provide *indirect* evidence that a memory delay resulted in the specification of object size via relative cues. Notably, and as will be discussed in detail in the following section, such an explanation is tempered by results from my JND analyses providing *direct* evidence that MH-, but not MH+ trials, adhered to Weber's law. As a final issue in this section, I note that MH+ and MH- conditions produced longer GTs than the CH+ condition. This is an expected finding and is commensurate with work from the visual domain showing that a memory delay elicits longer GTs due to increased uncertainty regarding target location and size (Berthier et al., 1996; Churchill et al., 2000; Holmes et al., 2011; Westwood et al., 2000; Wing et al., 1986). Thus, the analysis of GT evinces that the presence of real-time feedback (tactile or haptic) optimizes grasping efficiency.

2.4.3 Grasping JNDs: memory delay and the provision of terminal haptic feedback

JNDs for the CH+ condition did not vary systematically with object size and therefore violated Weber's law. This finding supports earlier work by my group (Davarpanah Jazi & Heath, 2014) and supports the SPM's contention that tactile-based actions are mediated

via absolute information. In turn, JNDs for the MH- condition increased linearly with increasing object size and therefore adhered to Weber's law. In other words, results evince that MG grasping is supported by the same relative information as manual estimations. To my knowledge such a finding provides the first evidence that the dorsal tactile cortical processing stream operates in the same 'real-time' mode as its visual counterpart (Westwood & Goodale, 2003; for review see Goodale, 2011). Interestingly, however, the use of relative cues for MG grasping was modulated by the provision of terminal haptic feedback. In particular, the MH+ condition yielded JNDs that violated Weber's law. More specifically, results show that the MH+ condition yielded JND/object size slopes that were equivalent to the CH+ condition and were shallower than the MH- condition. Thus, results for the MH+ condition provide rule-based evidence that the provision of terminal haptic feedback determines whether relative or absolute information supports MG grasping. As well, I note that the dissociable adherence of MH+ and MH- conditions to Weber's law cannot be accounted for by a speed/accuracy trade-off in motor output variability (Lemay & Proteau, 2001; Meyer et al., 1988). Indeed, if that were the case then the larger PGAs in the MH+ condition would have produced JNDs that were larger than the MH- condition.

2.4.4 Terminal haptic feedback supports an absolute tactile-haptic calibration

An important issue to address is how terminal haptic feedback supports the absolute specification of object size in a tactile-based MG grasping task. In reconciling this issue I first note that the different target objects used here were randomly varied from trial-to-trial. Thus, participants could not simply rely on haptic feedback from trial N-1 to plan a current grasping response; rather, results suggest a tactile-haptic integration. Second, and as outlined in the Introduction, some work from the visual domain has shown that terminal haptic feedback supports the absolute specification of object size via a visuo-haptic calibration process. In particular, Schenk (2012a) showed that DF's metrical grip aperture scaling was limited to trials wherein she was able to physically grasp a target object; that is, terminal haptic feedback from the target object supported the absolute specification of object size (but see Milner et al., 2012; Whitwell & Buckingham, 2013).

In addition, (1) Bingham et al. (2007) showed that responses performed in the absence of online limb vision demonstrated final grip apertures that were comparable to their CL counterparts only when terminal haptic feedback was available, and (2) a recent study by my group showed that pantomime-grasping responses performed with and without terminal haptic feedback respectively violated and adhered to Weber's law (Davarpanah Jazi et al., 2014). Accordingly then, some work from the visual domain has proposed that haptic error signals derived from physically grasping a target object support a *visuo-haptic* calibration that is used in a predictive fashion to specify absolute aperture shaping on future trials (Bingham et al., 2007; Davarpanah Jazi et al., 2014; Schenk, 2012a; Schenk, 2012b)³. In a similar vein, I propose that the absolute specification of object size in the current experiment was supported via a *tactile-haptic* calibration. More directly, I contend that haptic error signals support the absolute calibration between tactile cues and motor output. In further support for my proposal, Ernst and Bühlhoff's (2004) maximum-likelihood estimation model contends that the effective and efficient execution of actions is associated with a multisensory reweighting based on the most reliable sensory input. Hence, in my grasping task the static tactile cues associated with the target object resting on the palm of the non-grasping (left) hand may have been less reliable than the absolute haptic feedback associated with physically grasping the target object. Thus, the observation that JNDs for CH+ and MH+ conditions (but not the MH- condition) violated Weber's law provides rule-based evidence of an absolute tactile-haptic calibration specified via the preferential weighting of object size via terminal haptic feedback.

A final issue that I address relates to Whitwell et al.'s (2014) follow-up examination of Schenk's (2012a) work involving DF. In particular, Whitwell et al. showed that DF's ability to scale her grip aperture to object size is independent of whether the visual size of the object matches the haptic feedback derived from 'touching' the object. As such, Whitwell et al. contend that haptic feedback related to the attainment of a movement goal location, and not object size per se, is sufficient to allow DF to calibrate her visuomotor system. Of course, such an explanation cannot be extended to my tactile-haptic study because both the MH+ and MH- conditions provided sensory cues related to the attainment of the movement goal location (i.e., contact of the grasping limb with the palm

of the non-grasping limb). Indeed, although both the MH+ and MH- conditions received haptic cues related to the attainment of a movement goal only the ability to physically grasp the target object (i.e., the MH+ condition) resulted in an absolute tactile-haptic calibration. Further, I wish to emphasize that drawing direct corollaries between my work and Schenk (2012a) and Whitwell et al. (2014) must be tempered by the fact that the latter studies are based on: (1) the investigation of a visuo-haptic calibration, and (2) an individual who has experienced a long-term recovery from brain injury. Therefore, my results should be interpreted in the context of how terminal haptic feedback supports the dissociable cortical processing streams underlying somatosensory processing (i.e., the SPM).

2.5 Conclusions

Manual estimations adhered to Weber's law regardless of the memory and haptic feedback manipulations used here. Thus, manual estimation is a perceptual task mediated via an immutable and relative percept of object size. In addition, MG grasping performed with and without terminal haptic feedback respectively violated and adhered to Weber's law. Such results indicate that terminal haptic feedback supports an absolute calibration between a tactile defined object and the required motor output. What is more, my study highlights that multiple somatosensory cues (i.e., tactile and haptic) support goal-directed grasping.

2.6 Footnotes

1. In addition to manual estimation and grasping tasks, a classic method of adjustment task was used wherein participants manipulated the size of an object appearing on a computer screen to match the felt size of the target object resting on the palm or forearm of their left limb. The results for the method of adjustment task matched the results for the manual estimation task (Davaranah Jazi & Heath, 2014).
2. DF is an extensively studied individual with bilateral lesions to her lateral occipital cortex (James et al., 2003) and a documented visual agnosia. Evidence

has shown that DF's lesions impair her visual form perceptions but not her ability to use vision to interact with the environment (for extensive review of this issue see Goodale & Milner (2013)).

3. The calibration between the sensory and motor systems is intrinsic and reflects the normal process of motor skill acquisition (Held & Hein, 1958; see also Redding & Wallace, 2003). Moreover, intrinsic skill acquisition has been shown to occur on a trial-by-trial basis (Laubach et al., 2000).

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Chapter 3

3 Pantomime-grasping: the 'return' of haptic feedback supports the absolute specification of object size

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3.1 Introduction

Weber's law is an extensively studied principle of human perception asserting that the 'just-noticeable-difference' (JND) associated with discriminating between an original and a comparator stimulus is in constant proportion to the magnitude of the original stimulus. Moreover, the law states that the sensitivity of detecting a change in any physical continuum is *relative* as opposed to *absolute*. The law is recognized for its generalizability to perception-based processing across numerous stimulus properties (e.g., brightness, numerosity, shape, size) and sensory domains (e.g., auditory, haptic, visual) (for extensive review see Marks & Algom, 1998). Moreover, Weber's law provides an important framework for understanding the dissociable nature of the visual information mediating perceptions and actions. For example, Ganel et al. (2008a) showed that visually guided perceptions and actions (i.e., precision thumb and forefinger grasp) of differently sized 3D objects produced JNDs that respectively adhered to and violated Weber's law¹. In other words, results show that the *perceptual* resolution of smaller objects is greater than for larger objects within the same sensory continuum (i.e., relative visual processing), whereas the *visuomotor* system computes the metrical size of an object independent of its placement within the same continuum (i.e., absolute visual processing). Accordingly, Ganel et al. interpreted their findings within Goodale and Milner's (1992) perception-action model (PAM) and the contention that relative visual information processed via the ventral visual pathway mediates perceptions and that absolute visual information processed by dedicated visuomotor networks residing in the dorsal visual pathway mediates actions².

Recent work by my group replicated Ganel et al.'s (2008a) findings related to visually guided grasping (Heath et al., 2011; Heath et al., 2012). In addition, my group has shown that grasping responses completed after 2000 ms of visual delay (i.e., memory-guided (MG) grasping) similarly violate Weber's law (Holmes et al., 2011). Notably, however, grasping responses requiring the decoupling of the spatial relations between stimulus and response (pantomime-grasping: see Holmes et al., 2013) and responses requiring the 'grasp' of a 2D target (Holmes & Heath, 2013; but see Christiansen et al., 2014) have

been shown to adhere to Weber's law. For example, Holmes et al. (2013) had participants pantomime-grasp to an area adjacent to differently sized visual target objects and observed that JNDs adhered to Weber's law – a result interpreted as providing support for the theoretical tenets of the PAM and providing rule-based evidence that the top-down demands of dissociating a stimulus and a response is a perception-based task mediated via relative visual information.

The conclusion forwarded by Holmes et al. (2013) is commensurate with several other pantomime-grasping studies that have focused their analyses on the timing and magnitude of peak grip aperture (PGA). In particular, Goodale et al. (1994) employed two pantomime-grasping procedures wherein participants completed responses to an area once occupied by an object (Experiment 1 and 2; see also Cavina-Pratesi et al., 2011; Westwood et al., 2000) and when responses were directed to an area adjacent to a visual object (Experiment 3; see also Holmes et al., 2013). Results showed that PGA for both pantomime-grasping tasks was smaller than their closed-loop (CL) grasping counterparts, and more recent work has shown that the result is independent of online vision of the grasping environment (Fukui & Inui, 2013). Further, Goodale et al. reported that patient DF³ scaled her grip aperture to object size during CL grasping but not when performing either of the aforementioned pantomime-grasping tasks. As such, the smaller grip aperture associated with pantomime-grasping coupled with DF's impaired performance provides coalescent evidence that pantomime-grasping is a perception-based task.

The term pantomime-grasping derives from Liepmann's (1905/1980) definition of an action performed in the absence of physically interacting with a tool and/or object. Thus, the 'traditional' pantomime-grasping tasks outlined in the preceding paragraph differ *visually* from more 'natural' grasping tasks because the object has been removed from the grasping environment and/or is decoupled from the spatial location of the response. In addition, natural grasping entails physically touching a target object and therefore produces cues from proprioceptive feedback related to finger and thumb orientation (henceforth referred to as haptic feedback)⁴ – feedback that provides information related to the *absolute* size of the target object (Davaranah Jazi & Heath, 2014; for extensive

reviews see Dijkerman & deHaan, 2007 or Lederman & Klatzky, 2009). In contrast, haptic feedback is unavailable in traditional pantomime-grasping tasks (e.g., Cavina-Pratesi et al., 2011; Goodale et al., 1994; Holmes et al., 2013; Westwood et al., 2000). Thus, it is possible that the perception-based nature of traditional pantomime-grasping relates to the task's *visual* and/or *haptic* properties. In demonstration of this issue, Bingham et al (2007) employed a mirror-box apparatus that permitted grasping in the absence of online limb vision to an area represented by a physical or virtual (i.e., pantomime-grasping) object without disrupting continuous object vision. The results of their study demonstrated that PGAs for pantomime-grasping were smaller than when grasps were directed to a physical object. Accordingly, Bingham et al. proposed that the absence of a physical target precluded a visuo-haptic calibration necessary to support the absolute specification of object size. In addition, Schenk (2012a,b) demonstrated that the presence of haptic feedback influences DF's ability to scale her pantomime-grasping to object size. In particular, Schenk employed a mirror-box environment similar to Bingham et al. that permitted a to-be-grasped target object to be removed from the grasping environment without occluding its vision. Results showed that DF's pantomime-grasping (i.e., the target object was not present at the movement goal location) was no better than her well-documented visuoperceptual deficits. In contrast, DF's pantomime-grasping within a block of trials that afforded intermittent and predictable haptic feedback allowed her to produce PGAs that reliably scaled to object size. Although Schenk did not provide a mechanistic account for his observations, Whitwell et al. (2014) proposed that *if* haptic feedback supports DF's absolute specification of object size then it may do so by providing feedback related to finger and thumb endpoints that is used in a predictive manner to support aperture shaping on future trials. Additionally, Whitwell et al. proposed that the importance of haptic feedback for DF's performance might arise across a series of trials wherein an error signal related to an expected and observed outcome supports the absolute calibration between vision and motor output. In spite of the fact that Schenk's findings have received a number of serious challenges (Whitwell et al., 2014; see also Milner et al., 2012; Whitwell & Buckingham, 2013), there remains limited evidence as to whether haptic feedback in

neurologically intact individuals influences the nature of the information (i.e., absolute vs. relative) supporting pantomime-grasping.

The goal of the present investigation was to examine whether terminal haptic feedback related to absolute object size influences the extent to which a memory-based pantomime-grasping task adheres to - or violates - Weber's law. Indeed, such an inquiry provides a direct and rule-based framework to examine the nature of the sensory information supporting such actions. To accomplish my objective, I had neurologically intact participants grasp differently sized target objects (i.e., 20, 30, 40 and 50 mm) in three conditions organized in separate blocks of trials. As shown in Figure 3-1, all conditions entailed the visual preview of a target object after which time vision was occluded – and remained occluded for the duration of a trial – and responses were subsequently cued following a brief (i.e., 1000 ms) delay. The introduction of the delay provided the experimenter with sufficient time to remove the target object from the grasping environment. Moreover, because my group's previous work (Holmes et al., 2011) has shown that CL and MG grasps similarly violate Weber's law the occlusion of vision throughout a response provided the necessary framework to selectively examine the influence of haptic feedback on grasping. In the *no-target pantomime-grasp, without haptic feedback* condition (PH-), the target object was removed from the grasping environment prior to response cuing and participants were instructed to grasp to the target's remembered location. In the *no-target pantomime-grasp, with haptic feedback* condition (PH+), the target object was again removed from the grasping environment prior to response cuing; however, when the participant had completed their response, the experimenter placed the target object (i.e., the object that was removed from the grasping environment) between the thumb and forefinger of participants' grasping limb. In other words, the PH+ condition provided terminal haptic feedback related to the absolute size of the target object. In the MG condition, the target object remained physically present and was therefore immediately available for participants to grasp at the end of their response. The MG condition therefore served as a more naturalistic task for the integration of haptic feedback.

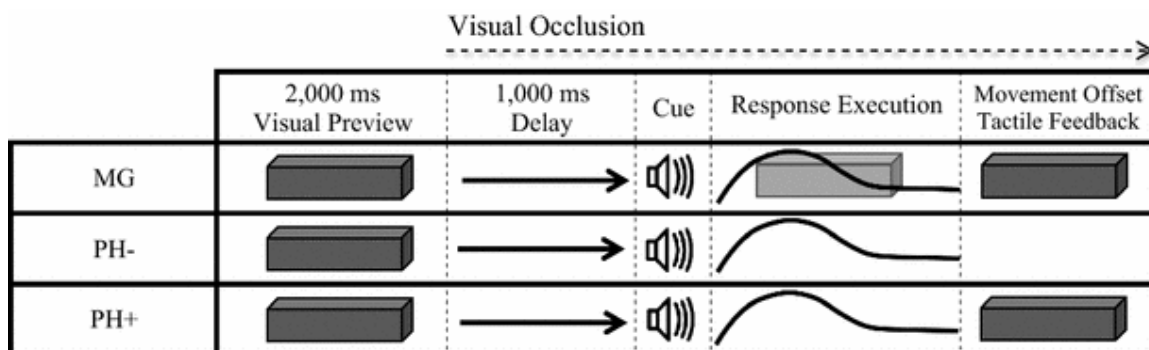


Figure 3-1: Schematic of the timeline of visual, auditory and haptic events in the memory-guided (MG), no-target pantomime-grasp, without haptic feedback (PH-), and no-target pantomime-grasp, with haptic feedback (PH+) conditions. For all conditions, participants were provided a 2000 ms visual preview of a target object after which vision of the grasping environment was occluded and remained occluded for the duration of a response. A tone provided 1000 ms following visual occlusion served as participants' movement imperative. In the MG condition, the target object remained on the tabletop and participants were able to naturally grasp it at the end of their response. In the PH- condition, the target object was removed from the tabletop during the 1000 ms delay interval and participants reached to the remembered target object location without being able to physically grasp it. In the PH+ condition, the target object was again removed during the delay interval. Importantly, at the end of a response in the PH+ condition, the experimenter positioned the previewed target object between participants' thumb and forefinger and therefore provided terminal haptic feedback related to absolute object size.

I computed JNDs at the time of PGA to determine whether the PH-, PH+ and MG conditions adhered to or violated Weber's law. In terms of research predictions, if terminal haptic feedback supports *absolute* aperture shaping via a forward updating of grasp endpoints or an error-related recalibration between vision and motor output, then JNDs for the PH+ condition should violate Weber's law in line with the MG condition. Moreover, such a finding would demonstrate that integrative multisensory cues support the absolute specification of object size. In contrast, if terminal haptic feedback related to absolute object size does not play a regulatory role in aperture shaping, then JNDs for PH- and PH+ conditions should adhere to the law and thereby demonstrate aperture shaping via relative object information.

3.2 Methods

3.2.1 Participants

Sixteen individuals (4 males, 12 females: age range 18–29 years) completed the memory-guided (MG) and no-target pantomime-grasp, without haptic feedback (PH-) conditions, and a separate group of twelve individuals (5 males and 7 females: age range 18–30 years) completed the no-target pantomime-grasp, with haptic feedback (PH+) condition. I used a between-participant design for the different pantomime-grasping conditions to avoid possible carryover effects associated with physically touching the target objects. For that same reason, participants who performed both the PH- and MG conditions always performed the former trials first (see details below). All participants were self-declared right-hand dominant with normal or corrected-to-normal vision. Participants signed consent forms approved by the Office of Research Ethics, University of Western University, and this work was conducted according to the ethical standards laid down in the Declaration of Helsinki.

3.2.2 Memory-guided (MG) and no-target pantomime-grasp, without haptic feedback (PH-)

Participants stood for the duration of the experiment in front of a table (height of 880 mm; surface width and depth of 1040 and 740 mm, respectively) and reached to grasp, or

pantomime-grasp, target objects via a precision grip. Target objects were differently sized (20, 30, 40 and 50 mm in length, 10 mm in depth and height), and weight-matched (7 g) black acrylic blocks placed on a neutral white surface and were located at participants' midline and 450 mm from the front edge of the table. The long-axis of target objects was perpendicular to participants. A pressure-sensitive switch located at midline and 50 mm from the front edge of the table served as the start location for each trial. Visual information was manipulated via liquid-crystal occlusion goggles (PLATO Translucent Technologies, Toronto, ON, Canada) and MATLAB (7.6: The Mathworks, Natick, MA, USA), and the Psychophysics Toolbox extensions (ver 3.0; Brainard, 1997) controlled visual and auditory events.

Prior to each trial, the goggles were set to their translucent state while the experimenter positioned a target object on the table. During this time, participants rested the medial surface of their right palm (i.e., the grasping limb) on the start location with their thumb and forefinger pinched lightly together. Once the target object was positioned, a trial sequence was initiated wherein the goggles were set to their transparent state for a 2000 ms visual preview. Following the preview, the goggles reverted to their translucent state and remained in this state until the preview for a subsequent trial; online visual feedback was therefore unavailable throughout a grasping response. Further, once the goggles closed, a 1000 ms delay interval was introduced after which time a tone cued participants to complete a response in one of the two conditions (see Figure 3-1. for schematic of visual, auditory and haptic events). For the MG condition, participants grasped but did not lift the target object. In the PH- condition, the target object was removed from the grasping environment prior to response cuing (i.e., during the 1000 ms delay interval). In line with the MG condition, at the end of a PH- response participants' thumb and forefinger were in contact with the tabletop surface; however, the absence of the target object precluded terminal haptic feedback related to absolute object size. The MG and PH- conditions were performed in separate blocks, and participants were therefore aware of whether a physical target object would be available to grasp at the end of their response. In both conditions, participants maintained their endpoint grasp position for approximately 2000 ms before returning to the start location. As mentioned above, the

PH- condition was completed prior to the MG condition to avoid possible carryover effects associated with physically grasping the target objects. For each condition, 20 randomly ordered trials were completed to each target object size (i.e., 160 experimental trials). Last, the 1000 ms delay interval was used to provide the experimenter sufficient time to remove the target object from the tabletop in the PH- condition. Further, I note that my group's previous work has shown that delays up to 2000 ms produce grasping responses that violate Weber's law (Holmes et al., 2011). Indeed, that previous work has shown that MG grasps following a brief delay violate Weber's law demonstrates that such actions are mediated via the same visual code (i.e., absolute) as their CL counterparts.

3.2.3 No-target pantomime-grasp, with haptic feedback (PH+)

The no-target pantomime-grasp, with haptic feedback (PH+) condition was identical to the PH- condition with the only exception that participants were provided terminal haptic feedback related to absolute object size. Thus, participants completed the same pantomime-grasp as the PH- condition; however, when participants attained their movement goal location, the experimenter positioned the target object between their thumb and forefinger. Indeed, and as in the PH- condition, at movement offset participants' thumb and forefinger were in contact with the tabletop surface and remained separated to reflect terminal grip aperture. Importantly, after movement offset (see definition in section 3.2.6), a computer-generated cue instructed the experimenter to return the target object to the tabletop surface (i.e., at a location approximately 50 mm from participants' limb). The experimenter then slid the target object until one side contacted participants' thumb and then adjusted the opposite side until it contacted participants' forefinger. I estimate that 2500 ms was the time required to position the object. Once positioned, participants were encouraged to use their thumb and forefinger to reposition the object to produce a stable grasp (i.e., a grasp that would allow for lifting). As in the MG condition, however, participants were instructed to hold – but not lift – the object for approximately 2000 ms before returning to the start location. Thus, the PH+ condition provided terminal haptic feedback related to absolute object size.

3.2.4 Data analysis

Position data of the grasping limb (i.e., right hand) were tracked via infrared emitting diodes (IREDs) attached to the medial surface of the distal phalanx of the thumb, the lateral surface of the distal phalanx of the index finger and the styloid process of the wrist. IRED data were sampled at 400 Hz via an Optotrak Certus (Northern Digital Inc. Waterloo, ON, Canada). Position data were filtered offline using a second-order dual-pass Butterworth filter with a low-pass cutoff frequency of 15 Hz. Position data were used to calculate instantaneous velocities via a five-point central finite difference algorithm. Movement onset was indicated by release of the start location pressure switch, and movement offset was defined as the first frame wherein wrist velocity dropped below 50 mm/s for 20 consecutive frames (i.e., 50 ms).

3.2.5 Just-noticeable-difference scores (JNDs)

In the perceptual literature, a JND represents the smallest change by which a performer can reliably discriminate between an original and a comparator stimulus. For example, in a size-discrimination task, a participant would be asked to provide a verbal report of whether the length of a line (i.e., the comparator stimulus) differs from a previously presented line (i.e., the original stimulus). In this context, JNDs are defined statistically with correct identification dependent on an arbitrary criterion such that some studies may employ a 75 % correct criterion for identification of the stronger stimulus, whereas other studies may employ an 85 % correct criterion (for review see Marks & Algom, 1998). In contrast, a statistical criterion is not available for the computation of JNDs in a grasping task; rather, JNDs represent the within-participant standard deviations (unbiased) of grip aperture size (Davarpanah Jazi & Heath, 2014; Davarpanah Jazi et al., 2015; Ganel et al., 2008a; Ganel et al., 2008b; Heath et al., 2011; Heath et al., 2012; Holmes & Heath, 2013; Holmes et al., 2011; Holmes et al., 2013; Pettypiece et al., 2010). Thus, JNDs represent the sensitivity related to comparing grip aperture size (i.e., the comparator stimulus) to the size of a to-be-grasped target object (i.e., the original stimulus). According to Ganel et al. (2008a), the foundation for this computation is based on the classic method of adjustment wherein variance provides a measure of sensorimotor uncertainty ‘...for

which the observer is unable to tell the difference between the size of the comparison and the target object' (p. 600). Thus, I interpret a linear increase in JNDs with object size as adherence to Weber's law. In demonstration of the computation of JNDs, Figure 3-2 presents trial-to-trial PGAs for an exemplar participant when grasping differently sized objects in the MG and PH- conditions. As well, the figure's offset panels show the standard deviation associated with trial-to-trial PGAs (i.e., the JNDs) and demonstrate that JNDs for the MG condition did not systematically vary with object size, whereas JNDs for the PH- condition increased linearly with increasing object size.

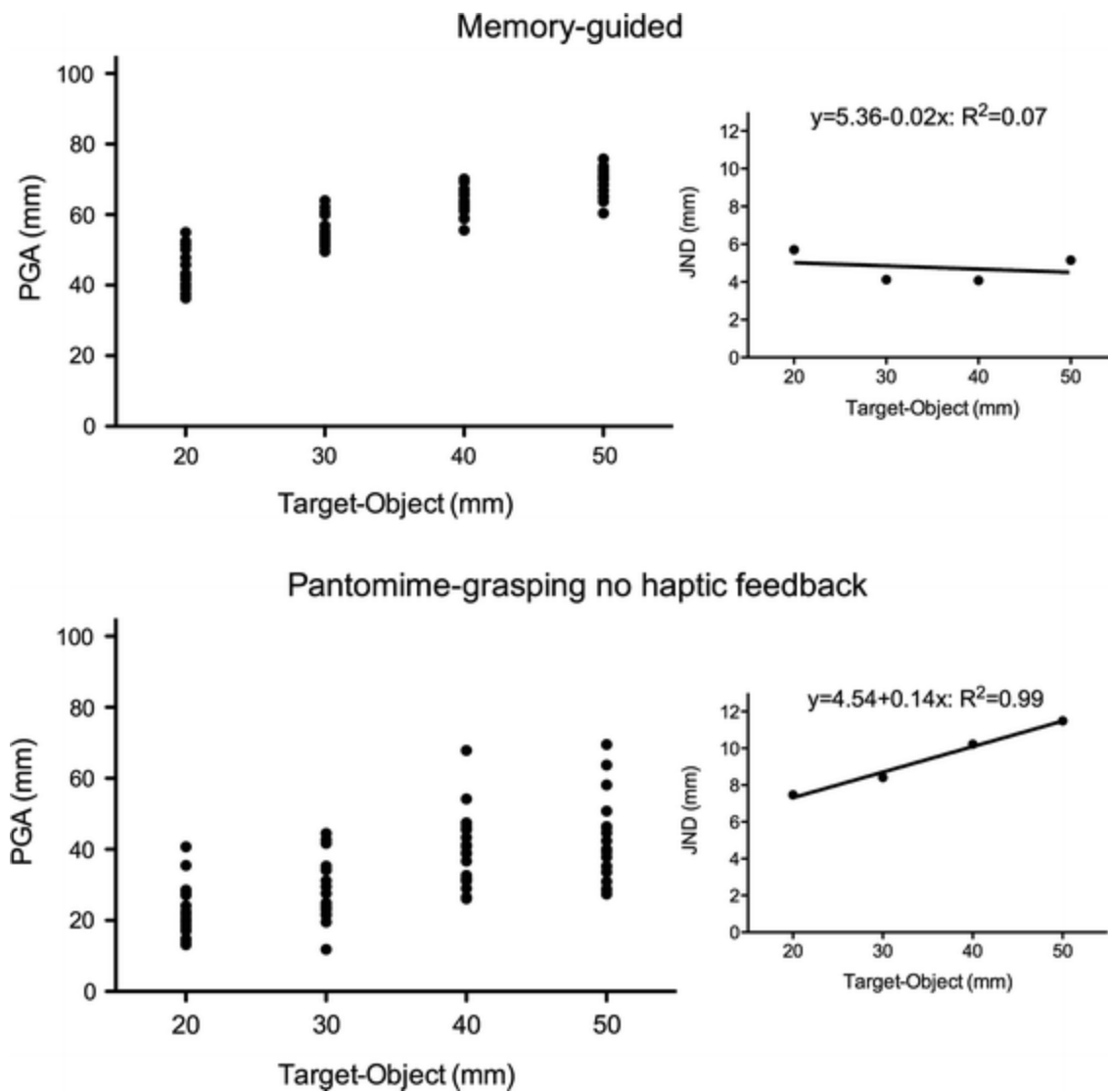


Figure 3-2: Main panels show trial-to-trial peak grip aperture (PGA: mm) values for an exemplar participant in the memory-guided (MG) (top panel) and no-target pantomime-grasp, without haptic feedback (bottom panel) conditions as a function of object size (20, 30, 40 and 50 mm). The smaller offset panels represent the standard deviation related to the trial-to-trial PGAs for each object size displayed in the main panel (i.e., the just-noticeable-difference scores: JNDs). The figures demonstrate that JNDs for the MG condition did not systematically vary with object size, whereas values for the pantomime-grasping no haptic feedback condition increased linearly with increasing object size.

3.2.6 Dependent variables and statistical analyses

I computed grasping time (GT: time between movement onset and offset), peak grip aperture (PGA: maximum resultant distance between the thumb and forefinger), time to peak grip aperture (tPGA: time from movement onset to PGA) and the within-participant standard deviations of PGA (i.e., the JNDs). Trials involving an anticipatory response (i.e., a response initiated before response cuing or a reaction time less < 180 ms: see Westwood et al., 2000) were excluded from subsequent data analyses and were less than 1% of trials for any participant. The PH- and MG conditions used the same group of participants, and results were examined via 2 (condition: PH-, MG) by 4 (object size: 20, 30, 40 and 50 mm) repeated measures ANOVA. In turn, participants in the PH+ condition were independent of the aforementioned conditions. As such, results were examined via one-way repeated measures ANOVA with object size as the repeated variable.

3.3 Results

3.3.1 No-target pantomime-grasp, without haptic feedback (PH-) vs. memory-guided (MG)

The PH- condition produced shorter GTs (697 ms, SD = 19) and smaller (39 mm, SD = 11) and later occurring (557 ms, SD = 72) PGAs than the MG condition (GT = 708 ms, SD = 23; PGA = 69 mm, SD = 15; tPGA = 497 ms, SD = 45), $F_{s(1,15)} = 6.25, 161.39$ and 15.05, respectively, for GT, PGA and tPGA, $p_s < 0.03$. As well, Figure 3-3 shows that PGA yielded a main effect of object size, $F(3,45) = 211.05, p < 0.001$, such that values (for both PH- and MG conditions) increased with increasing object size (only linear effect significant: $F(1,15) = 255.62, p < 0.001$).

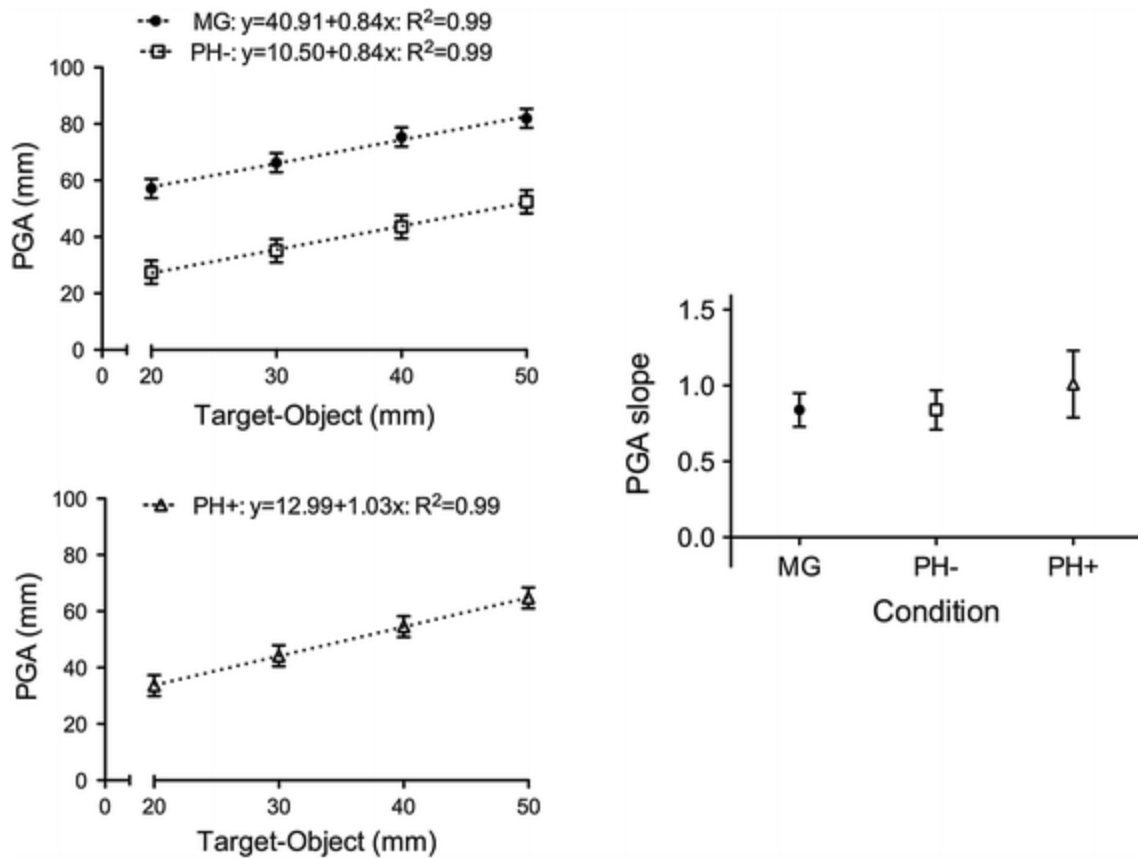


Figure 3-3: *Top panel* shows mean peak grip apertures (PGAs: mm) for memory-guided (MG) and no-target pantomime-grasp, without haptic feedback (PH-) conditions as a function of object size and their associated regression lines and equations. The *bottom panel* shows results for the no-target pantomime-grasp, with haptic feedback condition (PH+). *Error bars* represent the 95 % within-participant confidence intervals computed via the separate mean-squared error terms for object size in each condition (Loftus & Masson, 1994). The *smaller offset panel* represents the mean values for the computation of participant-specific slopes relating PGAs to object size for each condition. In this panel, *error bars* represent the 95 % between-participant CI, and the absence of overlap between an *error bar* and zero indicates that the slope differs from zero (Cumming, 2013).

JNDs yielded main effects of condition, $F(1,15) = 5.30, p < 0.05$, object size, $F(3,45) = 5.36, p < 0.01$ and their interaction, $F(3,45) = 5.66, p < 0.01$. In decomposing the interaction, Figure 3-4 shows that JNDs for the PH- condition elicited an effect of object size, $F(3,45) = 9.04, p < 0.001$, such that values increased with increasing object size (only linear effect significant: $F(1,15) = 19.78, p < 0.001$), whereas JNDs in the MG condition were refractory to object size, $F(3,45) < 1$. In other words, the PH- and MG conditions adhered to and violated Weber's law, respectively.

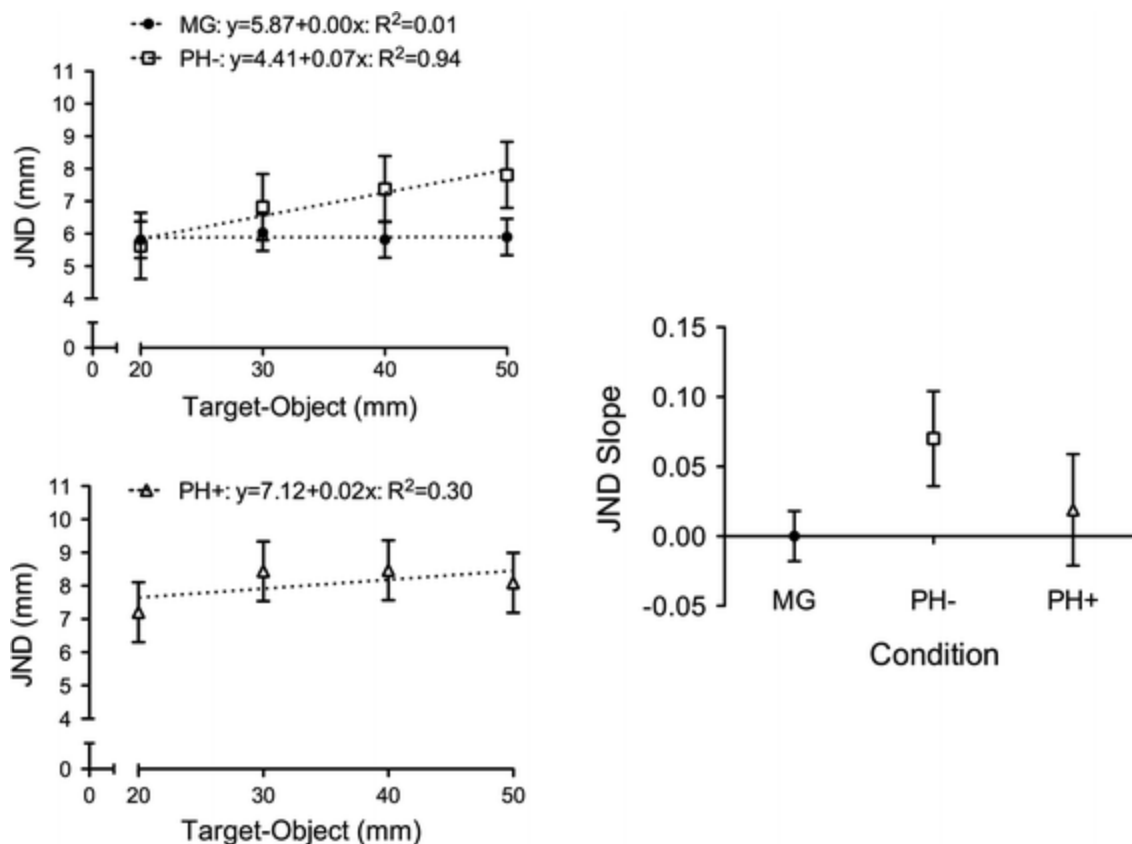


Figure 3-4: *Top panel* shows mean just-noticeable-difference scores (JNDs: mm) for memory-guided (MG) and no-target pantomime-grasp, without haptic feedback (PH-) conditions as a function of object size and their associated regression lines and equations. The *bottom panel* shows results for the no-target pantomime-grasp, with haptic feedback condition (PH+). *Error bars* represent the 95 % within-participant confidence intervals computed via the separate mean-squared error terms for object size in each condition (Loftus & Masson, 1994). The *smaller offset panel* represents the mean values for the computation of participant-specific slopes relating JNDs to object size for each condition. In this panel, *error bars* represent the 95 % between-participant CI, and the absence of overlap between an *error bar* and zero indicates that the slope differs from zero (Cumming, 2013).

3.3.2 No-target pantomime-grasp, with haptic feedback (PH+)

The average GT and tPGA values were 706 ms (SD = 24 ms) and 552 ms (SD = 81), respectively, and neither variable was reliably influenced by object size, $F_s(3,33) < 1$. PGAs yielded an effect of object size, $F(3,33) = 66.56$, $p < 0.001$, such that values increased with increasing object size (only linear effect significant: $F(1,11) = 71.09$, $p < 0.001$) (see Figure 3-3). Most notably, Figure 3-4 shows that JNDs did not reliably vary with object size, $F(3,33) = 1.17$, $p = 0.31$. Thus, the PH+ condition violated Weber's law.

3.3.3 PH+ vs. PH- and MG conditions

I computed participant-specific slopes relating PGAs and JNDs to object size and contrasted values for the PH+ condition to each of the PH- and MG conditions via independent-samples t tests. The slope analyses provided a basis to determine whether the scaling of PGAs and JNDs to object size differed between groups (i.e., PH+ vs. PH-, and PH+ and MG). In terms of PGAs, the slope for the PH+ condition (1.03, SD = 0.38) did not reliably differ from the PH- (0.84, SD = 0.25) or MG (0.84, SD = 0.21) conditions ($t_s(26) = 1.54$ and 1.64 , $p_s = 0.14$ and 0.11). Further, the offset panel of Figure 3-3 presents the mean slope and 95% confidence intervals for each condition and provides a graphic depiction that values for the PH+, PH- and MG conditions differed from zero. In terms of JNDs, the slope for the PH+ condition (0.02, SD = 0.05) did not reliably differ from the MG condition (0.01, SD = 0.03), $t(26) = 1.24$, $p = 0.14$; however, it was shallower than the PH- condition (0.07, SD = 0.06), $t(26) = -6.57$, $p < 0.001$. Moreover, the offset panel of Figure 3-4 shows that the slope for the PH- condition - but not for the PH+ or MG conditions - differed from zero. As such, only the PH- condition elicited a JND/object size slope that reliably differed from zero.

Because my PGA/object size slopes did not reliably differ across conditions, I computed participant-specific PGA/object size regression intercepts to determine whether PGA *magnitude* for the PH+ condition differed from either the PH- or MG conditions. The intercept for the PH+ (12.99, SD = 7.03) and PH- (10.50, SD = 8.30) conditions did not reliably differ ($t(26) < 1$); however, the intercept for the former was less than the MG

condition (40.91, SD = 14.8) ($t(26) = -7.25, p < 0.001$). That the PH+ and MG conditions exhibited different intercepts, but equivalent slopes, indicates that the former produced smaller PGAs at each matched object size. In addition, I computed participant-specific JND/object size intercepts for the PH+ and MG conditions. The intercept for the PH+ condition (7.12, SD = 3.0) was larger than the MG condition (5.87, SD = 1.75) ($t(26) = 2.10, p < 0.05$): a result indicating that JNDs for the PH+ condition were larger than their MG counterparts at each matched object size. Last, I did not contrast PH+ and PH- intercepts because my JND/object size slope analysis previously established a between-condition difference.

3.4 Discussion

3.4.1 MG and PH- conditions respectively violate and adhere to Weber's law: evidence for dissociable visual codes

PGA values in MG and PH- conditions increased with increasing object size. Thus, the visuomotor system reliably distinguished between the differently sized objects used here. In line with previous work (Holmes et al., 2013; Westwood et al., 2000), PGAs for the MG condition were larger than the PH- condition. The observed difference in PGA between the MG and PH- conditions is consistent with a seminal investigation by Marteniuk et al. (1987) showing that the precision and contextual features (i.e., fragile vs. non-fragile) of a target influence the manner a grasping response is planned and controlled. Thus, the absence of a physical target in the PH- condition served as a contextual cue that decreased task-based precision demands. Additionally, Smeets and Brenner's (1999) double-pointing hypothesis contends that the precision demands of grasping (i.e., grasping a real target object) requires that the thumb and forefinger approach a target object via orthogonal movement vectors to reduce spatial variability at the time of contact (i.e., increased precision) and to avoid an early collision (i.e., an appropriate safety margin). As well, orthogonal approach vectors ensure that the opposing forces of the thumb and forefinger are parallel to one another at the time of contact (i.e., prevents slipping). As such, that the PH- condition produced smaller PGAs than the MG condition indicates that the absence of physical target grasp points resulted

in diminished task-based precision demands and the need to adopt orthogonal finger and thumb approach vectors. After all, the participant and not the physical properties of a target object determines the ‘safety margin’ for a successful pantomime-grasp (Holmes & Heath, 2013), and pantomime-grasping entails knowledge that there is not the risk of an object collision. Further, PGAs in the PH- condition (557 ms or 80 % of GT) occurred later than the MG condition (497 ms or 70 % of GT) a finding indicating that reduced precision demands decreased feedback (Marteniuk et al., 1987; Wallace & Weeks, 1988; Wing et al., 1986) and/or feedforward-based (Arbib, 1985) corrections during the grasp approach phase (Jeannerod, 1984).

Although results for the MG and PH- conditions used in the current investigation show differences in the size and timing of PGA, such metrics do not provide a direct basis for examining the nature of the visual information mediating aperture formation. Thus, I computed JNDs to provide a rule-based framework to determine whether MG and PH- conditions were mediated via dissociable visual information. Figure 3-4 shows that JNDs for the MG condition did not vary systematically with object size, whereas JNDs for the PH- condition increased linearly with object size. In other words, the MG and PH- conditions respectively violated and adhered to Weber’s law. As noted in Introduction, results for the MG condition replicate earlier work (Holmes et al., 2011) and provide direct evidence that absolute visual information (or integrative visual and haptic: see below) mediates the grasping of a ‘real’ object. In terms of the PH- condition, the present findings replicate Holmes et al. (2013) and the contention that pantomime-grasping is a perception-based task supported by relative visual information (see also Holmes & Heath, 2013). Moreover, it is important to recognize that the difference in JNDs between the PH- and MG conditions reported here cannot be explained on the basis of a speed/accuracy trade-off related to motor output variability (see Meyer et al., 1988). Indeed, if that were the case then the larger and earlier occurring PGAs in the MG condition would have produced JNDs that were larger than the PH- condition. Instead, the JNDs reported here provide rule-based evidence that dissociable information supported the MG and PH- conditions.

Recall that the PH- condition was always performed prior to the MG condition – a methodology used to avoid the possibility that performing the MG condition first might result in haptic carryover effects influencing a subsequent block of PH- trials. Notably, however, such a methodology does not control for whether practice-related effects influence the nature of the information supporting grasping. To address that issue, I completed a supplemental experiment involving twelve naïve right-handed participants (7 male and 5 female: age range 19-25 years) who performed the same PH- and MG conditions as my main experiment with the only exception being that the ordering of conditions was counterbalanced. Results showed that PGAs for the PH- condition were smaller (47 mm, SD = 15) and later occurring (597 ms, SD = 59) than the MG condition (PGA = 70 mm, SD = 16; tPGA = 506 ms, SD = 47), $F_s(1,11) = 16.51$ and 74.57 , $p_s < 0.01$, respectively, for PGA and tPGA. Further, Figure 3-5 shows that PGAs for both conditions increased with increasing object size, $F(3,33) = 348.50$, $p < 0.001$ (only linear effect significant: $F(1,11) = 420.11$, $p < 0.001$). In terms of JNDs, Figure 3-5 demonstrates a condition by object size interaction, $F(3,33) = 9.76$, $p < 0.001$: JNDs for the PH- (linear effect significant: $F(1,11) = 23.51$, $p < 0.001$) but not the MG (linear effect: $F(1,11) < 1$) condition increased with increasing object size. In other words, my supplemental experiment matches my main experiment and the combined results demonstrate that neither haptic ordering experience nor practice-related effects account for the dissociable information mediating PH- and MG conditions.

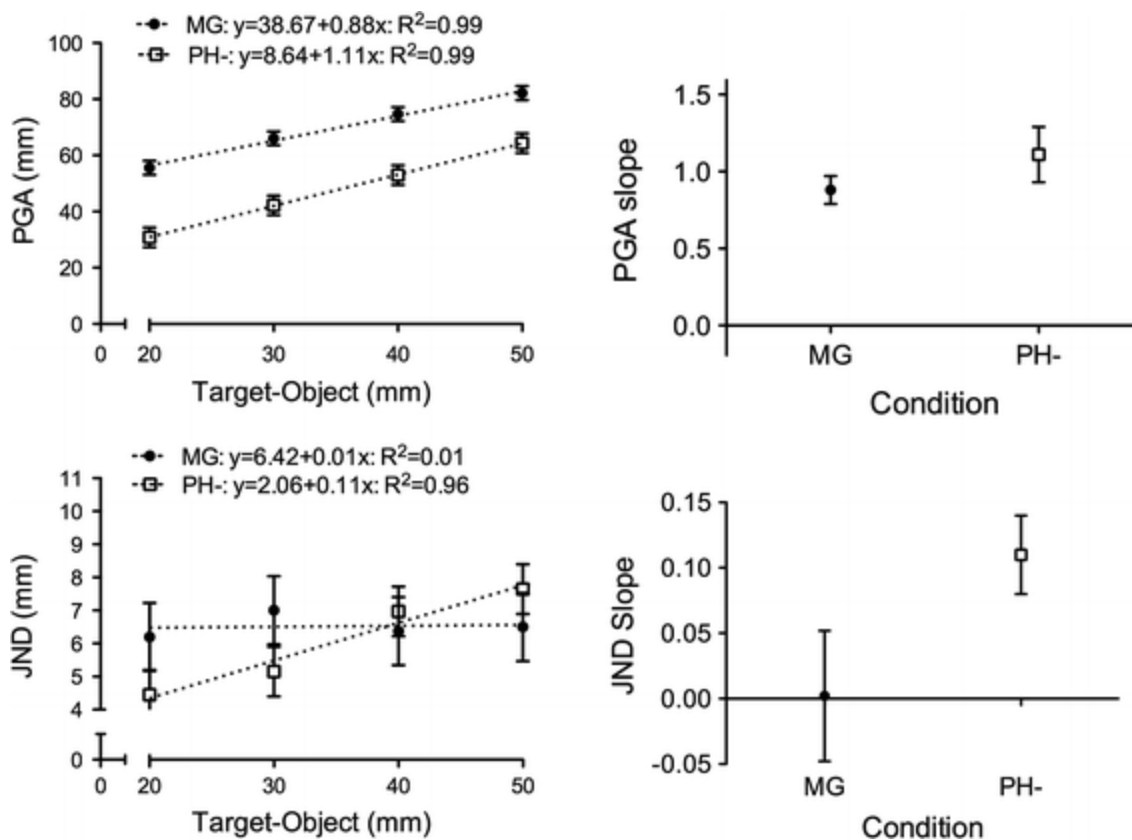


Figure 3-5: Results for the supplemental experiment wherein the order of memory-guided (MG) and no-target pantomime-grasp, without haptic feedback (PH-) conditions were counterbalanced. The *left top and bottom panels* show mean peak grip aperture (PGA: mm) and just-noticeable-difference scores (JNDs: mm) respectively for MG and PH- conditions as a function of object size. Further, the panels present regression lines and associated regression equations for each condition. *Error bars* represent 95 % within-participant confidence intervals computed via the separate mean-squared error terms for object size in each condition (Loftus & Masson, 1994). The *right top and bottom panels* represent the respective mean participant-specific slopes relating PGA and JND to object size for each condition. *Error bars* represent the 95 % between-participant CI, and the absence of overlap between an *error bar* and *zero* indicates that the slope differs from zero (Cumming, 2013).

3.4.2 PH+ grasping: evidence that haptic feedback influences the nature of the information supporting pantomime-grasping

The primary objective of this study was to determine whether terminal haptic feedback derived from proprioceptive cues of finger and thumb orientation influences the nature of the information mediating pantomime-grasping. To accomplish that objective, a group of participants separate from the MG and PH- conditions performed pantomime-grasping responses wherein the target object was placed in their grasping limb once they had achieved the movement goal location (i.e., PH+ condition). Thus, the provision of the physical object at the end of the response provided absolute terminal haptic feedback related to object size. As in the MG and PH- conditions, PGAs in the PH+ condition increased with increasing object size and the slope relating PGA to object size for the PH+ condition did not reliably differ from either the PH- or MG conditions. Thus, an increase in object size produced an equivalent increase in PGA across all conditions. Notably, however, the magnitude and timing (552 ms or 78 % of GT) of PGAs in the PH+ condition were similar to the PH- condition. The comparable PGA metrics suggest that PH+ and PH- conditions were characterized by a common strategic response reflecting that the absence of a physical target object provided no risk of object collision and/or resulted in diminished task-based precision demands.

Although PGA values for the pantomime-grasping conditions (i.e., PH- and PH+) were smaller than the MG condition, the PH+ condition elicited JNDs that did not systematically vary with object size. Moreover, the JND slope for the PH+ condition did not reliably differ from the MG condition and was shallower than the PH- condition. As such, absolute terminal haptic feedback related to object size resulted in grasp responses that violated Weber's law. In terms of explaining my findings, I note that the different target objects were randomly varied from trial-to-trial. Thus, participants could not simply rely on haptic feedback from trial N-1 to plan a current grasping response; rather, a visuo-haptic integration was required⁵. As mentioned in Introduction, Whitwell et al. (2014) proposed two possible mechanisms by which haptic feedback may support the absolute specification of object size. In the first case, it was proposed that haptic feedback related to finger and thumb orientation may be used in a predictive fashion to

specify object size or appropriate grasp points, whereas in the second case it was proposed that haptic error signals related to observed and expected outcomes generated over a series of trials may support the absolute calibration of the visual and motor systems. Furthermore, I note that because haptic feedback is task-relevant in the PH+ condition, it may therefore serve as the predominant cue in minimizing response variance and the calibration of motor output (Ernst & Banks, 2002). Although the present investigation is unable to disentangle between the aforementioned accounts, I believe that the results add importantly to the grasping literature inasmuch as they provide rule-based evidence that reintroducing haptic feedback related to absolute object size at the end of a pantomime-grasping response results in a visuo-haptic recalibration. Moreover, the present findings show that the recalibration supports the motor system's ability to specify the metrical properties of a target object. Such a result is important not only in terms of understanding pantomime-grasping but also suggests that the use of absolute target information (and violation to Weber's law) in more naturalistic grasping tasks may relate to the integration of visual and haptic information.

At least two issues require addressing. First, although Ganel et al. (2008a) reported that CL grasping violated Weber's law, their work showed that MG grasping adhered to the law. In contrast, the MG condition used here and in previous work by my group (Holmes et al., 2011) violated Weber's law on par to CL grasping. A possible account for the discrepant findings is that Ganel et al. employed a longer delay interval (i.e., 5000 ms) than used here (i.e., 1000 ms) and elsewhere (i.e., 2000 ms; Holmes et al., 2011). Indeed, the length of the delay may represent a notable issue in determining the visual information supporting grasping as some work has argued that the visuomotor system retains absolute information for up to 2000 ms of visual delay (Elliott & Madalena, 1987; Glover, 2004; for a review of this issue see Heath et al., 2010). Further, Hesse and Schenk (2014) reported that patient DF's memory-based reaching performance is unimpaired when her actions are performed in the absence of visual landmarks and/or online limb (i.e., by setting shutter-goggles to their translucent state as done in the present investigation). Such a result is compatible with the present results and my group's previous JND findings (Holmes et al., 2011) and provides evidence that MG actions are

not restrictively mediated via relative and allocentrically based visual cues. The second issue to address is the observation that JNDs for the PH+ condition were larger than the MG condition at each matched object size. In interpreting this finding, it is important to note that JNDs for MG and PH+ conditions did not vary systematically with object size. Thus, the difference between the two conditions cannot relate to the use of dissociable codes (i.e., absolute vs. relative) because each condition violated the psychophysical principles of Weber's law. Instead, a parsimonious explanation may relate to the fact that pantomime-grasping is not a practiced task and therefore introduces systematic motor uncertainty (Proteau et al., 1994; Schmidt et al., 1979). In support of this view, *a posteriori* analyses showed that the variability of PGA timing in the PH+ condition (95 ms, SD = 41) was greater than the MG condition (43 ms, SD = 20), $t(26) = 13.40$, $p < 0.001$. Because increased variability is related to increased rates of motor learning (Wu et al., 2014; see also Herzfeld & Shadmehr, 2014), it is possible that the larger JNDs in the PH+ condition reflect the development of learned associations between visual and haptic cues.

3.5 Conclusions

Pantomime-grasping in the absence of terminal haptic feedback related to absolute object size is a visuoperceptual task mediated by relative size information. Importantly, however, results suggest that the provision of terminal haptic feedback related to object size in a pantomime-grasping task results in the convergence of visual and haptic cues to support the absolute specification of object size. Further, the current study highlights the role of multisensory integration in target-directed grasping.

3.6 Footnotes

1. Ganel et al. (2008a) employed manual estimation and method of adjustment tasks. Results for both showed adherence to Weber's law (see also Davarpanah Jazi & Heath, 2014).
2. Smeets and Brenner (2008) contend that grasping violates Weber's law because the visuomotor system computes grasp points rather than the size (or magnitude)

of a to-be-grasped object. It is, however, important to note that pantomime-grasping (Holmes et al., 2013) and grasping a 2D object (Holmes & Heath, 2013) adhere to Weber's law - a result providing some evidence that the size of a target object is used to specify grip aperture. As such, the position adopted in the present study is that target size information is used, in part, to specify grasping. Of course, I recognize the basis of Smeets and Brenner's comments and therefore direct the reader to the aforementioned authors' target article (Smeets and Brenner, 1999) that provides a lively debate and outline of the divergent views regarding whether object size or grasp point information supports aperture shaping.

3. DF is an extensively studied individual with bilateral lesions to her lateral occipital cortex (James et al., 2003). As a result of her lesions, DF has a persistent deficit in visual form perception but demonstrates preserved visuomotor abilities. DF's preserved visuomotor abilities have been attributed to her intact dorsal visual pathway (for recent review see Goodale & Milner, 2013).
4. Mechanoreceptor-derived (i.e., tactile) cues associated with touching an object or the surface on which it rests serve as an additional source of haptic feedback. In previous work (Davarpanah Jazi & Heath, 2014; Davarpanah Jazi et al., 2015) as well as the current study, I note that such cues do not influence the nature of the information mediating visually or tactile-defined grasping (but see Whitwell et al., 2014). Instead, my work demonstrates that the proprioceptive component of haptic feedback supports the absolute specification of object size.
5. For the PH+ condition, I examined whether the size of the target object on trial N-1 influenced PGA or JND values for a current trial (i.e., trial N) - an approach matching a number of pro- and antisaccade task-switching experiments performed by my group (e.g., DeSimone et al., 2014; Weiler & Heath, 2014). Results showed that preceding target object size did not influence PGAs or JNDs for a current trial ($F_s < 1$).

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Chapter 4

4 Pantomime-grasping: advance knowledge of haptic feedback availability supports an absolute visuo-haptic calibration

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4.1 Introduction

Our visual system's ability to identify an object is dependent on the integration of *relative* information laid down and maintained by the visuoperceptual networks of the ventral visual pathway. In contrast, goal-directed grasping is supported by *absolute* visual information mediated by dedicated visuomotor networks residing in the posterior parietal cortex (PPC) of the dorsal visual pathway (for reviews of duplex visual processing see Goodale, 2011; Whitwell et al., 2014)¹. The importance of vision for action and the absolute processing of the dorsal visual pathway is characterized by work showing that chronic (i.e., optic ataxia; for recent review see Andersen et al., 2014) and transient (i.e., via transcranial magnetic stimulation) lesions to the PPC impairs grip aperture scaling and interferes with online trajectory amendments (Cavina-Pratesi et al., 2013; Desmurget et al., 1999; Jeannerod, 1986; Pisella et al., 2000). It is, however, important to recognize that in addition to vision, the motor system is provided object-based information via haptic feedback (i.e., integrative mechano- and proprioceptive cues). In particular, physically grasping an object provides: (1) mechanoreceptive cues related to the shape and texture of an object's grasp points; and (2) proprioceptive cues from thumb and forefinger position that provide absolute object size information (for review of haptic frames of reference see Lederman & Klatzky, 2009). As such, haptic feedback may serve as an important sensory source in determining the nature of the information (i.e., relative vs. absolute) supporting grasping control.

One area of research that has potentially underestimated the importance of haptic feedback is pantomime-grasping. The empirical evaluation of pantomimed (or simulated) actions was first introduced by Liepmann (1905/1980) and required that individuals perform a well-learned movement (e.g., hammering a nail) in the absence of a physical tool and/or object. The task was originally employed to provide clinical evaluation of apraxic motor deficits following stroke (Geschwind & Kaplan, 1962; Roy et al., 2000). The grasping literature has subsequently evolved the use of pantomime-grasping and requires that participants direct a response to an area adjacent to, or once occupied by, a target object. In particular, the dissociated stimulus-response relations of

pantomime-grasping have been frequently used as a framework for understanding the distinct *visual* characteristics associated with natural and simulated responses (for review see Goodale, 2011). It is, however, important to recognize that pantomime-grasping and natural grasping differ not only in terms of their visual properties but also because the former does not entail physically interacting with an object; that is, pantomime-grasping does not afford the integration of haptic feedback. In addressing the importance of this issue, Bingham et al. (2007) employed a mirror-box apparatus allowing the manipulation of haptic feedback without occluding object vision (see depiction of mirror-box in Figure 1 of Bingham et al., 2007). In that experiment, responses were completed in conditions wherein vision of an object overlapped with its physical location (i.e., haptic feedback condition: H+ trials) and when the physical object was unavailable at the movement goal location (i.e., no haptic feedback condition). Thus, the no haptic feedback condition in Bingham et al.'s (2007) study entailed a pantomime action and I henceforth refer to this condition as *no-target pantomime-grasp, without haptic feedback* (i.e., PH- trials). Notably, H+ and PH- trials were completed in separate blocks (i.e., blocked feedback schedule) and a block wherein task-types were randomly interleaved on a trial-by-trial basis (i.e., random feedback schedule). Thus, in the random feedback schedule participants were unaware as to whether they would receive haptic feedback at the end of their response. Blocked feedback schedule PH- trials exhibited a less accurate scaling of grip aperture to object size (i.e., smaller peak and terminal grip aperture values) than H+ trials. In contrast, random feedback schedule PH- trials exhibited aperture scaling commensurate to random and blocked schedule H+ trials. Accordingly, Bingham et al. (2007) concluded that haptic feedback - even when intermittently and unpredictably available - supports an absolute visuo-haptic calibration. In contrast, the absence of haptic feedback throughout a block of trials (i.e., blocked PH- trials) was interpreted to preclude any calibration and limit grip aperture specification to the relative visual (i.e., visuoperceptual) properties of an object (see also Cavina-Pratesi et al., 2011; Fukui & Inui, 2013; Goodale et al., 1994; Holmes et al., 2013; Westwood et al., 2000). In subsequent work, Schenk (2012) used a similar mirror-box apparatus to examine H+ and PH- trial performance in an individual with bilateral lesions to her ventral visual pathway

(i.e., patient DF; see James et al., 2003). The literature has shown that DF's ventral stream lesions impair her visual form perception but spare her use of vision for action due to her intact dorsal visual pathway (Goodale & Milner, 2006). Schenk reported that DF's grip aperture specification during PH- trials was no better than her well-documented visuo-perceptual deficits - a finding previously documented and attributed to the relative and perception-based nature of pantomime-grasping (Goodale et al., 1994). In turn, DF demonstrated absolute aperture scaling when PH- trials were performed in a feedback schedule that included intermittent - but predictably available - H+ trials². Based on these results, Schenk proposed that DF requires integrative visual and haptic cues to support her absolute aperture scaling. Although Schenk did not provide a mechanistic account for his findings, Whitwell et al. (2014) proposed that *if* haptic feedback supports DF's grip aperture scaling then it may do so by providing feedback related to thumb and index finger position that is used in a feedforward fashion to support performance on future trials, and/or generate an error signal that permits an absolute visuo-haptic calibration (for challenges to Schenk's findings and interpretation see Whitwell & Buckingham, 2013; Whitwell et al., 2014; see also Milner et al., 2012).

Recent work by my group showed that dissociable information supports grasping responses performed with and without haptic feedback (Davarpanah Jazi et al., 2015a,b; Hosang et al., 2016; see also Davarpanah Jazi & Heath, 2014). Notably, a distinction between my group's work and others (Bingham et al., 2007; Schenk, 2012) is that instead of contrasting PH- and H+ trials my group employed a pantomime-grasping condition wherein haptic feedback was provided after participants achieved their desired movement goal location (henceforth referred to as *no-target pantomime-grasp, with haptic feedback*: PH+). In particular, PH+ trials entailed an experimenter placing a physical object between participants' thumb and forefinger only after their grasping response was completed. Thus, and unlike H+ trials, PH+ trials provided: (1) no expectancy that the object would be available to grasp immediately at the end of the response; and (2) no risk of an early object collision (see Smeets & Brenner, 1999). For example, the PH- and PH+ trials employed by Davarpanah Jazi et al. (2015b) were completed in separate blocks. Additionally, just-noticeable-difference scores (JNDs) at the time of peak grip

aperture (PGA) were calculated to determine whether task-types adhered to, or violated, the psychophysical principles of Weber's law. Indeed, Weber's law asserts that the JNDs associated with discriminating between an original (i.e., the to-be-grasped target object) and a comparator stimulus (i.e., grip aperture) is in constant proportion to the magnitude of the original stimulus, and that the sensitivity of detecting a change in any physical continuum is *relative* as opposed to *absolute* (for review of this issue in grasping, see Heath et al., 2015a). As such, JNDs in grasping provide a law-based evaluation of the nature of the information supporting motor output (see Ganel et al., 2008a; Heath et al., 2011). Results showed that JNDs for the PH- and PH+ trials adhered to and violated Weber's law, respectively. In line with previous work, results for the PH- trials indicated aperture shaping via relative visual information (e.g., Bingham et al., 2007; Cavina-Pratesi et al., 2011; Goodale et al., 1994; Holmes et al., 2013). In turn, that PH+ trials violated Weber's law indicates that the provision of haptic feedback supports the absolute specification of object size. More specifically, my group proposed that PH+ trials engender an error signal related to a difference between an "expected" (in this case haptic) and "actual" sensory outcome that supports an absolute visuo-haptic calibration mediating future trials (for review of internal models see Wolpert et al., 1995). Indeed, such a view is consistent with evidence that haptic feedback is as a salient "intermodal alignment" signal that supports the learning and the predictions necessary for future motor responses (Flanagan et al., 2006).

The goal of the present investigation was to examine the issue of whether advanced knowledge related to the provision of haptic feedback influences the information supporting PH- and PH+ trials. The basis for my question was twofold. First, and as mentioned above, it is possible that the PH- trials used in Bingham et al.'s (2007) random feedback schedule were influenced by an expectation that the object would be available at the movement goal location. Indeed, because Bingham et al.'s random feedback schedule included PH- and H+ trials it is entirely possible that participants structured their responses based on a strategy designed to avoid colliding with the object in the event that it was present. In fact, the authors of that work acknowledge that such a strategy may account for the equivalent peak and terminal grip aperture values associated

with their random feedback schedule PH- and H+ trials. To that end, I contrasted PH- and PH+ trials performed in blocked (i.e., the same feedback schedule as used by Davarpanah Jazi et al., 2015b) and random feedback schedules. Importantly, the use of PH- and PH+ trials in the random feedback schedule provides equivalent movement strategies because the absence of a physical object in both tasks obviates the need for responses to be structured as if the object was always available to touch, or collide with. Second, I computed JNDs across all experimental conditions to provide a law-based measure of whether advance knowledge related to the provision of haptic feedback influences the information supporting grasping. In terms of research predictions, if PH+ trials in the random feedback schedule violate Weber's law then results would support the contention that intermittent – and unpredictable – haptic feedback is sufficient to support an absolute visuo-haptic calibration. In turn, if PH+ trials in the random feedback schedule adhere to Weber's law then results would indicate that advanced knowledge of haptic feedback availability is necessary to support an absolute visuo-haptic calibration. Moreover, evidence supporting the latter view would indicate that the inability to contrast actual and expected haptic events on a trial-by-trial basis precludes the development of an internal model necessary for the aforementioned calibration. In addition, I included memory-guided (MG) trials wherein haptic feedback was immediately available at the movement goal location. The MG trials were employed as a naturalistic control for the integration of haptic feedback.

4.2 Materials and Methods

4.2.1 Participants

Sixteen individuals (1 male and 15 females: age range = 18–29 years) from the University of Western Ontario community volunteered to participate in this study. All participants were self-declared right hand dominant and had normal or corrected-to-normal vision. Participants signed consent forms approved by the Office of Research Ethics, University of Western Ontario, and this work was completed according to the Declaration of Helsinki. The participants recruited here were a convenience sample and I recognize that it resulted in an asymmetrical number of female participants. That said, a

previous study by my group reported null sex-based differences in the integration of haptic feedback for grasping kinematics (Davarpanah Jazi & Heath, 2014). Thus, I do not believe that my results are tempered by sex-based differences in grasping control.

4.2.2 Apparatus and procedures

Participants stood in front of a table-top (height = 880 mm, depth = 760 mm, width = 1060 mm) for the duration of the experiment and used a precision grip (i.e., thumb and forefinger) to grasp the long-axis of differently sized target objects with their right hand (see Figure 4-1 for grasping posture). The target objects were black acrylic blocks that were different in width (20, 30, 40 and 50 mm) but had the same height and depth (10 mm). Target objects were positioned 300 mm from the front edge of the table and at participants' midline. The target objects' long-axis was oriented perpendicular to participants' midline. A pressure sensitive switch placed at table midline and 50 mm from the front edge of the table served as the start location for each trial. Vision of the grasping environment was controlled via liquid-crystal shutter goggles (PLATO Translucent Technologies, Toronto, ON, Canada; for further information see: Milgram, 1987). As well, a Sonalart (Mallory Sonalart Products, Indianapolis, IN, USA) was used to cue grasping responses. Computer and auditory events were controlled via MATLAB (7.9.0: The MathWorks, Natick, MA, USA) and the Psychophysics toolbox extensions (ver 3.0; Brainard, 1997). A National Instruments A/D board (NI PCI-6221, National Instruments, Austin, TX, USA) supported external hardware connections (i.e., start location switch, translucent goggles, and Sonalart).

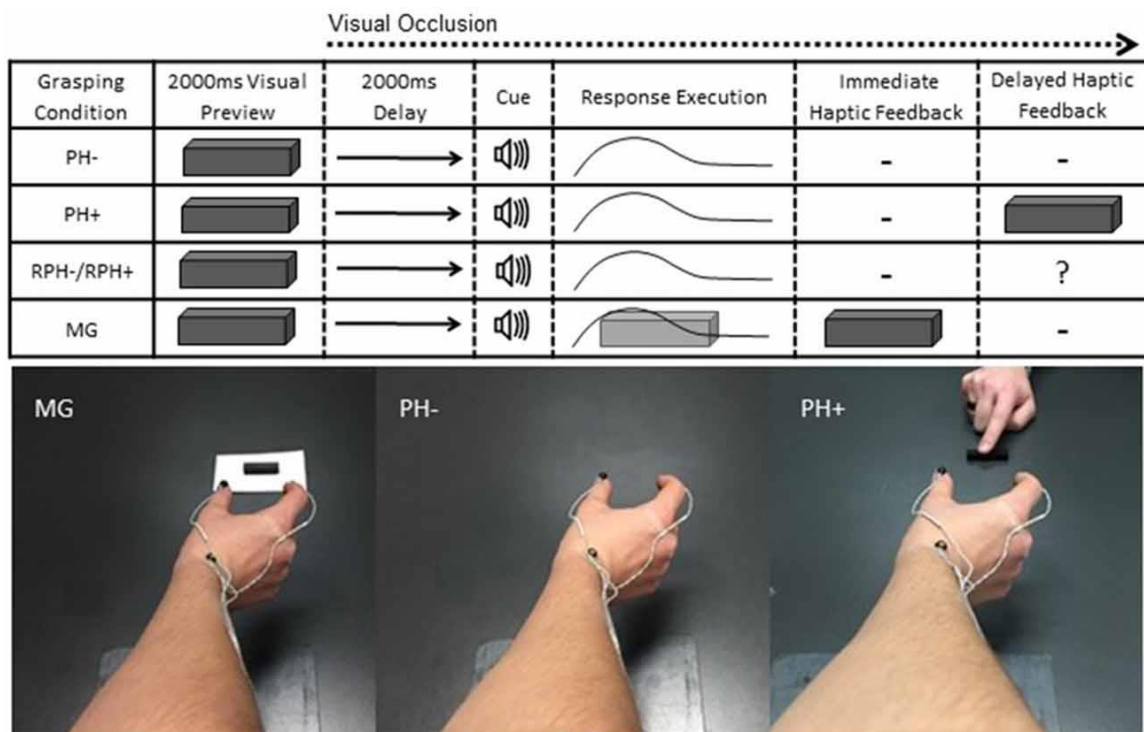


Figure 4-1: Schematic of visual, auditory and haptic events for the memory-guided (MG) and no-target pantomime-grasping trials with (i.e., PH+) and without (i.e., PH-) haptic feedback in blocked (i.e., BPH- and BPH+) and random (RPH- and RPH+) feedback schedules. Participants were provided a 2000 ms visual preview of a target object 20, 30, 40, or 50 (mm) in width after which time vision was occluded for a 2000 ms delay and followed by an auditory tone. For MG trials, the target object remained present on the grasping surface and therefore provided immediate haptic feedback. For the pantomime-grasping trials, the target object was removed from the grasping environment and was not available to “touch” at the movement goal location. At the end of BPH+ and RPH+ trials the experimenter placed the physical target object between participants’ thumb and forefinger to provide delayed haptic feedback. For RPH- and RPH+ trials, the *question mark* in the column headed “Delayed Haptic Feedback” indicates that participants were unaware of whether haptic feedback would be available. The photographs below the schematic provide an egocentric view of a participant’s limb position at the movement goal location for MG, PH- and PH+ trials. Notably, for the PH+ trials

the experimenter's limb can also be seen placing the target object between the participant's thumb and forefinger. Note: the goggles were in their translucent state throughout a movement; hence, the egocentric view presented here serves only to depict participants' grasp posture.

4.2.3 Memory-guided (MG) grasping

Prior to each trial the experimenter placed a target object on the tabletop surface while the participant rested the medial surface of their grasping limb on the start location - during this time the goggles were set to their translucent state. Once the target was appropriately placed, the goggles were set to their transparent state for a 2000 ms visual preview. Following the preview, the goggles reverted to their translucent state for a 2000 ms delay interval after which time a tone (2900 Hz for 100 ms) cued participants to initiate a grasping response. Participants were instructed to grasp - but not lift - and hold the target object for 2000 ms before returning to the start location. The goggles remained translucent for the duration of the response, thus participants planned and executed their response in the absence of online visual feedback. Notably, the target object remained on the table surface for the duration of the response and provided immediate terminal haptic feedback related to absolute object size. The MG condition was performed in a single block of trials and participants were therefore aware that a physical target object would be present at the movement goal location.

4.2.4 Pantomime-grasping

Participants completed two types of pantomime-grasping trials and both entailed the same visual and auditory events as the MG task. In particular, the no-target pantomime-grasp without haptic feedback trials (PH-) served as a more “traditional” pantomime-grasping response and involved the experimenter removing the target object from the grasping environment during the delay interval. As such, participants grasped to a remembered target location and were not afforded terminal haptic feedback related to object size. Further, participants were instructed to maintain their terminal aperture for 2000 ms before returning to the start location. In the *no-target pantomime-grasp, with haptic feedback* trials (PH+), the experimenter removed the target object from the grasping environment as in the PH- trials; however, after movement offset (see kinematic definition of movement offset below) the experimenter placed the target object between participants’ right thumb and forefinger. More specifically, a tone generated via the kinematic defined movement offset signaled the experimenter to place the target object

back on the table surface and the experimenter slid the object until it first contacted the thumb and then positioned the object until the opposite side contacted the forefinger of the grasping hand. The time required to complete this process was not longer than 2500 ms. Notably, this time window has been shown to be sufficiently brief to allow for feedback-based integration (for review see Heath et al., 2010). Participants were then instructed to make the appropriate adjustments to produce a stable precision grasp (i.e., a forefinger and thumb posture that would allow for lifting of the target object). The target object was held – but not lifted – for 2000 ms before the participant returned to the start location. Figure 4-1 provides a schematic representation of the sequence of visual, auditory and haptic events that occurred during a single trial across all task-types. The 2000 ms visual delay between target preview and response cuing provided the experimenter with sufficient time to remove the target object from the table-top during pantomime-grasping trials. Further, previous work by my group has shown that MG grasping movements (i.e., the control condition in this experiment) completed following a delay (of 2000 ms or less) violate Weber’s law and are mediated via absolute visual information - a finding my group has replicated on a number of occasions (Davarpanah Jazi et al., 2015b; Holmes et al., 2011; Hosang et al., 2016; for review see Heath et al., 2015a). Thus, my group has shown that the delay interval used here does not influence the nature of the information mediating motor output. Further, and in line with my group’s previous work (Davarpanah Jazi et al., 2015b), MG, PH- and PH+ trials were completed in a 600–800 ms grasping time bandwidth. Following each trial verbal feedback (i.e., “too fast”, “too slow”, “good”) was provided, and any trial falling outside the bandwidth was discarded and reentered into the trial matrix. Less than 5% of trials were repeated for this reason.

PH- and PH+ trials were performed in *blocked* (i.e., BPH- and BPH+) and *random* (i.e., RPH- and RPH+) feedback schedules. In the blocked feedback schedule (i.e., the same feedback schedule as used by Davarpanah Jazi et al., 2015b) participants were aware of whether or not terminal haptic feedback would be available, whereas in the random feedback schedule the presence of such feedback could not be predicted. More specifically, in the random feedback schedule PH+ and PH- trials were randomly

interleaved on a trial-by-trial basis. The different trial blocks entailed 15 trials to each object size (which were randomly ordered). Therefore, the MG, BPH- and BPH+ trial blocks each consisted of 60 trials and each required approximately 30 min to complete. In turn, the random feedback schedule entailed 120 trials (i.e., 60 trials of each of the RPH- and RPH+ tasks) and required approximately 60 min to complete. To reduce mental and physical fatigue, the four trial blocks were performed in separate sessions separated by at least 24 h (i.e., two blocks per session). The ordering of trial blocks was randomized.

4.2.5 Data analysis

The position of the right limb was measured via infrared emitting diodes (IREDs) placed on the lateral surface of the distal phalanx of the forefinger, the medial surface of the distal phalanx of the thumb, and the styloid process of the wrist. IRED position data were sampled at 400 Hz via an OPTOTRAK Certus for 1500 ms following response cuing. IRED position data were filtered offline via a second-order dual-pass Butterworth filter employing a low-pass cutoff frequency of 15 Hz (for further information see Winter & Patla, 1997). Subsequently, instantaneous velocities were computed from the position (i.e., displacement) data via five-point central finite difference algorithm. Movement onset was marked when participants released pressure from the start location switch and movement offset was determined when wrist velocity fell below a value of 50 mm/s for 20 consecutive frames (i.e., 50 ms).

4.2.6 Just-noticeable-difference scores (JNDs)

Weber's law asserts that JNDs represent the smallest detectable difference between an original and a comparator stimulus and are proportional to the magnitude of the original stimulus. Moreover, the law states that the sensitivity of detecting a change in any physical continuum is relative as opposed to absolute. In the perceptual literature JNDs are computed via an arbitrary statistical criterion related to participants' ability to discriminate between an original and a comparator stimulus (e.g., 75% of trials or any other possible value). Notably, however, a statistical criterion is not possible for a grasping task. Thus, in the current and other research (Davaranah Jazi & Heath, 2014;

Davarpanah Jazi et al., 2015b; Ganel et al., 2008a; Ganel et al., 2008b; Heath et al., 2012; Holmes & Heath, 2013; Holmes et al., 2011; Holmes et al., 2013; Pettypiece et al., 2009) JNDs represent the within-participants standard deviation of PGA. In addition, I computed JNDs at movement offset (i.e., terminal grip aperture: TGA) to evaluate whether a visuo-haptic calibration extends from the predictive (i.e., PGA; see Jeannerod, 1986) to the end stage of aperture shaping. Importantly, the JND approach used here is based on the Fechnerian principle that variance reflects the uncertainty by which a performer is unable to detect a difference between an original and comparator stimulus (Ganel et al., 2008a; Heath et al., 2015a; for extensive review see Marks & Algom, 1998). In particular, Marks and Algom assert that a linear increase in variability with increasing stimulus intensity "... is Weber's law" (p. 102). Figure 4-2 provides data from an exemplar participant performing MG, BPH- and BPH+ trials. The large panels show trial-to-trial PGAs associated with 20, 30, 40 and 50 mm target objects. Further, the offset panels of Figure 4-2 show standard deviations (i.e., JNDs) associated with the trial-to-trial values. The figure shows that trial-to-trial values for the BPH- trials – but not MG or BPH+ trials – increased linearly with increasing object size and I interpret the linear increase as adherence to Weber's law.

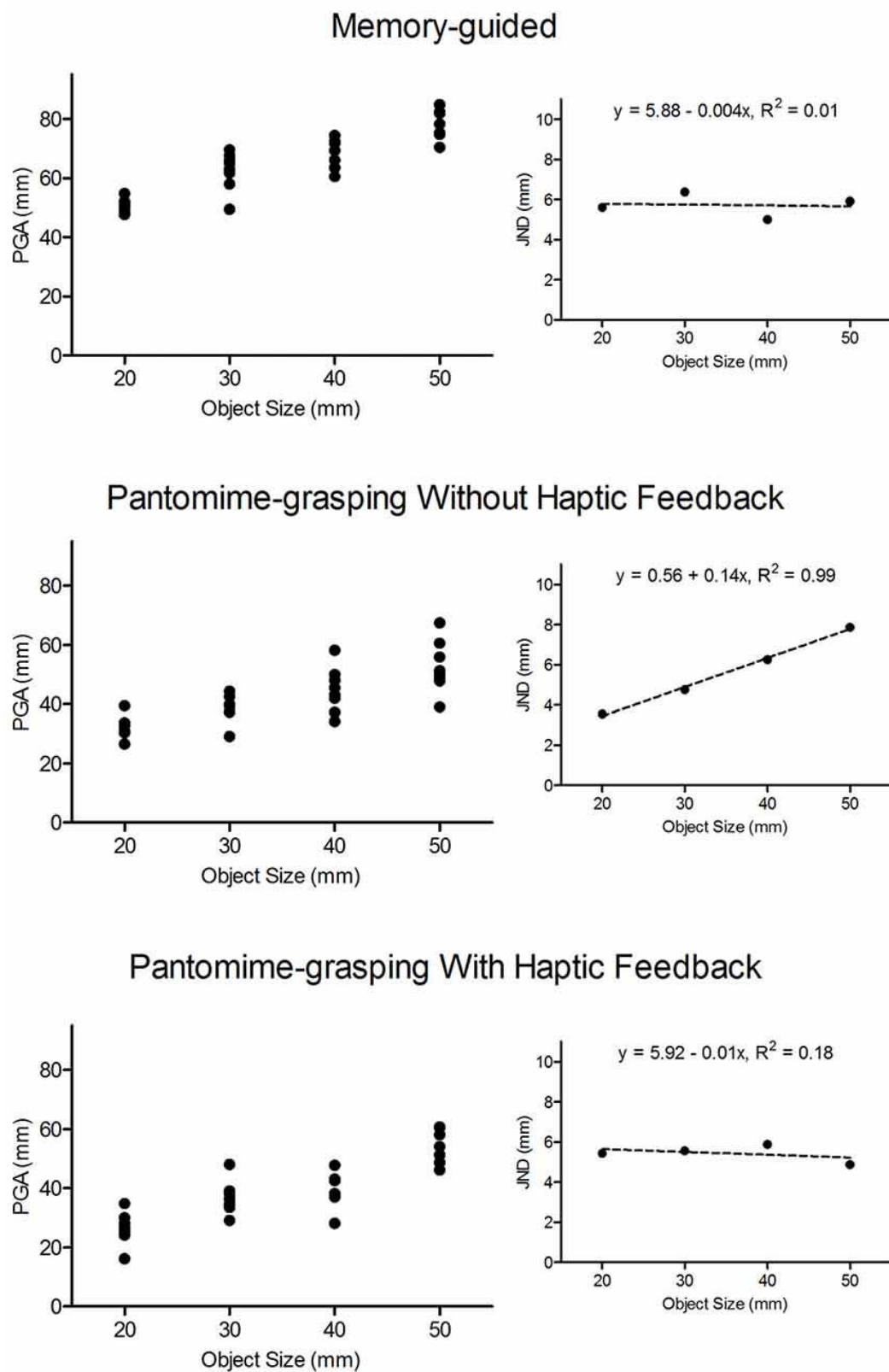


Figure 4-2: Trial-to-trial peak grip aperture (PGA: in mm) values for an exemplar

participant in MG (top panel), blocked feedback schedule pantomime-grasping without haptic feedback (BPH-: middle panel) and blocked feedback schedule pantomime-grasping with haptic feedback (BPH+: bottom panel) trials as a function of object size. The figure demonstrates that trial-to-trial PGAs for MG and BPH+ trials did not systematically vary with object size, whereas values for BPH- trials increased with increasing object size. The smaller offset panels represent the mean within-participant standard deviation for each object size (i.e., the just-noticeable-difference scores: JNDs). The dashed lines represent the linear regression of JNDs to object size and the top of each panel presents the associated linear regression equation and proportion of explained variance. The figure graphically demonstrates my computation and interpretation of JNDs. In particular, null scaling of JNDs to object size (i.e., MG and BPH+ trials) is taken as a violation of Weber's law, whereas values that systematically increase with object size (i.e., BPH- trials) are taken as adherence to the law.

4.2.7 Dependent variables and statistical analyses

In line with our previous work, I examined grasping time (GT: time between movement onset and offset), peak grip aperture (PGA: maximum resultant distance between thumb and forefinger), terminal grip aperture (TGA: distance between thumb and forefinger at movement offset), time to peak grip aperture (tPGA: time from movement onset to PGA) and computed JNDs at PGA and TGA. All dependent variables were examined via 5 (condition: MG, BPH-, BPH+, RPH- and RPH+) by 4 (object size: 20, 30, 40, and 50 mm) repeated measures ANOVA. Main effects and interactions were considered significant at an alpha level of 0.05 or less. *Post hoc* contrasts for object size were examined via power-polynomials (i.e., trend analysis: see Pedhazur, 1997), whereas between-condition effects were decomposed via paired samples *t*-tests. I also computed participant-specific slopes relating JNDs (at PGA and TGA) to object size across the five grasping conditions (i.e., MG, BPH-, BPH+, RPH- and RPH+). The slope analyses were designed to support a series of planned contrasts. The first planned contrast examined all pairwise comparisons between MG, BPH- and BPH+ trials, whereas the second examined all pairwise comparisons between BPH-, RPH- and RPH+ trials. The basis for these analyses was to: (1) determine whether advance knowledge of haptic feedback in a pantomime-grasping task (i.e., BPH+ trials) elicits a null JND/object size scaling commensurate to a more naturalistic grasping task (i.e., MG trials); and (2) determine whether the absence of advance haptic feedback information (i.e., RPH- and RPH+ trials) renders aperture scaling commensurate to a “traditional” pantomime-grasping task (i.e., BPH- trials).

4.3 Results

The average GT was 693 ms ($SD = 27$) and this variable did not produce any manipulation related effects (all $F < 1$). Results for tPGA yielded main effects for condition, $F(4,60) = 26.76$, $p < 0.001$, and object size, $F(3,45) = 7.46$, $p < 0.01$. In particular, tPGA values for pantomime-grasping conditions did not reliably vary (BPH- = 599 ms, $SD = 46$; BPH+ = 609 ms, $SD = 36$; RPH- = 574 ms, $SD = 39$; RPH+ = 578 ms, $SD = 40$; all $t(15) < 1$) and occurred later than the MG condition (507 ms, $SD = 45$; all

$t(15) > 5.80$, all $p < 0.001$). In addition, across all trial-types t PGA increased linearly with increasing object size (only linear effect significant: $F(1,15) = 9.44$, $p < 0.01$). Results for PGA produced main effects for condition, $F(4,60) = 31.82$, $p < 0.001$, object size, $F(3,45) = 399.19$, $p < 0.001$, and their interaction, $F(12,180) = 2.76$, $p < 0.01$. Figure 4-3 shows that PGAs for all trial-types increased with increasing object size (only linear effects significant: all $F(1,15) = 206.79, 338.38, 207.78, 355.77$ and 328.93 for BPH-, BPH+, RPH-, RPH+ and MG trials, respectively, all $p < 0.001$). As well, at each matched object size PGAs for the MG condition were larger than all pantomime trial-types (all $t(15) > 4.91$, all $p < 0.001$), which did not reliably differ from one another (all $t < 1$). In terms of TGA, results indicated a main effect for object size, $F(3,45) = 428.94$, $p < 0.001$, such that values increased linearly with increasing object size (only linear effect significant: $F(1,15) = 514.16$, $p < 0.001$; see Figure 4-3). As well, I note that the absence of a reliable effect of condition, $F(4,60) < 1$, for TGA demonstrates that the larger aperture values associated with MG trials early in the grasping trajectory (i.e., at PGA) were no longer present at movement offset.

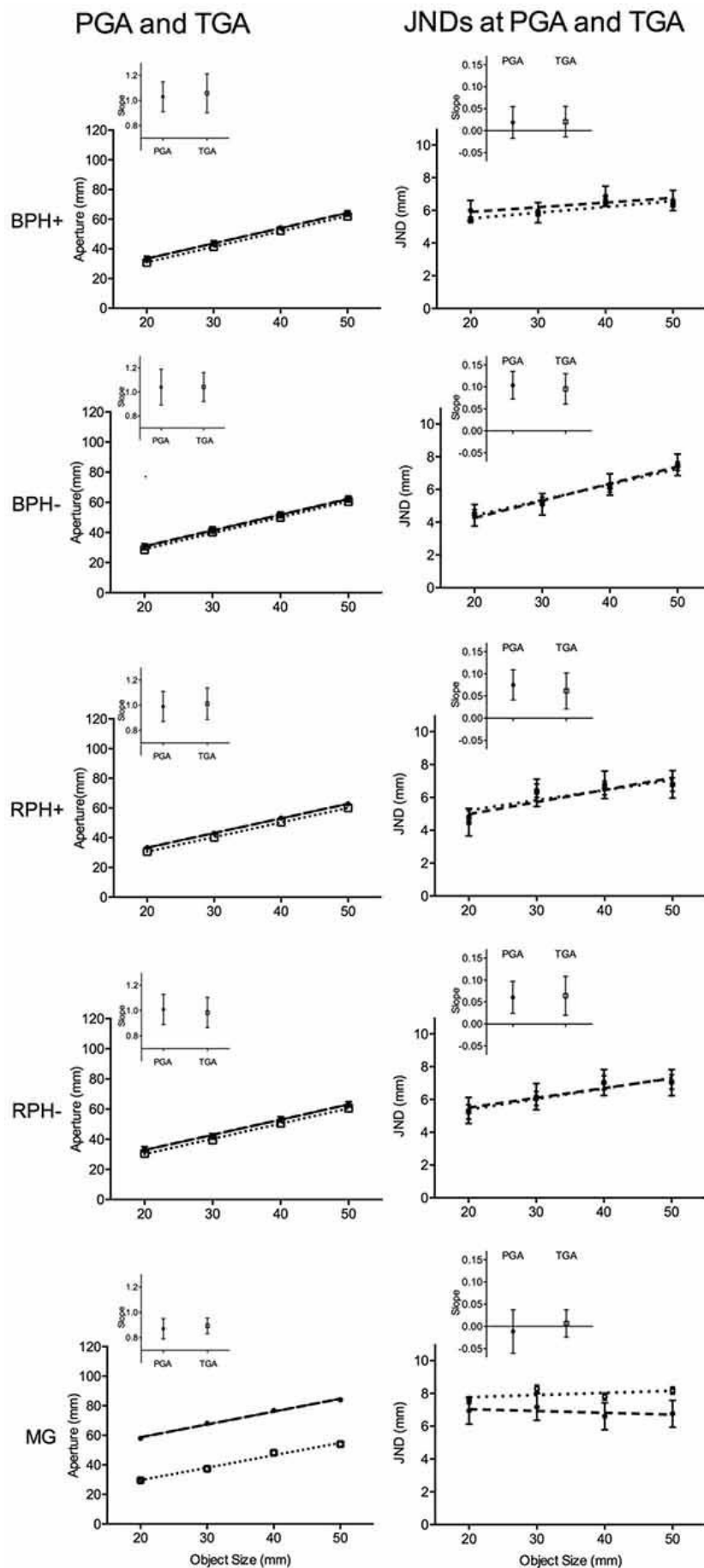


Figure 4-3: The left panels present mean peak grip aperture (PGA in mm; see closed circle symbols and dashed regression line) and terminal grip aperture (TGA in mm; see open square symbols and dotted regression line) and the right panels depict just-noticeable-difference scores (JNDs in mm) computed at PGA (see closed circle symbols and dashed regression line) and TGA (see open square symbols and dotted regression line) for: (1) blocked feedback schedule pantomime-grasping trials performed with (BPH+) and (2) without (BPH-) haptic feedback, and (3) random feedback schedule pantomime-grasping trials performed with (RPH+) and (4) without (RPH-) haptic feedback, and (5) MG trials. Error bars represent 95% within-participants confidence intervals as a function of the mean-squared error term for object size computed separately for each trial-type (Loftus & Masson, 1994). Note: for the PGA and TGA panels the size of the error bars is less than the width of the symbol depicting the mean value, as well, for all pantomime-grasp trial-types a significant degree of overlap exists between PGA and TGA values. The inset panels represent the mean participant-specific slope relating PGA and TGA to object size and JNDs (computed separately at PGA and TGA) to object size. Error bars represent 95% between-participant confidence intervals and the absence of overlap between a confidence interval and the horizontal line indicates that the slope reliably differed from zero, and is a result that can be interpreted inclusive to a test of the null hypothesis (Cumming, 2013).

Results for JNDs computed at PGA and TGA yielded main effects of object size, all $F(3,45) = 11.26$ and 11.01 for JNDs at PGA and TGA, respectively, all $p < 0.001$, and condition by object size interactions, all $F(12,180) = 3.49$ and 2.70 for JNDs at PGA and TGA, respectively, all $p < 0.01$. Figure 4-3 demonstrates that JNDs computed at PGA for BPH-, RPH- and RPH+ trials increased linearly with increasing object size (only linear effects significant: all $F(1,15) = 50.63, 12.02$ and 21.63 for BPH-, RPH- and RPH+ conditions, respectively, all $p < 0.001$), whereas JNDs for the BPH+ and MG conditions did not reliably vary with object size, all $F(3, 45) = 1.46$ and 0.36 , $ps = 0.24$ and 0.78 . In addition, JNDs computed at TGA match the aforementioned analyses; that is, values for BPH-, RPH- and RPH+ conditions increased linearly with increasing object size (only linear effects significant: all $F(1,15) = 14.75, 10.40$, and 9.52 for BPH-, RPH- and RPH+ conditions, respectively, all $p < 0.01$), whereas BPH+ and MG conditions did not reliably vary with object size, all $F(3,45) = 1.72$ and 0.08 for BPH+ and MG conditions, respectively, $ps = 0.17$ and 0.50 .

The inset panels for JNDs in Figure 4-3 provide mean JND/object size slopes (for values computed at PGA and TGA) and associated 95% confidence intervals for each trial-type. These figures graphically support my analyses of mean JND values; that is, slopes for the BPH-, RPH+ and RPH- trials – but not the BPH+ and MG trials - reliably differed from zero. As well, I used participant-specific slopes for a series of planned comparisons and for ease of presentation I present here only JND/object size slopes computed at the time of PGA³. The first set of planned comparisons show that the slope for BPH- trials (0.10 , $SD = 0.06$) was steeper than MG (-0.01 , $SD = 0.09$) and BPH+ trials (0.02 , $SD = 0.05$; all $t(15) = 4.37$ and 4.05 , all $p < 0.002$), and the latter two trial-types did not reliably differ ($t(15) = -1.22$, $p = 0.24$). A second set of planned comparisons indicated that RPH- (0.06 , $SD = 0.07$), RPH+ (0.08 , $SD = 0.06$) and BPH- trials did not reliably differ from one another (all $t(15) = 1.65, 1.31$, and -1.00 , all $p > 0.33$, respectively for RPH- vs. BPH-, RPH+ vs. BPH-, and RPH- vs. RPH+).

4.4 Discussion

My group has previously demonstrated that PH- and PH+ trials performed in separate blocks adhere to, and violate Weber's law, respectively. This demonstrates that haptic feedback supports an absolute visuo-haptic calibration (Davarpanah Jazi et al., 2015b). The present study contrasted PH- and PH+ trials across blocked and random feedback schedules to determine whether advanced knowledge of haptic feedback is necessary to support the aforementioned calibration.

4.4.1 Memory-guided (MG) and blocked feedback schedule pantomime-grasping with (BPH+) and without (BPH-) haptic feedback

I first outline findings for MG and blocked pantomime-grasping trials (i.e., BPH- and BPH+) to demonstrate that results replicate an earlier study by my group (Davarpanah Jazi et al., 2015b). In particular, PGA and tPGA values for MG, BPH- and BPH+ trials increased linearly with increasing object size – a finding demonstrating that the motor system reliably discriminated between the differently sized objects used here (for resolution of visuomotor system see Ganel et al., 2012). Notably, however, MG trials produced larger and earlier occurring PGAs than BPH- and BPH+ trials (Cavina-Pratesi et al., 2011; Davarpanah Jazi et al., 2015b; see also Goodale et al., 1994; Holmes et al., 2013; Westwood et al., 2000). These results are consistent with previous work and demonstrate that the absence of a physical object (i.e., BPH- and BPH+ trials) offers no risk of an object “collision” and thereby renders PGA values that are smaller and later occurring than MG trials (for review of double-pointing hypothesis see Smeets & Brenner, 1999). In further support of this assertion, MG trials produced comparable terminal grip apertures (i.e., TGA) to BPH- and BPH+ trials – a result further indicating that the larger PGA of MG trials is related to an obligatory strategy designed to reduce the possibility of a collision. More notably, the timing and magnitude of PGAs, as well as the magnitude of TGA, for BPH- and BPH+ trials did not differ. This is a salient finding for two reasons. First, it demonstrates that trial-types were associated with comparable movement strategies. Second, it demonstrates that any difference in JND values across BPH- and BPH+ trials (see details below) cannot be attributed to a range

effect in aperture size (i.e., larger JND for a response with a larger PGA or TGA; Lemay & Proteau, 2001) or the stochastic properties of motor-output variability (Schmidt et al., 1979)⁴.

I computed JNDs at the time of PGA and TGA to provide a law-based measure of whether MG, BPH-, and BPH+ trials adhere to or violate Weber's law. Results for JNDs computed at PGA and TGA matched one another and showed that BPH- trials adhered to Weber's law, whereas MG and BPH+ trials violated the law. Further, the mean JND/object size slope for BPH- trials was larger than MG and BPH+ trials, and the latter two trial-types did not differ. These findings provide a direct replication of my group's previous work (Davarpanah Jazi et al., 2015b; see also Holmes et al., 2011) and are taken to evince that the absence of haptic feedback (i.e., BPH- trials) renders pantomime-grasps selectively mediated via relative visual information (see also Cavina-Pratesi et al., 2011; Fukui & Inui, 2013; Goodale et al., 1994; Holmes et al., 2013; Westwood et al., 2000). In turn, that haptic feedback provided immediately at the movement goal location (i.e., MG trials) or when experimentally induced (i.e., BPH+ trials) resulted in a violation of Weber's law indicates an absolute visuo-haptic calibration. Moreover, in accounting for the calibration hypothesis I emphasize that object size was randomly varied on a trial-by-trial basis. Thus, during BPH+ (and MG) trials it was not possible for participants to use haptic feedback from trial N-1 in order to support aperture scaling on a subsequent trial. Instead, I propose that an error signal related to the difference between a predicted and an actual haptic outcome activates a learning corrective process supporting the refinement and calibration of an internal forward model (see Flanagan et al., 2006). The internal model is proposed to mediate a visuo-haptic calibration serving the absolute specification of object size on future trial performances (see also Davarpanah Jazi & Heath, 2014; Whitwell et al., 2014).

4.4.2 Blocked vs. random haptic Feedback schedule: preparing for the "worst case"

Recall that the objective of this study was to determine whether advanced information related to haptic feedback availability influences the nature of the information supporting

PH- and PH+ trials. In addressing this objective, I note that previous work by Bingham et al. (2007) showed that PH- trials performed in a blocked feedback schedule exhibited smaller PGAs (and TGAs) than trials wherein the object was available to grasp at the movement goal location (i.e., H+ trials). In contrast, PH- trials in a random feedback schedule exhibited PGAs that were as large as blocked and random feedback schedule H+ trials. Accordingly, the authors proposed that intermittent – and unpredictable – terminal haptic feedback (i.e., random H+ trials) is sufficient to support absolute calibration in PH- trials. As outlined in section 4.1 however, it could be argued that the larger PGAs associated with random feedback schedule PH- trials reflects a strategy designed to avoid the possibility of a hand/object collision. To avoid that potential confound, I contrasted PH- and PH+ trials in a random feedback schedule (i.e., RPH- and RPH+ trials) to preclude expectancy-based differences in grasping control. To that end, I found that the timing and magnitude of PGA, and the magnitude of TGA, for RPH- and RPH+ trials was equivalent to their blocked feedback schedule counterparts (i.e., BPH- and BPH+ trials). As such, the PGA findings demonstrate that the pantomime-grasping trial-types used here were associated with comparable control strategies, and my results provide no evidence that intermittent and unpredictable haptic feedback supports an absolute visuo-haptic calibration.

As indicated previously, JNDs (computed at PGA and TGA) for BPH- and BPH+ trials respectively adhered to and violated Weber's law. In contrast, RPH- and RPH+ trials adhered to the law. Moreover, JND/object size slopes for RPH- and RPH+ trials did not reliably differ in magnitude from BPH- trials. That RPH- and RPH+ trials adhered to Weber's law on par to BPH- trials provides law-based evidence that the inability to predict haptic feedback availability precluded an absolute calibration process and rendered aperture shaping via relative visual information. Thus, an important issue to address is why advance knowledge of haptic feedback is required to support an absolute visuo-haptic calibration. In addressing this question, I have drawn on work contrasting reaching/grasping movements performed with (i.e., CL action) and without (i.e., open-loop) continuous limb and target vision across blocked and random feedback schedules. In particular, results have shown that CL trials performed in a blocked feedback schedule

are more accurate (Elliott & Allard, 1985; Zelaznik et al., 1983), exhibit more online trajectory amendments (Khan et al., 2002) and produce more effective PGAs (Jakobson & Goodale, 1991) than counterparts performed in a random feedback schedule. Accordingly, the inability to predict the availability of visual feedback has been interpreted to reflect the adoption of a “worst-case” control strategy wherein a response is specified largely in advance of movement execution via central planning mechanisms (Elliott et al., 2009). As well, work has shown that CL reaching (Neely et al., 2008) and grasping (Heath et al., 2006) responses in a blocked feedback schedule are refractory to the context-dependent (i.e., relative) features of pictorial illusions, whereas random feedback schedule counterparts are “tricked” in a direction consistent with the illusion’s perceptual effects. As such, a “worst-case” control strategy has been tied to motor output subserved via relative visual information (for review see Heath et al., 2011). Indeed, it is entirely possible that in a “worst-case” control strategy the unpredictable nature of feedback diminishes participants’ ability to contrast an expected to an actual *visual* outcome and therefore limits the efficiency and effectiveness of an internal forward model supporting trial-by-trial performance improvements (Cheng & Sabes, 2007). In the context of the current investigation, an internal forward model would serve to trigger a learning corrective process when a mismatch is detected between a predicted and actual haptic outcome (Westling & Johansson, 1987). Thus, the predicted availability of haptic feedback (BPH+ trials) may represent the environment necessary for an optimal integration between visual and haptic systems (Ernst & Banks, 2002) and therefore supports the trial-by-trial learning corrective process required for an absolute visuo-haptic calibration. In contrast, I propose that completing a response in an environment wherein haptic feedback is unavailable (i.e., BPH- trials) or cannot be predicted (i.e., RPH- and RPH+ trials) limits - or precludes - an optimal integration process and results in motor output specified via the relative visual features of a target object.

4.5 Conclusions

This work provides the first examination of whether pantomime-grasping performed with and without advance knowledge of haptic feedback adheres to or violates the

psychophysical principles of Weber's law. Results showed that grasping adhered to Weber's law when haptic feedback was unavailable or could not be predicted – a finding I interpret to reflect the selective use of relative visual cues for aperture shaping. In contrast, responses violated Weber's law when haptic feedback was predictably available. As such, I propose that trial-to-trial knowledge of haptic feedback serves as an optimal environment to support an absolute visuo-haptic calibration. Moreover, I again emphasize that my work identifies a critical limitation of the only other study to have examined the role of haptic feedback in a random feedback schedule (Bingham et al., 2007). Bingham et al.'s study is taken as explicit evidence for the sensory requirements associated with an absolute visuo-haptic calibration. Notably, and counter to Bingham et al. (2007), I show that advanced knowledge of haptic feedback is required to support an absolute haptic feedback calibration/integration. I therefore see my results as an important contribution to the grasping literature. Future work in this area will examine the concurrent behavioral and electroencephalographic (i.e., event-related brain potentials: ERP; see Heath et al., 2015b) properties of pantomime-grasping responses performed with and without haptic feedback. In particular, the P300 ERP waveform is a component of interest because it reflects the updating of an internal mental model (Donchin & Coles, 1988). As such, modulation of the P300 amplitude in grasping paradigms similar to that used here would identify the neural mechanism associated with an absolute visuo-haptic calibration. Such a result would provide a more encompassing theoretical view of feedback in grasping, and may serve to emphasize its role and integration in future prosthetic and robotic interfaces.

4.6 Footnotes

1. The visual and tactile information mediating perceptions and actions differ with respect to their metrical properties. The term “relative” used for perceptions refers to target features (i.e., size, shape, and location) in relation to its surrounding environment and the manner in which it is encoded (e.g., the object is judged to be bigger or smaller than another object). Relative information is based on comparisons within the environment or memory-based experiences. In

contrast, absolute information reflects the metrical (or Euclidean) properties of a target object. Notably, the use of “relative” and “absolute” information is reflected in the visual (Goodale, 2011) and somatosensory (i.e., tactile; see Lederman & Klatzky, 2009) literature.

2. Although Schenk’s (2012) intermittent feedback schedule included randomly ordered H+ and PH- trials, participants were provided advanced knowledge of whether a trial would involve haptic feedback. Thus, and unlike the present study, Schenk’s work was not designed to evaluate whether the expectancy of haptic feedback influences an absolute visuo-haptic calibration.
3. Although not provided in the main Results, JND/object size slopes computed at TGA match those computed at PGA. In particular, the slope for BPH- trials (0.09, SD = 0.06) was steeper than MG (0.00, SD = 0.05) and BPH+ (0.02, SD = 0.05) trials, (all $t(15) = 2.50$ and 4.66 , all $p < 0.03$). In turn, slopes for RPH- (0.07, SD = 0.07), RPH+ (0.07, SD = 0.06) and BPH- trials did not reliably differ from one another (all $t(15) = 1.22$, 1.01 and -0.15 , all $p > 0.24$, respectively for RPH- vs. BPH-, RPH+ vs. BPH-, and RPH- vs. RPH+).
4. An issue raised in the review process was that the larger PGAs associated with MG trials in combination with the condition’s null scaling of JNDs relates to a mechanical constraint and/or the neuromotor noise accompanying a larger aperture opening. In addressing this issue, I first note that BPH+ trials elicited PGAs that matched the other pantomime-grasping conditions and were smaller than MG trials. In spite of this result, JNDs for BPH+ trials did not vary with object size. Moreover, all trial-types produced comparable TGA values. Thus, a mechanical-based explanation cannot account for the null JND/object size scaling observed at PGA and TGA for the MG and BPH+ trials. Second, a previous study by my group (Heath et al., 2012) was purpose-designed to examine if JND/object size scaling is related to the stochastic properties of motor output variability (for review see Schmidt et al., 1979). In that study participants completed grasps in movement time criterion of 400 ms and 800 ms. It was hypothesized that if impulse-variability impacts JND/object size scaling then

grasping responses requiring higher velocities (i.e., 400 ms) would be associated with larger JND/object size slopes. Counter to that prediction, JND/object size slopes were refractory to the movement time criterion. Accordingly, my group proposed that the scaling of JNDs to object size is independent of neuromotor noise.

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Chapter 5

- 5 The spatial relations between stimulus and response determine an absolute visuo-haptic calibration in pantomime-grasping

A version of this chapter is under review for publication:

Davarpanah Jazi S., & Heath, M. The spatial relations between stimulus and response determine an absolute visuo-haptic calibration in pantomime-grasping. *Brain and Cognition*.

5.1 Introduction

Our ability to recognize and identify a visual object requires that we process the object's *relative* and perceptual properties within an *allocentric* frame of reference (i.e., with respect to other objects). For example, identifying an apple from among different fruits at our local greengrocer is mediated by previous experiences with apples and via allocentric and relative comparisons (e.g., colour, shape, and size) to 'other' fruits. In contrast, if we reach to grasp the apple (i.e., an action task) then maximally effective and efficient motor output requires the computation of the apple's *absolute* properties (e.g., size, shape and location) within an *egocentric* frame of reference (i.e., with respect to our own body). Goodale and Milner's (1992) perception-action model (PAM) asserts that the aforementioned tasks are supported via functionally and anatomically distinct visual processing streams. In particular, the PAM contends that relative and allocentric cues mediating top-down object identification are supported via visuo-perceptual networks residing in the inferotemporal cortex of the ventral visual pathway (James et al., 2003). In turn, the PAM asserts that absolute and egocentric cues supporting actions are subserved via dedicated visuomotor networks in the posterior parietal cortex (PPC) of the dorsal visual pathway.

It is, however, important to recognize that some goal-directed actions require motor output that is, in part, specified via an object's relative and allocentric properties. For example, Figure 5-1 presents two pantomime-grasping tasks. In the first example (see left panel), a performer is depicted grasping to an area adjacent to a target object (i.e., spatially dissociated pantomime-grasp), whereas in the second example (see right panel) the performer is shown grasping to an area previously occupied by a target object (i.e., no-target pantomime-grasp). In both examples, the performer must regulate their response via top-down (i.e., perception-based) allocentric comparisons between the dissociated stimulus and response (SR) and/or retrieve relative information about the target from memory. In demonstrating this point, Goodale et al. (1994) had patient DF and healthy controls complete spatially dissociated and no-target pantomime-grasps. DF is an extensively studied individual with a visual form agnosia (i.e., perceptual deficit)

arising from bilateral lesions to her lateral occipital cortex (James et al., 2003). In spite of DF's visuoperceptual impairment, she demonstrated preserved naturalistic reaching and grasping – a finding attributed to her intact dorsal visual pathway. Notably, Goodale et al. showed that DF's spatially dissociated and no-target pantomime-grasps did not scale to the veridical size of target objects; but more specifically, her performance was no better than her well-documented visuoperceptual deficit. Moreover, evidence from healthy controls has shown that pantomime-grasps produce smaller peak grip apertures (PGAs) than their naturalistic grasping counterparts (Cavina-Pratesi et al., 2011; Davarpanah Jazi & Heath, 2016; Davarpanah et al., 2015a,b; Fukui & Inui, 2013; Westwood et al., 2000). Accordingly, work involving DF and healthy controls indicate that the top-down and perceptual nature of pantomime-grasps renders motor output via relative and allocentric visual information. Further, Holmes et al. (2013) provided a law-based measure of the nature of the information supporting spatially dissociated pantomime-grasps by examining whether such actions adhere to, or violate, the relative psychophysical principles of Weber's law. The results of that study showed that pantomime-grasps and naturalistic grasps adhered to and violated Weber's law, respectively. In other words, Holmes et al. provided direct evidence that spatially dissociated pantomime-grasps are mediated via relative visual information, whereas their naturalistic counterparts are mediated via absolute visual information.

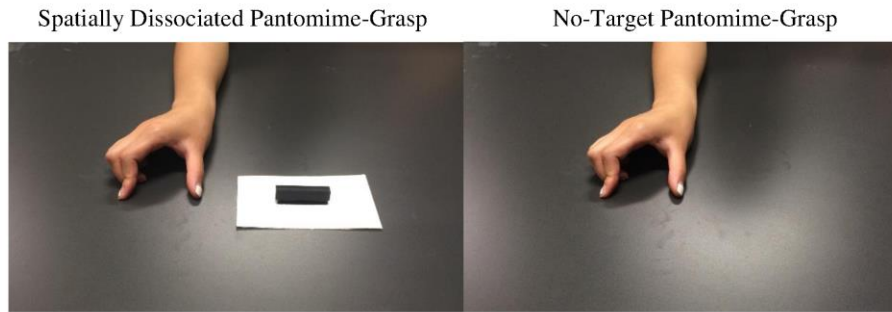


Figure 5-1: Exemplar depictions of spatially dissociated and no-target pantomime-grasps. Both conditions entail a common start and movement goal location. For spatially dissociated pantomime-grasps the target object is adjacent to the movement goal location, whereas for no-target pantomime-grasps the participant is required to grasp to the area originally occupied by the target object. Notably, in both conditions the target object is unavailable to grasp at the movement goal location.

A notable feature of the pantomime-grasps outlined in the previous paragraph is that such actions differed from naturalistic grasping not only in terms of their ‘visual’ properties, but also because the absence of a physical object in pantomime-grasping precluded the opportunity to integrate terminal haptic feedback. Indeed, in a naturalistic grasping task the performer integrates absolute haptic cues via physically grasping the target object, whereas no such feedback is available in pantomime-grasping. Thus, it is possible that terminal haptic feedback serves as an important sensory cue in determining the nature of the information mediating aperture shaping¹. In addressing this issue, Schenk (2012) examined DF’s pantomime-grasping performance by employing a mirror-box apparatus (see Figure 1 of that work; see also Bingham et al., 2007) allowing for the dissociation between the visual and physical location of a to-be-grasped target object. Schenk reported that DF’s pantomime-grasps performed in a block of trials that precluded haptic feedback resulted in motor output that was no better than her visuo-perceptual deficit. In turn, DF’s pantomime-grasps performed in a block of trials that provided intermittent – but predictable – terminal haptic feedback resulted in metrical aperture scaling. Schenk proposed that DF integrates haptic feedback into her pantomime-grasps to support an absolute ‘visuo-haptic’ calibration. Although Schenk did not provide a mechanistic account for his findings (cf. Milner et al., 2012; Whitwell & Buckingham, 2013; Whitwell et al., 2014), Whitwell et al. proposed that if haptic feedback supports DF’s aperture scaling then it may do so via: (1) proprioceptive-based thumb and forefinger feedback serving a feedforward control process mediating future trial performance and/or (2) an error signal derived from predicted and actual haptic feedback cues that supports an absolute visuo-haptic calibration.

In line with Schenk (2012), recent work by my group (Davarpanah Jazi & Heath, 2016; Davarpanah Jazi et al., 2015b; Hosang et al., 2016) and others (Bingham et al., 2007) involving neurologically healthy individuals has shown that no-target pantomime-grasps performed with and without terminal haptic feedback are supported via distinct sensory properties (absolute vs. relative). For example, Davarpanah Jazi et al. had participants complete no-target pantomime-grasps without limb and target vision in conditions wherein terminal haptic feedback was unavailable (i.e., PH-) and available (i.e., PH+) at

the movement goal location. In particular, the PH- condition represented an exemplar pantomime-grasp involving a response to a location previously occupied by a target object. In contrast, for the PH+ condition the experimenter placed the physical target object between participants' thumb and forefinger once they had achieved their movement goal location – a manipulation that provided terminal haptic feedback. Results showed that PH- and PH+ conditions respectively adhered to and violated Weber's law. Thus, results provided law-based evidence that trials in the PH- condition were subserved via relative visual information, whereas the PH+ condition was supported via an absolute specification of object size. Accordingly, it was proposed that an error signal related to the difference between an 'expected' and 'actual' sensory outcome (in this case haptic) mediated an absolute visuo-haptic calibration (for review of internal models see Wolpert et al., 1995).

My group's previous work (Davarpanah Jazi & Heath, 2016; Davarpanah Jazi et al., 2015b) exclusively relied on a no-target pantomime-grasping task. Therefore, it is unclear whether spatially dissociated pantomime-grasps elicit a similar absolute visuo-haptic calibration. To that end, Experiment 1 provided terminal haptic feedback in spatially dissociated pantomime-grasps performed with continuous online limb and target vision. It was hypothesized that dissociated SR relations would result in the preferential weighting of motor output via an allocentric frame of reference and thus diminish – or preclude – the integration of haptic feedback to support an absolute calibration. The basis for this hypothesis was drawn from Ernst and Banks' (2002) maximum-likelihood-estimation model (MLE). More specifically, the MLE states that an optimal motor response is based on an aggregate of all sensory sources (e.g., visual and haptic) and that motor output is preferentially weighted to the more reliable sensory source. Results for Experiment 1 supported my hypothesis and showed that spatially dissociated pantomime-grasps adhered to Weber's law regardless of the provision of haptic feedback. The results of Experiment 1 motivated Experiments 2 and 3 which sought to determine whether visual feedback (i.e., limb and target) availability influences an absolute visuo-haptic calibration in spatially dissociated pantomime-grasping. Thus, I employed the same pantomime-grasp responses as Experiment 1 with the exception that Experiment 2

occluded online target vision, and Experiment 3 occluded limb and target vision at movement onset (i.e., visual open-loop grasping) and introduced a memory delay. Indeed, I sought to determine whether manipulating the reliability of the visual information supporting spatially dissociated pantomime-grasps provides the environment necessary to support a visuo-haptic calibration. Put another way, Experiments 2 and 3 were designed to determine whether a systematic depletion of limb and target vision renders a sensory (re)weighting in which haptic feedback serves as the more reliable sensory source.

5.2 Experiments 1 – 3

5.2.1 Methods

5.2.1.1 Participants

Three separate experiments were conducted and the participants included in any given experiment were independent of the other experiments. All participants were between 19 and 37 years of age, declared being right-hand dominant, with normal or corrected-to-normal vision, and reported that they were not previously or currently diagnosed with a neurological disorder or orthopedic impairment of the upper-limb (see Table 5-1 for participant demographics). Participants signed consent forms approved by the Office of Research Ethics, University of Western Ontario, and this project was completed according to the Declaration of Helsinki.

Table 5-1: Demographic information of participants in Experiments 1 through 4.

	Age Range (years of age)	Female	Male	Total Participants
Experiment 1	19 - 30	11	1	12
Experiment 2	19 - 35	11	2	13
Experiment 3	20 - 37	6	6	12
Experiment 4	18 - 29	11	1	12

5.2.1.2 Apparatus and procedures

For all experiments, participants sat in a height adjustable chair placed in front of a table (height = 780 mm, depth = 760 mm, width = 1060 mm) and used their right forefinger and thumb (i.e., precision grip) to grasp, or pantomime-grasp, the long-axis of target objects. Target objects were acrylic blocks painted flat black with widths of 20, 30, 40, and 50 mm (all were 10 mm in height and depth) and were oriented perpendicular to the primary grasping direction (for pictorial representation see Figure 5-2). To ensure a constant visual presentation, each target object was affixed to a laminated sheet of white paper (i.e., a cue card: depth = 76 mm, width = 127 mm) and then secured to 'lock' points on the tabletop. The start location for the grasping limb was a pressure sensitive switch located at participants' midline and 50 mm from the front edge of the table. Prior to each trial, participants rested the medial surface of their right wrist on the start location with their forefinger and thumb pinched comfortably together. Vision of the grasping environment was controlled via liquid-crystal shutter goggles (PLATO Translucent Technologies, Toronto, ON, Canada) (Milgram, 1987), and a Sonalert electrical buzzer (2,900 Hz) (Mallory Sonalert Products, Indianapolis, IN, USA) served as the movement imperative (i.e., 100 ms in duration). Experimental events were controlled using MATLAB (7.9.0: The MathWorks, Natick, MA, USA) and the Psychophysics Toolbox extensions (ver 3.0) (Brainard, 1997).

	Condition	2,000ms Visual Preview		Response Execution	Response Offset	Delayed Haptic Feedback
Experiment 1	CL					-
	P _D H-					-
	P _D H+					
Experiment 2	P _{DT} -H-		2,000ms Delay 			-
	P _{DT} -H+		2,000ms Delay 			
Experiment 3	P _{Do} H+					
	P _{DM} H+		2,000ms Delay 			
Experiment 4	PH-		2,000ms Delay 			-
	PH+		2,000ms Delay 			

Figure 5-2: Schematic of the sequence of visual, auditory and haptic events across Experiments 1 through 4. For all experiments participants were provided a 2,000 ms visual preview of spatially dissociated or overlapping target objects. Experiment 1: following the visual preview, an auditory cue signalled participants to grasp the target object presented at (i.e., closed-loop condition: CL) or adjacent to the movement goal location (i.e., pantomime-grasps). Pantomime-grasps were

performed with (i.e., spatially dissociated pantomime-grasp, with haptic feedback: $P_D H+$) and without (i.e., spatially dissociated pantomime-grasp, without haptic feedback: $P_D H-$) terminal haptic feedback. Experiment 2: following the visual preview, the goggles were set to their translucent state for 2,000 ms and the target object was removed from the grasping environment. Subsequently, the goggles reverted to their transparent state and participants were required to complete spatially dissociated pantomime-grasps with (i.e., spatially dissociated pantomime-grasp, no target, with haptic feedback: $P_{DT} H+$) and without (i.e., spatially dissociated pantomime-grasp, no target, without haptic feedback: $P_{DT} H-$) terminal haptic feedback. Experiment 3: following the visual preview in the open-loop condition an auditory imperative was provided and the goggles were set to their translucent state coincident with movement onset (i.e., spatially dissociated pantomime, open-loop, with haptic feedback: $P_{DO} H+$). In contrast, for the memory-guided condition (i.e., spatially dissociated pantomime, memory-guided, with haptic feedback: $P_{DM} H+$) the visual preview period was followed by a 2,000 ms visual delay after which time an auditory imperative signaled participants to pantomime-grasp and vision remained occluded. In this condition, vision was neither available during response planning nor response execution. Notably, both conditions provided terminal haptic feedback. Experiment 4: following the visual preview, the goggles were set to their translucent state for 2,000 ms and the experimenter removed the target object from the grasping environment. Subsequently, participants were instructed to complete no-target pantomime-grasps with (i.e., no-target pantomime-grasp, with haptic feedback: $PH+$) and without (i.e., no-target pantomime-grasp, without haptic feedback: $PH-$) terminal haptic feedback while the goggles remained in their translucent state. Further and as shown in the ‘Haptic Feedback’ column, for the $H+$ trials of Experiments 1 through 4 the experimenter placed the target object between participants’ forefinger and thumb after the completion of the grasp. The light-gray background indicates when vision was occluded.

5.2.1.3 Experiment 1: spatially dissociated pantomime-grasps with online limb and target vision

The goal of this experiment was to examine whether dissociating SR relations influences the integration of haptic feedback when completing pantomime-grasps with online limb and target vision. To that end, participants completed three experimental conditions. In the *closed-loop* (i.e., CL) condition, the experimenter placed a target object at participants' midline and 450 mm from the front edge of the table. During this time the goggles were set to their translucent state. Once the target object was positioned the goggles were set to their transparent state for a 2000 ms visual preview after which time an auditory imperative signaled participants to grasp and hold – but not lift – the target object for 2000 ms before returning to the start location. The goggles remained transparent until movement offset (see kinematic definition of movement offset below). As such, the CL condition afforded online limb and target vision, and because the target object remained on the table during the response it provided immediate terminal haptic feedback related to object size (i.e., a 'naturalistic' grasping task). In the *spatially dissociated pantomime-grasp, without haptic feedback* (i.e., P_{DH}-) condition, the same visual preview as the CL condition was employed; however, the target object was positioned 120 mm to the left of participants' midline (and at the same depth as the CL condition). As shown in Figure 5-2, participants were instructed to grasp to the same midline location as the CL condition, albeit with dissociated SR relations. In other words, participants 'imagined' grasping the target object (i.e., pantomime) as if it were located at their midline. In line with the CL condition, the goggles remained transparent during the response and were then set to their translucent state at movement offset. As well, participants held their final grip aperture for 2000 ms before returning to the start location. Notably, because the grasping location was physically dissociated from the target object participants did not receive terminal haptic feedback. In the *spatially dissociated pantomime-grasp, with haptic feedback* (i.e., P_{DH}+) condition, the same procedures as the P_{DH}- condition were employed with one exception. In particular, following movement offset (and after the goggles were set to their translucent state) the physical target object was placed between participants' thumb and forefinger. More

specifically, the experimenter placed the target object (i.e., the same-sized target object as presented at preview) approximately 50 mm in front of participants' grasping limb and then slid it until one side contacted their thumb and then positioned the other side until it contacted their forefinger. The time required to position the target object was less than 2500 ms. Subsequently, participants were instructed to produce a stable grasp of the target object (i.e., a grasp that would permit object lifting) for 2000 ms before returning to the start location. Thus, the P_{DH+} condition provided terminal haptic feedback.

For all conditions, a movement time criterion of 600-800 ms was employed and feedback was provided following each trial (i.e., "too fast", "too slow", "good"). Any trial falling outside the movement time criterion was discarded and re-entered into the trial matrix: less than 5% of trials were repeated for this reason. The ordering of CL, P_{DH-} and P_{DH+} conditions was randomized as was the presentation of target objects in each block. Twenty trials were completed to each target object in each condition (i.e., 240 experimental trials). Further, I note that the different grasping conditions were performed in separate blocks because previous work by my group demonstrated that *a priori* knowledge of haptic feedback is necessary to support a visuo-haptic calibration (Davaranah Jazi & Heath, 2016).

5.2.1.4 Experiment 2: spatially dissociated pantomime-grasps without online target vision

The goal of this experiment was to determine whether removing online target vision influences the integration of terminal haptic feedback in a spatially dissociated pantomime-grasping task. Experiment 2 employed the same pantomime-grasp procedures as Experiment 1 with one exception. In particular, following the visual preview the goggles were set to their translucent state for a 2000 ms period during which time the experimenter removed the target object from the grasping environment. Following the occlusion period, the goggles were set to their transparent state simultaneous with the auditory imperative. Thus, participants grasped to the same midline position as Experiment 1; however, the response was mediated via a memory-based representation of the target object. Responses were completed in conditions wherein terminal haptic

feedback was unavailable (i.e., spatially dissociated pantomime-grasp, no target, without haptic feedback: P_{DT-H-}) and when provided at movement offset (i.e., spatially dissociated pantomime-grasp, no target, with haptic feedback: P_{DT-H+}) (see Figure 5-2 for a pictorial demonstration). The P_{DT-H-} and P_{DT-H+} conditions were performed in separate and randomly ordered blocks and included the ordering of target objects as per the conventions outlined in Experiment 1.

5.2.1.5 Experiment 3: spatially dissociated pantomime-grasps with open-loop and memory-guided visual conditions

The goal of this experiment was twofold. First, I sought to determine whether online vision of the grasping environment (i.e., limb *and* target vision) influences the nature of the information mediating spatially dissociated pantomime-grasps performed with terminal haptic feedback. Second, I sought to determine whether a memory delay influences the integration of terminal haptic feedback. To accomplish the first goal, the same P_{DH+} condition as employed in Experiment 1 was used here with one exception. In particular, following movement onset (see kinematic definition below) the goggles were set to their translucent state. Thus, limb and target vision was available during response planning but not during response execution (i.e., open-loop pantomime-grasping). Notably, open-loop pantomime-grasping responses were performed in a condition wherein terminal haptic feedback was provided at movement offset (i.e., *spatially dissociated pantomime-grasp, open-loop, with haptic feedback*: P_{DOH+}) as per the conventions described in Experiments 1. To accomplish my second objective, I included a spatially dissociated memory-guided pantomime-grasping condition. As shown in Figure 5-2, this condition entailed the same visual preview as all previous experiments; however, following the preview the goggles were set to their translucent state and participants were cued to initiate their response 2000 ms later. The goggles remained in their translucent state throughout the response and vision was neither available during movement planning nor movement execution. Memory-guided pantomime-grasps were performed with terminal haptic feedback (i.e., *spatially dissociated pantomime-grasp, memory-guided, with haptic feedback*: P_{DMH+}). The P_{DOH+} and P_{DMH+} conditions were

performed in separate and randomly ordered blocks and included the presentation and ordering of target objects as per the conventions outlined in Experiment 1.

5.2.1.6 Data analysis

Infrared emitting diodes (IREDs) were placed on the medial surface of the distal phalanx of the thumb, the lateral surface of the distal phalanx of the forefinger, and the styloid process of the radius. IRED position data were recorded at 400 Hz via an OPTOTRAK Certus (Northern Digital Inc., Waterloo, ON, Canada). A dual-pass Butterworth filter employing a low-pass cut-off frequency of 15 Hz was used to filter position data and instantaneous velocities were computed from the position data via a five-point central finite difference algorithm. Movement onset was determined when participants released pressure from the start location switch and movement offset was marked as the first frame wherein wrist velocity fell below 50 mm/s for 20 consecutive frames (i.e., 50 ms).

5.2.1.7 Just-noticeable-difference scores (JNDs)

Weber's law asserts that a JND represents the smallest detectable difference between an original and a comparator stimulus, and that values are proportional to the magnitude of the original stimulus. Moreover, the law states that the sensitivity of detecting a change in any physical continuum is relative as opposed to absolute. In the perceptual literature JNDs are computed via an arbitrary statistical criterion related to participants' ability to discriminate between an original and a comparator stimulus (e.g., 75% of trials or any other possible value); however, a statistical criterion is not possible for a grasping task. Thus, and in line with previous research (Davarpanah Jazi & Heath, 2014; Davarpanah Jazi et al., 2015a,b; Ganel et al., 2008a,b; Heath et al., 2012; Holmes & Heath, 2013; Holmes et al., 2013; Holmes et al., 2011; Pettypiece et al., 2009), the JNDs computed here represent the within-participant standard deviation of peak grip aperture (PGA). This approach is based on the Fechnerian principle that variance reflects the uncertainty by which a performer is unable to detect a difference between an original and a comparator stimulus (Ganel et al., 2008a; Heath et al., 2015; for extensive review see Marks & Algom, 1998). Figure 5-3 presents data of an exemplar participant from the CL and P_DH- conditions of Experiment 1. The large panels show trial-to-trial peak grip

apertures for the two conditions as a function of object size. For the CL condition, the spread of trial-to-trial PGAs do not systematically vary with object size, whereas for the P_{DH}- condition, trial-to-trial PGAs increased with increasing object size. Further, the offset panels of Figure 5-3 show standard deviations (i.e., the JNDs) associated with the trial-to-trial values and demonstrate that JNDs for the P_{DH}- trials – but not CL trials – increased linearly with increasing object size. The linear increase in JNDs is interpreted as adherence to Weber's law.

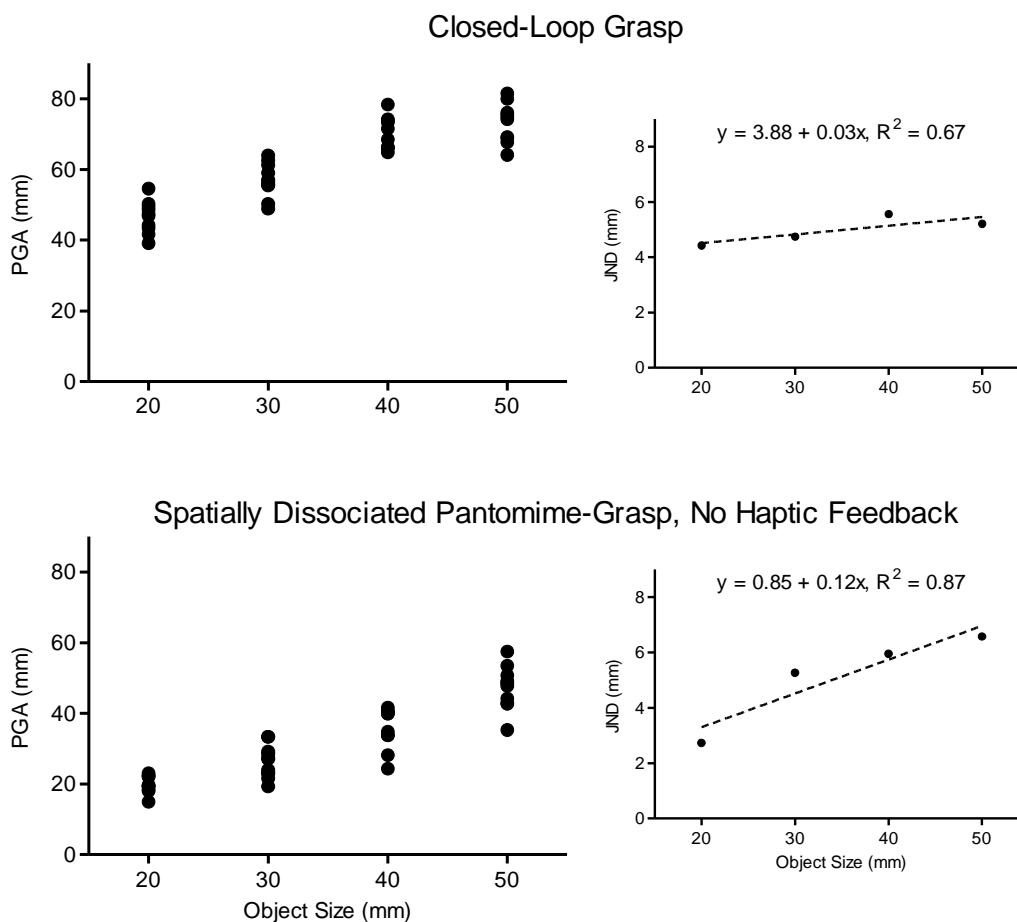


Figure 5-3: The large panels show trial-by-trial peak grip aperture (PGA: mm) for an exemplar participant in the closed-loop (CL) and spatially dissociated pantomime-grasp, without haptic feedback conditions of Experiment 1. Trial-by-trial PGAs for the CL condition did not vary with object size, whereas values for the P_DH- condition increased systematically with object size. The smaller offset panels represent the mean within-participant standard deviation for each object size (i.e., the just-noticeable-difference scores: JNDs). The dashed lines represent the linear regression of JNDs to object size and the top of each panel presents the associated linear regression equation and proportion of explained variance. This figure graphically illustrates my computation and interpretation of JNDs. In particular, null scaling of JNDs to object size (i.e., CL condition) is taken as a violation of

Weber's law, whereas values that systematically increase with object size (i.e., P_{DH}) is interpreted as adherence to the law.

5.2.1.8 Dependent variables and statistical analysis

The dependent variables included grasping time (GT: time from movement onset to movement offset), peak grip aperture (PGA: maximum resultant distance between thumb and forefinger) and corollary JNDs. Main effects and interactions were considered significant at an alpha level of 0.05 or less. Post-hoc contrasts for object size were examined via power-polynomials (i.e., trend analysis: see Pedhazur, 1997), whereas between-condition effects were decomposed via paired samples *t*-tests. I also computed participant-specific slopes relating JNDs to object size.

5.2.2 Results

5.2.2.1 Experiment 1: spatially dissociated pantomime-grasps with online limb and target vision

Dependent variables were examined via 3 (condition: CL, P_DH-, P_DH+) by 4 (object size: 20, 30, 40, 50 mm) repeated measures ANOVAs. The grand mean for GT was 694 ms (SD = 21) and this variable did produce any manipulation-related effects, $F_s < 1.83$, $p_s > 0.16$, all $\eta_p^2 < 0.14$. Results for PGAs and JNDs indicated main effects for condition, all $F(2,22) = 31.93$ and 4.91 , $p_s < 0.05$, $\eta_p^2 = 0.74$ and 0.31 , object size, all $F(3,33) = 377.00$ and 14.49 , $p_s < 0.001$, $\eta_p^2 = 0.97$ and 0.57 , and their interactions, all $F(6,66) = 9.77$ and 4.21 , $p_s < 0.01$, $\eta_p^2 = 0.47$ and 0.28 . As demonstrated in Figure 5-4, PGAs increased linearly with increasing object size for all conditions (significant linear effects: all $F(1,11) = 2289.81$, 325.39 and 162.58 for CL, P_DH- and P_DH+, respectively, $p_s < 0.001$). As well, PGAs for the 20, 30 and 40 mm objects were larger in the CL than P_DH+ condition (all $t(11) = 5.90$, 4.88 , and 2.98 , $p_s < 0.05$); however, a between-condition difference was not observed for 50 mm object ($t(11) < 1$). In turn, PGAs for the P_DH+ condition were larger than the P_DH- condition at each matched object size (all $t(11) > 6.18$, $p_s < 0.001$). In terms of JNDs, Figure 5-4 shows that values for the P_DH- and P_DH+ conditions increased linearly with increasing object size (significant linear effects: all $F(1,11) = 24.59$ and 22.25 , for P_DH- and P_DH+ conditions, respectively, $p_s < 0.01$); however, JNDs for the CL condition did not reliably vary with object size (non-significant linear effect: $F(1,11) = 1.75$, $p = 0.21$).

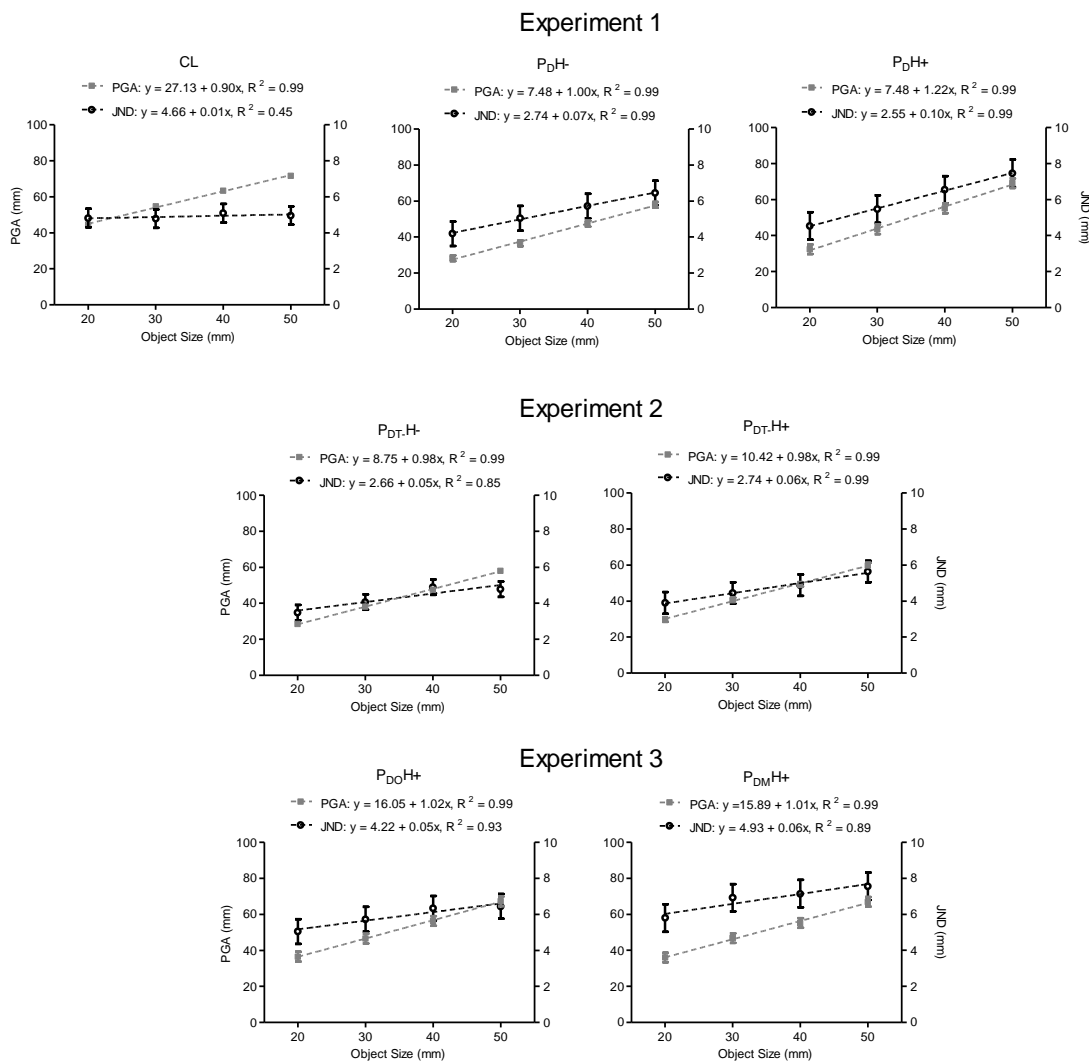


Figure 5-4: The Mean peak grip aperture (PGA in mm: see left ordinate) and just-noticeable-difference scores (JNDs in mm: see right ordinate) as a function of object size (20, 30, 40, and 50 mm) for Experiment 1 (top panels), Experiment 2 (middle panels), and Experiment 3 (bottom panels). Experiment 1: PGA and JND values associated with closed-loop (CL, and see left panel), spatially dissociated pantomime-grasp, without haptic feedback (P_DH-, and see middle panel), and spatially dissociated pantomime-grasp, with haptic feedback (P_DH+, and see right panel) conditions. Experiment 2: PGA and JND values associated with spatially dissociated pantomime-grasp, no target, without haptic feedback (P_DT- H-, and see

left panel) and spatially dissociated pantomime-grasp, no target, with haptic feedback ($P_{DT}H+$, and see right panel) conditions. Experiment 3: PGA and JND values associated with spatially dissociated pantomime-grasp, open-loop, with haptic feedback ($P_{DO}H+$, and see left panel) and spatially dissociated pantomime-grasp, memory-guided, with haptic feedback ($P_{DM}H+$, and see right panel) conditions. For all panels PGAs are presented as filled light-gray squares, whereas JNDs are shown as open dark circles. The light and dark hatched lines within each panel represent the regression line for PGAs and JNDs, respectively, and their associated regression equations and proportion of explained variances are presented at the top of the panel. Error bars represent 95% within-participant confidence intervals as a function of the mean-squared error term for object size computed separately for each condition (Loftus & Masson, 1994). Note: error bars for PGAs are less than the size of symbols associated with each mean value.

Figure 5-5 shows the mean JND/object size slope for each condition (and associated 95% confidence intervals) and provides a graphical demonstration that JNDs for the P_DH- and P_DH+ conditions – but not the CL condition – reliably differed from zero. Results from a one-way repeated-measures ANOVA, $F(2,22) = 12.40$, $p < 0.001$, $\eta_p^2 = 0.55$, indicated that P_DH- (0.07, SD = 0.05) and P_DH+ (0.10, SD = 0.07) conditions produced equivalent slopes ($t(11) = 1.11$, $p = 0.29$) that were larger than the CL condition (0.01, SD = 0.02) (all $t(11) = 5.05$ and 4.66 for P_DH- vs. CL, and P_DH+ vs. CL, respectively, $p_s < 0.01$).

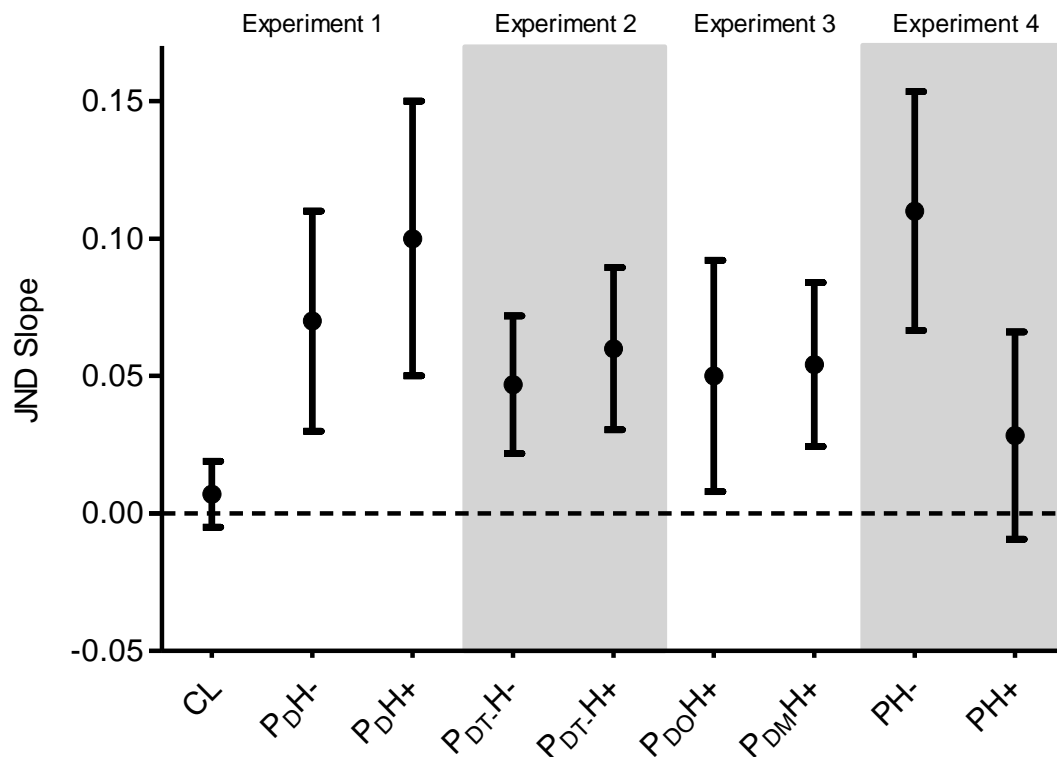


Figure 5-5: The Mean participant-specific slopes relating just-noticeable-difference scores (JNDs) to object size for the different experimental conditions across Experiments 1 through 4. Error bars represent the 95% between-participants confidence intervals (Cumming, 2013). The absence of overlap between error bars and zero represents a reliable linear effect that can be interpreted inclusive to a test of the null hypothesis.

Experiment 1 demonstrates that grasping a physical object with continuous limb and target vision results in a grip aperture specification that violates Weber's law; that is, CL responses are mediated via absolute information. In contrast, spatially dissociated pantomime-grasps performed with online limb and target vision adhered to Weber's law regardless of the provision of terminal haptic feedback. These findings suggest that relative and allocentric-based visual information is a reliable, and preferentially weighted, sensory source that supports spatially dissociated pantomime-grasps.

5.2.2.2 Experiment 2: spatially dissociated pantomime-grasps without online target vision

In this experiment spatially dissociated pantomime-grasps with (i.e., P_{DT-H+}) and without (i.e., P_{DT-H-}) terminal haptic feedback were completed in the absence of online target vision. Dependent variables were examined via 2 (condition: P_{DT-H-}, P_{DT-H+}) by 4 (object size: 20, 30, 40, 50 mm) repeated measures ANOVAs. The grand mean for GT was 693 ms (SD = 27) and this variable did not reveal any manipulation-related effects (all $F < 1.73$, $ps > 0.21$, all $\eta_p^2 < 0.13$). PGA and JND values produced main effects for condition, all $F(1,12) = 4.56$ and 6.83 , $ps < 0.05$, $\eta_p^2 = 0.28$ and 0.36 , and object size, all $F(3,36) = 676.21$ and 17.76 , $ps < 0.001$, $\eta_p^2 = 0.98$ and 0.60 . Figure 5-4 shows that PGAs and JNDs for the P_{DT-H+} condition were larger than the P_{DT-H-} condition, and that values for both conditions increased linearly with increasing object size (PGA significant linear effects: all $F(1,12) = 846.45$ and 691.55 , $ps < 0.001$; JND significant linear effects: all $F(1,12) = 16.81$ and 15.99 , $ps < 0.01$). Further, and given the objective of this study, I note that PGAs and JNDs did not produce a reliable condition by object size interaction (all $F < 1$). The mean participant-specific slopes relating JND to object size are presented in Figure 5-5 and demonstrate that values for P_{DT-H-} (0.05, SD = 0.04) and P_{DT-H+} (0.06, SD = 0.05) conditions were comparable ($t(12) < 1$) and reliably differed from zero.

Experiment 2 demonstrates that P_{DT-H-} and P_{DT-H+} conditions were mediated via relative visual information. Thus, in the absence of online target vision, relative and allocentric-based visual cues serve as a more reliable sensory source than terminal haptic feedback in mediating spatially dissociated pantomime-grasps.

5.2.2.3 Experiment 3: spatially dissociated pantomime-grasps with open-loop and memory-guided visual conditions

In this experiment, spatially dissociated pantomime-grasps with terminal haptic feedback were performed: (1) without online limb and target vision (i.e., P_{DOH+}), and (2) following a memory delay (i.e., P_{DMH+}). Dependent variables were examined via 2 (condition: P_{DOH+} and P_{DMH+}) by 4 (object size: 20, 30, 40, 50 mm) repeated measures ANOVAs. The mean GT was 696 ms (SD = 27) and this variable did not produce any manipulation-related effects (all $F < 0.71$, $ps < 0.56$, all $\eta_p^2 < 0.06$). Figure 5-4 shows that PGAs and JNDs produced main effects of object size, $F_s(3,33) = 251.33$ and 7.04 , $ps < 0.01$, $\eta_p^2 = 0.96$ and 0.39 , such that values for each metric increased linearly with increasing object size (PGA significant linear effects: all $F(1,11) = 250.89$ and 248.08 , $ps < 0.001$; JND significant linear effects: all $F(1,11) = 15.80$ and 6.35 , $ps < 0.05$). As well, neither variable produced a reliable effect of condition nor a condition by object size interaction (all $F < 2.02$, $ps > 0.16$, all $\eta_p^2 < 0.17$). Figure 5-5 shows that JND/object size slopes for P_{DOH+} and P_{DMH+} conditions differed from zero and the magnitude of the slope did not reliably vary between conditions (P_{DOH+}: 0.05 , $SD = 0.07$; P_{DMH+}: 0.06 , $SD = 0.05$) ($t(11) < 1$).

Experiment 3 demonstrates that P_{DOH+} and P_{DMH+} conditions adhered to Weber's law. Thus, the absence of online limb and target vision during movement execution, as well as the introduction of a memory delay, rendered spatially dissociated pantomime-grasping responses mediated via relative and allocentric-based visual information. Accordingly, the visual manipulations used here did not engender a sensory reweighting from relative visual information to absolute haptic feedback.

5.2.3 Discussion

Previous work by my group (Davarpanah Jazi & Heath, 2016; Davarpanah Jazi et al., 2015b; see also Hosang et al., 2016) demonstrated that haptic feedback provided following a no-target pantomime-grasp (with memory delay) renders grasping responses that violate Weber's law. Accordingly, it was proposed that haptic feedback serves as a more reliable sensory source than stored (i.e., memory-based) visual information and thus

supports an absolute visuo-haptic calibration. In the current investigation I sought to determine whether such a calibration extends to spatially dissociated pantomime-grasps and to determine whether the calibration is influenced by the systematic manipulation of limb and target vision, and the introduction of a memory delay. The basis for my research question was derived from the MLE model's contention that multimodal cues are optimally integrated to support motor control with increased weighting placed on the more reliable cue (Ernst & Banks, 2002). Thus, it was expected that limiting online limb and target vision (i.e., Experiment 2 and 3) and/or the introduction of a memory delay (i.e., Experiment 3) would result in an increased weighting of haptic feedback and engender an absolute visuo-haptic calibration.

5.2.3.1 PGAs: immediate and terminal haptic feedback influence grip aperture size

In Experiments 1 through 3, PGAs for all conditions increased linearly with increasing object size. This finding demonstrates that participants were able to discriminate between the differently-sized target objects used here (see also Ganel et al., 2012). Notably, however, the CL condition (i.e., the naturalistic grasping task) in Experiment 1 produced larger PGAs than the P_{DH+} condition for all but the largest object size. In turn, the P_{DH+} condition produced larger PGAs than the P_{DH-} condition. The fact that the CL condition produced larger PGAs than either pantomime condition is in line with work in the visual and tactile domains demonstrating that grasping a physical object results in larger PGAs compared to spatially dissociated or no-target pantomime-grasps (Cavina-Pratesi et al., 2011; Davarpanah Jazi et al. 2015a,b; Goodale et al., 1994; Holmes & Heath, 2013; Holmes et al., 2013; Westwood et al., 2000). According to Smeets and Brenner (1999), grasping a physical object requires that the thumb and forefinger adopt orthogonal approach vectors to avoid an early target collision, and to permit the adoption of grasp points normal to the long-axis of the target object (i.e., to prevent the object from slipping). Thus, CL grasping requires PGA values that are larger than the veridical size of a to-be-grasped target object (see also Jeannerod, 1984). In contrast, an orthogonal approach strategy is not required for pantomime-grasps because the absence of a physical object (i.e., immediately at the movement goal location) offers no risk of a collision.

More specifically, it is the participant, and not the physical properties of an object that determine a successful pantomime-grasp (Holmes & Heath, 2013). Further, I note that pantomime-grasps in Experiments 1 and 2 produced larger PGAs when terminal haptic feedback was provided (i.e., P_{DH+} and P_{DT-H+} trials) compared to when such feedback was unavailable (i.e., P_{DH-} and P_{DT-H-} trials). This result is in line with previous work by my group (Davarpanah Jazi et al., 2015b; see also Davarpanah Jazi et al., 2015a; Hosang et al., 2016) demonstrating that terminal haptic feedback, in part, supports a visuo-haptic calibration (see also Bingham et al., 2007). Notably, however, and as will be discussed in the following section, my examination of JNDs indicate that the calibration process was not absolute in nature.

5.2.3.2 JNDs: haptic feedback does not support an absolute visuo-haptic calibration for spatially dissociated pantomime-grasps

JNDs in the CL condition did not scale to object size (Heath et al., 2012; Heath et al., 2011; Holmes & Heath, 2013; Holmes et al., 2011; Hosang et al., 2016; see also Ganel et al., 2008a). In other words, CL grasps violated Weber's law and is a finding consistent with the PAM's contention that visually guided CL grasps are mediated via absolute visual information. Of course, CL grasps provided immediate haptic feedback, and as such it is not entirely clear whether visual information alone, or conjoint visual and haptic feedback rendered the absolute specification of object size. In terms of the spatially dissociated pantomime-grasps used in Experiment 1, JNDs scaled linearly to object size independent of whether haptic feedback was available (P_{DH+}) or unavailable (P_{DH-}). These findings indicate that spatially dissociated pantomime-grasps performed with continuous limb and target vision adhere to the relative psychophysical principles of Weber's law. As well, Experiments 2 and 3 demonstrate that the manipulation of online limb *and* target vision as well as the introduction of a memory delay did not modulate the extent to which spatially dissociated pantomime-grasps performed with terminal haptic feedback adhered to Weber's law. Thus, a parsimonious interpretation for my findings is that the top-down requirements of dissociating the visuo-spatial relations between SR is a predominant perceptual (and allocentric-based) task. Indeed, clinical and neuroimaging

evidence has shown that perception-based information provides a temporally durable representation of our visual world that supports future object (or place) identification (Cohen et al., 2009; Epstein & Kanwisher, 1998; Milner et al., 2001; Singhal et al., 2006; for review see Goodale, 2011; Goodale et al., 2004). As such, perceptual-based visual information may serve as a reliable – and preferentially weighted – sensory source for spatially dissociated pantomime-grasps.

5.3 Experiment 4

5.3.1 Introduction

To support the conclusions derived from Experiments 1 through 3 I thought it imperative to replicate the findings from my group's previous work showing an absolute visuo-haptic calibration (Davarpanah Jazi & Heath, 2016; Davarpanah Jazi et al., 2015b). Recall that in my group's previous work terminal haptic feedback was provided following a no-target pantomime-grasp. Thus, a salient difference between no-target and the spatially dissociated pantomime-grasps used in Experiments 1 through 3 is that the former entails spatial overlap between the presented visual target object and the to-be-completed grasping response. Thus, no-target pantomime-grasps do not require the top-down and perceptual demands of dissociating SR visuo-spatial relations. To that end, Experiment 4 employed no-target pantomime-grasps in conditions wherein terminal haptic feedback was available (i.e., PH+) and unavailable (i.e., PH-). In line with my group's previous work, I expected that PH+ and PH- trials would respectively violate and adhere to Weber's law.

5.3.2 Methods

5.3.2.1 Participants

Participant inclusion criteria were the same as Experiments 1 through 3 and participant demographics are reported in Table 5-1.

5.3.2.2 No-target pantomime-grasps with and without terminal haptic feedback

The same target objects, experimental equipment and general timeline of visual and haptic events as used in Experiments 1 through 3 were used here. In particular, in advance of each trial the goggles were set to their translucent state for a 2000 ms visual preview of a midline presented target object. Subsequently, the goggles reverted to their translucent state for a 2000 ms delay interval to provide the experimenter with sufficient time to remove the target object from the grasping environment. Following the delay, a tone served as an imperative to grasp to the location previously occupied by the target object. Thus, the pantomime-grasps used here entailed overlapping SR relations. Participants completed no-target pantomime-grasps in separate and randomized conditions involving the presence (i.e., PH+) or absence (i.e., PH-) of terminal haptic feedback (see Figure 5-2 for a pictorial representation). The order of target presentation and the analyses of data as per Experiments 1 through 3.

5.3.3 Results

Dependent variables were examined via 2 (condition: PH-, PH+) by 4 (object size: 20, 30, 40, 50 mm) repeated measures ANOVAs. The average GT value was 697 ms (SD = 29) and this variable did not produce any manipulation-related effects (all $F < 1$). In terms of PGAs, a main effect of object size, $F(3,33) = 209.41$, $p < 0.001$, $\eta_p^2 = 0.95$, indicated that values across PH- and PH+ conditions increased linearly with increasing object size (significant linear effects: $F_s(1,11) = 221.07$ and 251.07 , $p_s < 0.001$) (Figure 5-6). Further, PGAs did not produce a reliable main effect of condition or an interaction, ($F_s < 1.69$, $p_s > 0.22$, all $\eta_p^2 < 0.13$). Results for JNDs revealed a main effect of object size, $F(3,33) = 10.64$, $p < 0.001$, $\eta_p^2 = 0.15$, and a condition by object size interaction, $F(3,33) = 5.32$, $p < 0.01$, $\eta_p^2 = 0.33$. As presented in Figure 5-6, JNDs in the PH- condition increased linearly with increasing object size (significant linear effect: $F(1,11) = 31.36$, $p < 0.001$), whereas values for the PH+ condition did not reliably vary with object size (non-significant linear effect: $F(1,11) = 1.11$, $p = 0.31$). Further, Figure 5-5 shows that the mean JND/object size slope for the PH- condition (0.11, SD = 0.07) – but

not the PH+ condition (0.02, SD = 0.06) – differed from zero, and the magnitude of the slope was greater in the former condition, $t(11) = 2.92$, $p < 0.05$.

Experiment 4

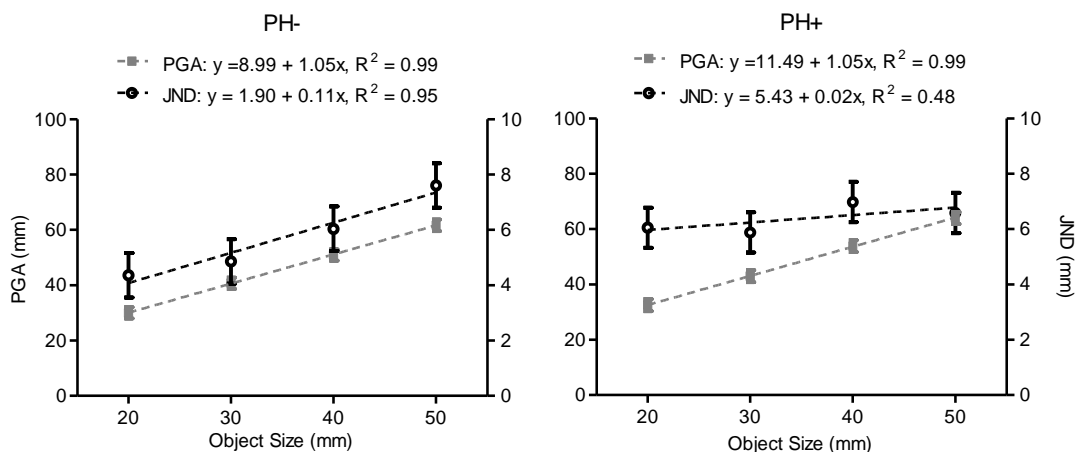


Figure 5-6: Experiment 4. Mean peak grip aperture (PGA in mm: see left ordinate) and just-noticeable-difference scores (JNDs in mm: see right ordinate) as a function of object size (20, 30, 40, and 50 mm) for the no-target pantomime-grasp, without haptic feedback (PH-, and see left panel) and no-target pantomime-grasp, with haptic feedback (PH+, and see right panel) conditions. PGAs are presented as filled light-gray squares, whereas JNDs are shown as open dark circles. The light and dark hatched lines within each panel represent the regression line for PGAs and JNDs, respectively and their associated regression equations and proportion of explained variance are presented at the top of each panel. Error bars represent 95% within-participant confidence intervals as a function of the mean-squared error term for object size computed separately for each condition (Loftus & Masson, 1994). Note: error bars for PGAs are less than the size of the square symbols associated with each mean value.

5.3.4 Discussion

Experiment 4 entailed pantomime-grasps with overlapping SR relations wherein limb and target vision was removed prior to response initiation. In terms of PGAs, results showed that values increased linearly with increasing object size and were not influenced by the presence or absence of terminal haptic feedback. Moreover, and in line with my group's previous work, JNDs for the PH- condition adhered to Weber's law – a finding taken to evince grasping control mediated via relative and allocentric-based visual information (Davarpanah Jazi & Heath, 2016; Davarpanah Jazi et al., 2015b). In turn, JNDs for PH+ trials did not systematically vary with object size and therefore demonstrates a violation of Weber's law. Accordingly, the present findings provide convergent evidence that the provision of terminal haptic feedback following pantomime-grasps with overlapping SR relations is supported via an absolute visuo-haptic calibration. Further, in accounting for my findings I wish to emphasize that across all experimental conditions target objects were presented in a randomized order. Thus, for the PH+ condition participants could not simply rely on the haptic feedback presented on trial N-1 to compute their grip aperture on trial N. Instead, I propose that an error signal derived from comparing an expected and an actual haptic outcome supports a visuo-haptic calibration that is used to guide future trial performance².

5.4 General discussion

Results from Experiments 1 through 3 show that spatially dissociated pantomime-grasps performed with terminal haptic feedback adhered to Weber's law independent of the provision of online vision (target and/or target and limb) or when a memory delay was introduced. In contrast, Experiment 4 demonstrated that terminal haptic feedback for pantomime-grasps with overlapping SR relations (i.e., no-target pantomime-grasp) rendered apertures that violated Weber's law. In accounting for my results, I have drawn upon the MLE model's contention that optimal sensory processing is based on the more reliable sensory source (i.e., vision vs. haptic). Accordingly, I propose that the requirements of dissociating the visuo-spatial relations between a stimulus and a response is a top-down task rendering motor output via temporally durable – and reliable –

perception-based and allocentric visual information. Indeed, it may be that perception-based visual information in this context provides a preferentially weighted sensory source that precludes a visuo-haptic calibration. In turn, pantomime-grasps with overlapping spatial relations may decrease the preferential reliance on allocentric visual information and provide the requisite environment necessary for an optimal integration of visual and haptic cues.

5.5 Footnotes

1. Dijkerman and deHaan's (2007) somatosensory processing model (SPM) states that tactile perceptions and actions are mediated via functionally and anatomically dissociable cortical pathways that rely on allocentric and egocentric reference frames, respectively (for review of tactile and haptic frames of reference see Lederman & Klatzky, 2009). According to the SPM, *relative* cues are mediated via a ventral pathway that extends from the anterior parietal cortex (APC) and the secondary somatosensory cortex (SII) to the posterior insula and underlies perceptions. In turn, a dorsal stream extending from the APC and SII to the PPC subserves actions and processes *absolute* tactile cues. Thus, tactile cues for perceptions and actions are mediated via processing characteristics that are comparable to their visual counterparts.
2. Previous work by my group has shown that naturalistic grasps performed following a memory delay (i.e., memory-guided (MG) grasping) are supported via absolute information related to the size of a target object (Davarpanah Jazi & Heath, 2016; Davarpanah Jazi et al., 2015b; Holmes et al., 2013; Holmes et al., 2011). It is, however, important to recognize that MG grasps differ from traditional no-target and spatially dissociated pantomime-grasps (i.e., actions performed without terminal haptic feedback) in that the former provides immediate terminal haptic feedback related to the absolute size of a target object. Thus, the haptic feedback associated with MG grasps provides an environment supporting a visuo-haptic calibration.

5.6 References

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Chapter 6

6 General Discussion

6.1 Summary of dissertation studies

The goal of this dissertation was to uncover the role of haptic feedback in the control of goal-directed grasping. Chapters 2 to 5 were systematically designed to study how the introduction of terminal haptic feedback influences tactile- and visually guided grasping.

The experiment presented in Chapter 2 had two goals. First, I sought to investigate whether presenting a memory delay prior to movement onset differentially influenced tactile-guided grasping and manual estimation responses. This was to provide evidence that support/reject the tenets of the somatosensory processing model (SPM: Dijkerman & de Haan, 2007). According to the SPM, motor responses mediated by a dorsal processing stream employ absolute and real-time tactile information to guide actions. In turn, the SPM asserts that removing tactile feedback and/or introducing a memory delay results in the processing of relative cues via a ventral stream that maintains tactile-based perceptual information over a long period of time. Results in Chapter 2 demonstrated that while tactile-guided grasps under closed-loop (CL) conditions were mediated via real-time absolute information, presenting a temporal delay resulted in manual estimation and grasping responses supported by relative tactile information. More specifically, these findings support the SPM's contention that an immutable and relative percept supports tactile perceptions and MG grasps. As a second goal, I sought to determine whether presenting haptic feedback at the end of the response would alter processing in tactile-guided grasping and manual estimation. Indeed, work in the visual domain has shown that when DF is denied terminal haptic feedback of a target object she is able to see, her grasping performance is significantly impaired (as is her manual estimation responses) (Schenk, 2012). Schenk concluded that terminal haptic feedback provides DF the requisite sensory feedback to support an absolute calibration between the visual and haptic systems (see also Davarpanah Jazi & Heath, 2014). As such, Chapter 2 presented participants with haptic feedback (via physically grasping a target object) following their memory-guided (MG) grasping and manual estimation responses. My results revealed that introducing haptic feedback following MG grasps – but not manual estimations – shifted processing from relative to absolute target properties. Such findings reveal how

information from multiple sources (i.e., haptic and tactile) are integrated in grip aperture formation and are indicative of a *within* sensory calibration in tactile-guided grasping.

A question that emerged from the results of Chapter 2 was whether sensory integration/calibration extends beyond one sense and is observed *between* sensory modalities (i.e., vision and haptic). Thus, in Chapter 3 the effect of terminal haptic feedback on visually guided pantomime-grasps was investigated. In line with Schenk's (2012) aforementioned findings, I hypothesized that presenting terminal haptic feedback following pantomime-grasps would lead to the integration of haptic signals and support the absolute specification of object size (i.e., via a visuo-haptic calibration). Results from Chapter 3 demonstrated that no-target pantomime-grasps performed without terminal haptic feedback were mediated via relative visual information. In contrast, pantomime-grasps which permitted terminal haptic feedback processed absolute sensory information and thus supported the conclusion of a calibration between visual and haptic modalities. Therefore, given the findings in Chapters 2 and 3, I demonstrated that haptic feedback supports a within- and between-sensory system calibration.

In Chapter 3 I concluded that the presentation of haptic feedback leads to an absolute visuo-haptic calibration in no-target pantomime-grasping. However, an issue that I did not address was whether knowledge about haptic feedback availability is necessary to support the aforementioned calibration. Previous work comparing reaching/grasping movements performed under visual CL vs. open-loop conditions have shown that if the two trial-types are presented in a randomized order then participants diminish their reliance on visual feedback to support online trajectory modifications in CL trials (Elliott & Allard, 1985; Khan et al., 2002; Jakobson & Goodale, 1991; Zelaznik et al., 1983). In other words, when online feedback availability cannot be predicted a response is specified largely in advance of movement via central planning mechanisms (as in OL trials) (Elliott et al., 2009; see also Heath et al., 2006; Neely et al., 2008). Therefore, in Chapter 4 participants completed no-target pantomime-grasps under conditions wherein haptic feedback was available or unavailable in blocked and random haptic feedback schedules. Results demonstrated that when participants had no knowledge of haptic

feedback availability (i.e. during random haptic feedback schedules) their pantomime-grasps were supported by the target's relative properties independent of terminal haptic feedback presentation. In other words, the results of Chapter 4 indicate that *a priori* knowledge of haptic feedback is necessary to support a visuo-haptic calibration in pantomime-grasping. Indeed, when terminal haptic feedback is predictably available I propose that participants build an internal forward model according to the "expected" sensory signals. Following response completion, participants compare the "expected" and "actual" haptic feedback signals in a manner that supports an absolute visuo-haptic calibration.

In Chapters 3 and 4 I demonstrated that terminal haptic feedback (presented in a blocked feedback schedule) leads to visuo-haptic calibration of no-target pantomime-grasps. Of course, in both chapters pantomime-grasps were performed towards the location of a previously presented target object (i.e. no-target pantomime grasp), and as such spatial overlap existed between the previously viewed stimulus and the location of the grasping response. Notably, however, it was unclear whether dissociating the spatial relations between stimulus and response (SR) differentially influenced a visuo-haptic calibration in pantomime-grasping. I hypothesized that the relative and allocentric-based computations in spatially dissociated pantomime-grasps are more reliable and preferentially weighted – a response mediation that would preclude a visuo-haptic calibration. My hypothesis was based on Ernst and Banks' (2002) maximum-likelihood-estimation (MLE) model stating that all sensory afferent signals are optimally combined to support motor control with the outcome depending on the reliability and weighting of each signal. Put another way, the more reliable sensory source receives more weighting in multisensory processing. Therefore, in Experiment 1 of Chapter 5 the target object was presented to the left of participants' midline and participants had to pantomime-grasp to a location with continuous target and limb vision (i.e., spatially dissociated pantomime-grasp). Responses were completed in conditions wherein terminal haptic feedback was available and unavailable. Findings revealed that spatially dissociated pantomime-grasps were mediated via relative information computed in allocentric frames of reference independent of terminal haptic feedback. Further, I attempted to determine how

systematically depleting vision influences visuo-haptic calibration in spatially dissociated pantomime-grasps. More specifically, in Experiment 2 target vision was removed during the movement, whereas in Experiment 3 target and limb vision was occluded at movement onset (i.e., open-loop pantomime-grasp) or 2,000 ms prior to response cuing (i.e., memory-guided pantomime-grasp). Results revealed that relative and allocentric-based cues support pantomime responses across Experiments 2 and 3 regardless of terminal haptic feedback presentation. Based on the tenets of the MLE, I proposed that the top-down demands of dissociating spatial SR relations is a perceptual task supported via temporally durable (and reliable) allocentric-based information that is immutable to the provision of terminal haptic feedback.

6.2 The role of visuo-spatial relations and haptic feedback in grasp control

A naturalistic grasping motion entails three components necessary for the planning and control of the movement. First, vision informs the individual about the state of their limb and the target prior to as well as during movement execution. Second, the visuo-spatial attributes of the target and effector determine the reference frames (i.e., ego- vs. allocentric) in which the response characteristics are computed. In particular, during a naturalistic grasp the grasping limb (i.e., response) is always directed towards the spatial location of the target object (i.e., stimulus) and thus the SR are presented in egocentric frames of reference. That is, individuals compute their movement characteristics via comparing target properties (i.e., size, position, distance) with respect to their own body at each moment in time. Third, when the grasping limb reaches movement endpoint it physically encounters the target object and thereby provides absolute feedback related to the physical properties of the target object. In the case that all three criteria are met the response is mediated via dedicated visuo- and haptic-motor networks that mediate target properties within an egocentric frame of reference. Notably, findings from my dissertation indicate that precluding any one of these components can differentially influence the underlying processing mechanisms of grasping. Further, I demonstrated that sensory processing is dependent on the relative weighting and dominance of

incoming signals received from vision, haptic feedback or visuo-spatial relations (Ernst & Banks, 2002).

A considerable amount of research has examined the role of visual limb and target properties in information processing (for example see Berthier et al., 1996; Fukui & Inui, 2013; Jeannerod, 1984), whereas a paucity of work has investigated how haptic feedback supports aperture shaping. For this reason, I examined the effect of haptic feedback on tactile-guided grasping in Chapter 2. I was able to show that, as a result of a within-sensory integration/calibration, absolute haptic signals are incorporated when grasping towards the location of a previously presented tactile target. Analogous to tactile-guided grasping, results from Chapter 3 demonstrated that haptic feedback mediates grasps performed to the empty location of a previously viewed target and thus supports an absolute visuo-haptic calibration. As well, findings from Chapter 4 indicated that such sensory calibration would not occur unless individuals are aware of the availability of terminal haptic feedback and thus prepare to employ absolute haptic cues in response production. Notably, the grasping responses of Chapters 3 and 4 had overlapping SR spatial relations and vision was removed prior to movement initiation. Such finding highlights the role of haptic feedback in grasps completed under MG visual conditions. In contrast, results in Chapter 5 revealed that dissociating the spatial relations between SR leads to the processing of relative and allocentric-based visual information in the ventral visual pathway (see also Cavina-Pratesi et al., 2011; Fukui & Inui, 2013; Goodale et al., 1994; Holmes et al., 2013; Westwood et al., 2000) – a finding independent of the provision of continuous limb and target vision or terminal haptic feedback. Such findings can be attributed to the perceptual demands of dissociating SR spatial relations. Taken together, the visuo-spatial relations between a stimulus and a response is highly weighted when determining the nature of the sensory information supporting grasp control. In other words, the egocentric-based visuo-spatial attributes between the target and response allow for visuo-haptic calibration to occur. Thus, it is important to recognize that, apart from visual feedback signals, visuo-spatial relations and haptic feedback are influential in determining the information supporting goal-directed grasping. In conclusion, a

multisensory control process that extends beyond the use of vision underlies grasp control.

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Appendices

Appendix A: Western University ethics approval form



**Western
Research**

Research Ethics

**Western University Non-Medical Research Ethics Board
NMREB Delegated Initial Approval Notice**

Principal Investigator: Dr. Matthew Heath

Department & Institution: Health Sciences/Kinesiology, Western University

NMREB File Number: 107719

Study Title: Comparing Haptic Versus Visual Feedback in Tactile-based Grasping

Sponsor: Natural Sciences and Engineering Research Council

NMREB Initial Approval Date: March 24, 2016

NMREB Expiry Date: March 24, 2017

Documents Approved and/or Received for Information:

Document Name	Comments	Version Date
Western University Protocol		2016/02/08
Advertisement		2016/03/08
Letter of Information & Consent		2016/03/08

The Western University Non-Medical Research Ethics Board (NMREB) has reviewed and approved the above named study, as of the NMREB Initial Approval Date noted above.

NMREB approval for this study remains valid until the NMREB Expiry Date noted above, conditional to timely submission and acceptance of NMREB Continuing Ethics Review.

The Western University NMREB operates in compliance with the Tri-Council Policy Statement Ethical Conduct for Research Involving Humans (TCPS2), the Ontario Personal Health Information Protection Act (PHIPA, 2004), and the applicable laws and regulations of Ontario.

Members of the NMREB who are named as Investigators in research studies do not participate in discussions related to, nor vote on such studies when they are presented to the REB.

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Curriculum Vitae

Post-secondary Education and Degrees

Bachelor of Science – Kinesiology 2003-2007
 University of Isfahan
 Isfahan, Iran

Master of Science – Kinesiology 2007-2009
 University of Isfahan
 Isfahan, Iran
 Supervisor: Dr Vahid Zolaktaf
 Thesis: Determination of proper height of hurdles for continuous double-legged jump in Plyometric training

Doctorate of Philosophy – Kinesiology 2012 to present
 The University of Western Ontario
 London, Ontario, Canada
 Supervisor: Dr Matthew Heath
 Thesis Topic: The effect of Haptic feedback on goal-directed grasping

Honours and Awards

Faculty of Health Sciences Graduate Conference Travel Award, The University of Western Ontario 2012-2015

Western Graduate Research Scholarship, The University of Western Ontario 2012-2015

Kinesiology Travel Award, The University of Western Ontario 2012-2013

Awarded as the highest overall GPA, Kinesiology, (B.Sc.) Class of 2007

Related Work Experience

Teaching Assistant 2012-2015
 School of Kinesiology, The University of Western Ontario

Undergraduate Student Supervision 2012-2016
 School of Kinesiology, The University of Western Ontario

Guest Lecturer October, 2014
 School of Kinesiology, The University of Western Ontario

Course Instructor 2007-2011
 University of Isfahan, Isfahan, Iran

Publications

Davarpanah Jazi S., & Heath, M. The spatial relations between stimulus and response determine an absolute visuo-haptic calibration in pantomime-grasping. *Brain & Cognition*. (under review)

Davarpanah Jazi S., & Heath M. (2016). Pantomime-grasping: Advance knowledge of haptic feedback availability supports an absolute visuo-haptic calibration. *Frontiers in Human Neuroscience*. 10: 197.

Hosang S., Chan J., **Davarpanah Jazi S.**, & Heath M. (2016). Grasping a 2D object: terminal haptic feedback supports an absolute visuo-haptic calibration. *Experimental Brain Research*. 234: 945-954.

Heath M., **Davarpanah Jazi S.**, & Holmes S. A. (2015). An inverse grip starting posture gives rise to the time-dependent adherence to Weber's law: A reply to Ganel et al. (2014). *Journal of Vision*. 15 (6): 1.

Davarpanah Jazi S., Yau M., Westwood D. A., & Heath M. (2015). Pantomime-grasping: the 'return' of haptic feedback supports the absolute specification of object size. *Experimental Brain Research*. 233 (7): 2029-40.

Davarpanah Jazi S., Hosang S., & Heath M. (2015). Memory delay and haptic feedback influence the dissociation of tactile cues for perception and action. *Neuropsychologia*. 71: 91-100.

Davarpanah Jazi S., & Heath M. (2014). Weber's law in tactile grasping and manual estimation: feedback-dependent evidence for functionally distinct processing streams. *Brain & Cognition*. 86: 32-41.

Davarpanah Jazi S., Purrajabi F., Movahedi A., & Jalali S. (2012). Effect of selected balance exercises on the dynamic balance of children with visual impairment. *Journal of Visual Impairment & Blindness*. 106 (8): 466-474.

Talks

Davarpanah Jazi S., Chan J., & Heath M. Pantomime-grasping: tactile processing is altered from relative to absolute only when haptic calibration is allowed.

Canadian Society for Psychomotor Learning and Sport Psychology
Waterloo, ON, Canada.

October, 2016

Manzone J., **Davarpanah Jazi S.**, Whitwell R., & Heath M. Visual codes or biomechanical constraints: a test of two hypotheses regarding the utility of Weber's law in grasping.

Canadian Society for Psychomotor Learning and Sport Psychology
Waterloo, ON, Canada

October, 2016

Davarpanah Jazi S., Hosang S., & Heath M. Introducing haptic feedback through object touch changes visual information supporting 2D object grasp from relative to absolute.
Canadian Society for Psychomotor Learning and Sport Psychology
Edmonton, Canada October, 2015

Legros A., Corbacio M., **Davarpanah Jazi S.**, Modolo J., & Thomas A. Acute effect of a 60 Hz magnetic field of up to 100 mT on human neuromotor control: an EEG/EMG/tremor study.
The Annual Meeting of Bioelectromagnetics Society
California, USA June, 2015

Davarpanah Jazi S., Hosang S., & Heath M. Absolute cues support delayed tactile grasping only when the target object is touched.
Canadian Society for Psychomotor Learning and Sport Psychology
London, ON, Canada October, 2014

Davarpanah Jazi S., Kalchman K., & Heath M. Tactile feedback influences haptic-based judgments of target size.
Canadian Society for Psychomotor Learning and Sport Psychology
Kelowna, BC, Canada October, 2013

Davarpanah Jazi S., & Heath M. Compliance of three haptically-guided size estimation tasks with Weber's law.
Southern Ontario Motor Behavior Symposium
Toronto, Canada May, 2013

Posters

Davarpanah Jazi S., Chan J., & Heath M. Absolute haptic cues mediate pantomime-grasping only when egocentric visual cues are delayed.
Society for Neuroscience
California, USA November, 2016

Chan J., **Davarpanah Jazi S.**, & Heath M. Haptic feedback influences calibration to veridical object size in pantomime-guided grasping of Müller-Lyer figures.
Canadian Society for Psychomotor Learning and Sport Psychology
Waterloo, ON, Canada October, 2016

Hosang S., Chan J., **Davarpanah Jazi S.**, & Heath M. Tactile vs. visual feedback in grasping and estimation: equivalent size resolution in the face of increased neuromotor noise.
Canadian Society for Psychomotor Learning and Sport Psychology
Edmonton, Canada October, 2015

Davarpanah Jazi S., Hosang S., & Heath M. Knowledge of haptic feedback availability does not influence size information supporting pantomime grasping.
Canadian Association for Neuroscience

Vancouver, Canada

May, 2015

Davarpanah Jazi S., Yau M., Goldsand H., & Heath M. Terminal tactile feedback influences the nature of the visual information mediating aperture shaping: evidence from memory-guided and pantomime grasping.

Canadian Society for Psychomotor Learning and Sport Psychology

London, ON, Canada

October, 2014

Davarpanah Jazi S., Gillen C., Desimone J., & Heath M. Visual and haptic target/distractor interactions and spatial congruency effects in goal-directed grasping.

International Multisensory Research Forum

Amsterdam, Netherland

June, 2014

Davarpanah Jazi S., Hosang S., & Heath M. Weber's law in delayed tactile grasping and manual estimation.

Southern Ontario Neuroscience Association

London, ON, Canada

May, 2014

Davarpanah Jazi S., Bryce J., & Heath M. Goal-directed grasping: receptor density influences the fidelity of haptic signals for perceptual and motor processing.

Progress in Motor Control

Montreal, Canada

June, 2013

Davarpanah Jazi S., Yau M., Goldsand H., Holmes S. A., & Heath M. Manual asymmetries during goal-directed grasping are expressed through the early stages of aperture shaping

Canadian Society for Psychomotor Learning and Sport Psychology

Halifax, Canada

November, 2012

Davarpanah Jazi S., Zolaktaf V., & Marandi S. M. Determination of proper height of jump for plyometric training

European Congress of Sport Medicine

Istanbul, Turkey

November, 2009

Professional Activities:

- Guest reviewer for the International Journal of Environmental Research and Public Health January, 2016
- Guest reviewer for the Journal of Neurophysiology December, 2015
- Member of the Society for Neuroscience (SFN) 2015 to present
- Member of the Canadian Society for Psychomotor Learning and Sport Psychology 2012 to present
- Member of the Canadian Association for Neuroscience (CAN) 2014 to present