

Western  Graduate&PostdoctoralStudies

Western University
Scholarship@Western

Electronic Thesis and Dissertation Repository

3-2-2021 1:00 PM

Statistical summary representations are perceived but not grasped.

Maryam Hamidi, *The University of Western Ontario*

Supervisor: Dr. Matthew Heath, *The University of Western Ontario*

A thesis submitted in partial fulfillment of the requirements for the Master of Science degree in Neuroscience

© Maryam Hamidi 2021

Follow this and additional works at: <https://ir.lib.uwo.ca/etd>

Recommended Citation

Hamidi, Maryam, "Statistical summary representations are perceived but not grasped." (2021). *Electronic Thesis and Dissertation Repository*. 7690.

<https://ir.lib.uwo.ca/etd/7690>

This Dissertation/Thesis is brought to you for free and open access by Scholarship@Western. It has been accepted for inclusion in Electronic Thesis and Dissertation Repository by an authorized administrator of Scholarship@Western. For more information, please contact wlsadmin@uwo.ca.

Abstract

A statistical summary representation (SSR) is a phenomenon wherein a target property (e.g., size) is encoded based on the average of the stimulus-set to which it belongs. Here, I examined method of adjustment (MoA), visually and memory-guided grasping tasks in separate blocks in which differently sized targets (i.e., 20 30 and 40 mm) were presented with equal frequency (*control weighting* condition) and when the 20 mm and 40 mm targets were asymmetrical presented (i.e., *small-target* and *large-target weighting* conditions). The weighting conditions were used to determine whether the different tasks are influenced by an SSR. In the MoA task, responses for the *small-* and *large-target* weighting conditions were biased in the direction of the most frequently presented target in the stimulus-set. In contrast, grip apertures for visually and memory-guided grasps were refractory to the different weighting conditions. Accordingly, an SSR influences perceptions but not goal-directed grasping.

Keywords

Action

Goal-directed

Grasping

Method of adjustment

Vision

Summary for Lay Audience

When scanning our visual environment, the judgments we make about the properties (e.g., size, shape) of a target object are influenced by non-target items. In fact, several studies have shown that when we view a display including a 'target' circle and differently sized non-target circles (i.e., a stimulus-set) our perception of the size of the target circle is biased by the average of all circles (i.e., target and non-target) – a phenomenon referred to as a statistical summary representation (SSR). The majority of the SSR research has focused on visuoperceptual judgments; however, it is unclear whether the phenomenon influences grasping movements directed to three-dimensional target objects. This represents a notable question because functionally and anatomically distinct visual pathways are thought to mediate perceptions and actions. To address this issue, participants were presented differently sized three-dimensional targets (20, 30, and 40 mm in width) and were asked to complete a classic perceptual judgment that involved adjusting the size of a line appearing on a computer monitor until it matched the size of the target object (i.e., method of adjustment task). As well, participants completed grasps of the same targets in conditions with (i.e., visually guided) and without (i.e., memory-guided) vision during the response. The method of adjustment, visually and memory-guided grasping tasks were completed in separate blocks and in conditions wherein the different targets were presented with equal frequency (i.e., control weighting) and when the 20 and 40 mm targets were presented five times as often as the other targets in the stimulus-set (i.e., *small-target* weighting and *large-target* weighting). Results showed that responses in the method of adjustment task were biased in the direction of the most frequently presented target in the stimulus-set; that is, responses were influenced by an SSR. In contrast, the transport and aperture shaping components of visually and memory-guided grasps were not influenced by the different target weighting conditions. Accordingly, results show that an SSR influences perceptual judgments but does not influence goal-directed actions.

Co-Authorship Statement

The author, under the supervision and mentorship of Dr. Matthew Heath, conducted the work in this master's thesis. With the guidance of Dr. Matthew Heath, I designed the experiments, recruited participants, collected, analyzed and interpreted data. I received support from an undergraduate research assistant (Lauren Giuffre) in recruiting participants and collection of data for Chapter Two.

Acknowledgments

I would like to thank Dr. Matthew Heath for supervising this research project and patiently supporting my transition into graduate studies. His insight and assistance have shaped me as an independent researcher. I truly feel honored to have had the opportunity to be part of his lab and to work with and learn from him. It is an experience that has incredibly improved many aspects of my life.

I wish to express my sincerest gratitude to my family and loved ones, for their unconditional love and support. They have made significant sacrifices for me and made it possible for me to learn from the very best and the very brightest minds in the world.

I would like to thank everyone in the NeuroBehavioral Lab, my lab mates, and my friends. I would also like to thank all those who willingly participated in my studies. Your time and patience were greatly appreciated, and this work would not have been completed without you.

Contents

Statistical summary representations are perceived but not grasped.	Error! Bookmark not defined.
Abstract	ii
Summary for Lay Audience	iii
Co-Authorship Statement.....	iv
Acknowledgments.....	v
List of Figures	viii
List of Abbreviations	x
List of Appendices	xi
Chapter 1	1
Literature Review.....	1
1. Literature Review.....	2
1.1 Goal-directed grasping movement	2
1.2 Two streams visual processing	5
1.2.1 Evidence supporting PAM	6
1.2.2 Evidence countering the PAM	9
1.3 Statistical summary representation	11
References.....	15
Chapter 2.....	19
1. Introduction.....	20
2. Methods.....	24
2.1. Participants.....	24
2.2. Apparatus and procedures.....	25
2.3. Method of Adjustment Task	26
2.4. Visually and Memory-Guided grasping.....	26
2.5. Data collection, data reduction and statistical analyses	27
3. Results.....	28
3.1. Method of Adjustment Task	28
3.2. Visually and Memory-Guided Grasping.....	29
3.2.1. Transport kinematics.....	29
3.2.2. Grasping kinematics.....	31
4. Discussion.....	35
4.1. Summary statistics influence visuoperceptual judgments: evidence from the method of adjustment task.....	35

4.2. Summary statistics do not influence visually or memory-guided grasps.....	36
5. Conclusions.....	39
References.....	40
Appendices.....	45
Curriculum Vitae	48

List of Figures

Figure 1. The anatomical location of the ventral and dorsal streams. Permission requested from Gallivan & Goodale, (2018), Handbook of Clinical Neurology	6
Figure 2. Schematic of the stimuli used in Ariely's (2001) study. The display on the left and right include the stimulus-set and the test circle, respectively. Permission requested from Ariely (2001), Psychological Science.....	12
Figure 3. Chong & Treismans' (2003) experiment timeline. Example of simultaneous presentation (On the left) and example of successive presentation (On the right). Permission requested from Chong & Treisman (2003) Vision Research.....	13
Figure 4. The solid black lines show hypothesized percent frequency histograms for line width (left panels) and peak grip aperture (right panels) as a function of target size (20, 30 and 40 mm) in method of adjustment and visually guided grasping tasks and for small and large-target weighting conditions. The text in each panel reports the frequency a target size was presented in the small- and large-target weighting conditions. The dotted red line in each panel depicts percent frequency histogram for the control weighting condition. For the method of adjustment task, small-target weighting condition distributions for each target size are shown as biased to the left of their control condition distribution (see leftward arrow), whereas large-target weighting condition distributions for each target are shown as biased to the right of their control condition distribution. Such findings would demonstrate a percept biasing target size in the direction of the most frequently presented target in a stimulus-set (i.e., an SSR). For visually guided grasps, peak grip aperture across weighting condition are shown to overlap because they are supported by absolute visual information independent of an SSR. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)	24
Figure 5. An exemplar participant's trial-by-trial line width for method of adjustment and peak grip aperture for visually and memory-guided grasps as a function of target size and weighting condition.	28
Figure 6 Group average line width for method of adjustment task and peak grip aperture (PGA) for visually and memory-guided grasps as a function of target size and weighting condition. Error bars represents 95% within-participant confidence intervals. Each panel includes linear regression lines and associated regression equations. The offset panels	

represent weighting condition group mean difference scores computed wherein line width and PGA values for the *control* condition were subtracted from the *small-* and *large-target* weighting conditions. Error bars represent 95% between-participant confidence intervals and the absence of overlap between error bars and zero (i.e., the horizontal dotted line) represent a reliable difference inclusive to a test of the null hypothesis. 30

Figure 7 Group average reaction time (A), movement time (B), and time to peak grip aperture (C) for visually (left panels) and memory-guided (right panel) grasps as a function of target size and weighting condition. Error bars represent 95% within-participant confidence intervals and each panel depicts linear regression lines and associated regression equations. 33

Figure 8 Group average aperture size at decile increments of normalized movement time for visually and memory-guided grasps as a function of target weighting conditions are shown separately for the 20- (top panel), 30- (middle panels) and 40-mm (bottom panels) target objects. The error envelope in each panel is the 95% between-participants confidence interval for the *control weighting* condition. We provide the confidence interval only for the *control* weighting condition because it graphically depicts that aperture size for the *small-* and *large-target* weighting conditions were within this envelope at each decile of the response..... 34

List of Abbreviations

2D: two-dimensional

3D: three-dimensional

ANOVA: analysis of variance

fMRI: functional magnetic resonance imaging

IREM: infrared emitting diode

MG: memory guided

MoA: method of adjustment

PAM: perception-action model

PGA: peak grip aperture

SSR: statistical summary representation

List of Appendices

Appendix A 1. Approval notice from the Office of Research Ethics, Western University 45
Appendix A 2. License for reuse figure 3, form Elsevier publisher. 46
Appendix A 3. License for reuse figure 1, from Elsevier Books publisher..... 47

Chapter 1

Literature Review

1. Literature Review

The goal of my thesis was to determine whether a statistical summary representation (SSR) influences the visual information supporting perceptual judgments and visually and memory-guided grasps of 3D target objects. Accordingly, I recruited a corpus of individuals to perform method of adjustment and grasping tasks to differently sized targets (20, 30 and 40 mm in width) in conditions wherein target size was presented with equal frequency (i.e., *control weighting*) and when the smallest (i.e., *small-target weighting*) and largest (*large-target weighting*) target sizes were presented five times as often as the other targets included in the stimulus-set. In developing my thesis document, Chapter 1 provides a general overview of: (1) goal-directed grasping, (2) the perception/action model (PAM), (3) evidence countering the PAM, and (4) evidence supporting an SSR in perceptual judgments and 2D ‘grasping’ Subsequent to the general overview, Chapter 2 provides the manuscript version of my thesis document.

1.1 Goal-directed grasping movement

Grasping and manipulating objects is an essential activity of daily living and it is therefore not surprising that an understanding of the behavioural, mechanical, and physiological properties supporting this action is an extensively studied area of research. The act of reaching to and grasping an object is formally known as manual prehension and the efficient and effective conduct of this behaviour is supported by a wealth of sensory inputs (i.e., proprioceptive, tactile, visual and vestibular) (for review see Grafton, 2010). From research in this area, it is clear that the visual system plays a pivotal role in successful grasping as it provides the motor system with a wealth of information about the location, size, shape, and physical properties of a to-be-grasped target object (Jeannerod, 1988). Prehension consists of two relatively independent components: (1) reaching to bring the limb into the vicinity of the target (i.e., transport component) and (2) shaping the hand to produce a stable grasp (i.e., aperture shaping component). The foundation of our current knowledge regarding prehension is based on seminal work by Marc Jeannerod (Jeannerod, 1981; 1984). In particular, Jeannerod (1984) employed high-speed photography while participants performed a precision grasp (i.e., via thumb and forefinger) of differently sized objects placed at different locations. Results showed that increasing the size of the target object resulted in an increase in peak

grip aperture (PGA: i.e., the distance between thumb and forefinger) but did not influence peak limb velocity. In contrast, increasing target object distance resulted in an increase in peak limb velocity but not PGA. Based on these results, Jeannerod proposed the existence of independent visuomotor channels for controlling transport and aperture shaping and further noted that each component is temporally synchronized and immutable to manipulations of visual feedback (i.e., dual-channel hypothesis: Jeannerod, 1999).

An alternative to Jeannerod's dual-channel hypothesis is Smeets & Brenner's (1999) double-pointing model. The double pointing model states that it is not reaching and grasping that governs prehension; rather, the model contends that control is governed at the digit level such that the thumb and forefinger trajectories are controlled independently and with regard to their respective points of contact on a target object. In a test of the double-pointing hypothesis, Jackson & Shaw (2000) used the Ponzo illusion to directly measure the impact of the illusion on grip aperture and grip force scaling. The authors required that participants select the stimulus that was perceived to be the larger/smaller of the two. Results for a grasping task showed that PGAs were not "tricked" by the illusion; however, the authors observed that grip force was biased in a direction consistent with the illusion's perceptual effects. These findings are compatible with the double-pointing model in that they suggest that the visuomotor system's primary task is to determine where to place the fingers to achieve a stable grasp. It is, however, important to note that several studies have not provided empirical support for the double-pointing model (e.g., Van de Kamp & Zaal, 2007; Zaal & Bongers, 2014). For example, Van de Kamp and Zaal observed that perturbing the end position of either the index finger or thumb resulted in significant adaptations of both digits – a finding at odds with the double pointing model's assertion that grasping represents independent reaching movements of the thumb and forefinger.

A wealth of studies have expanded Jeannerod's (1984) work by examining the role of vision in controlling transport and aperture shaping. For example, Jakobson and Goodale (1991) had participants grasp differently sized objects in separate blocks (Experiment 1) wherein visual feedback was available throughout their response (i.e., visually guided grasping) and when vision was extinguished at movement onset (i.e., open-loop grasping). Results showed that visually guided and open-loop PGAs scaled to target size; however, values were larger in the latter condition. The authors interpreted the larger open-loop PGAs

as reflecting that in the absence of visual feedback there is uncertainty about target size and thus requires a larger aperture to avoid an unexpected hand/target collision. In a subsequent experiment (Experiment 2), Jakobson and Goodale had participants grasp the same targets as Experiment 1 in a condition wherein the availability of vision during the response could not be predicted in advance of movement execution (i.e., visually guided and open-loop trials were randomly interleaved on a trial-by-trial basis). The results of Experiment 2 showed that PGAs for visually guided and open-loop grasps were comparable and larger than the visually guided grasps performed in Experiment 1. Accordingly, the authors proposed that when visual feedback is not predictably available, participants adopt a safety margin strategy to ensure an aperture size that prevents an unwanted (and potentially early) collision with the target object – a finding in line with earlier reaching (Elliott & Allard, 1985; Khan et al., 2002; Zelaznik et al., 1983) and subsequent grasping (Heath et al., 2006; Neely et al., 2008) studies.

From Jakobson and Goodale's (1991) work, it is clear that grasps performed with and without vision are structured differently. Thus, an interesting question is for how long visual information can be accurately maintained in memory to support goal-directed reaching/grasping. In an early study, Elliott and Madalena, (1987) asked participants to perform manual aiming movements to targets located 25 and 35 cm from a start position in five different visual conditions, visually guided, open-loop (i.e., vision occluded at movement onset), and 2000, 5000, 10,000 ms of memory delay. Results indicated that the open-loop condition produced comparable endpoint accuracy to the visually guided condition and was more accurate than the 2000, 5000 and 10,000 ms delay conditions. This result led the authors to suggest that an accurate memory-based substitute for direct vision is available to the motor system for up to 2000 ms of visual delay. However, it is important to recognize that Elliott and Madalena did not include a “brief” memory delay condition as vision was available at movement planning during their open-loop condition. Accordingly, Westwood, Heath and Roy, (2001) had participants reach to targets in visually guided, open-loop, and conditions involving 500, 1000, 1500 and 2000 ms of memory delay. Notably, in the memory-guided conditions vision of the movement environment was removed (i.e., via occlusion goggles), and responses were subsequently cued 500, 1000, 1500 and 2000 ms thereafter. Results showed visually guided responses were more accurate than open-loop

responses, and responses in the latter were more accurate than the memory-guided conditions (which did not differ). Based on these findings, Westwood et al., concluded that there is no period of memory delay that provides an accurate and equivalent substitute for direct vision of the movement environment (see also Westwood & Goodale, 2003). In support of these findings, Heath (2005) had participants perform limb visible and occluded reaches in visually guided, open-loop, 0 ms, 500, 1500 and 2500 ms memory-guided conditions. Results for limb visible and limb occluded trials showed that endpoint accuracy diminished as soon as vision of the target was occluded; that is, no interval of memory delay supported a response with accuracy commensurate with visually guided or open-loop responses. Notably, however, analysis of reach trajectories showed that limb visible (but not limb occluded) trials evoked online trajectory corrections. This result was taken to evince that although not as accurate as direct target vision, a stored target representation can support online trajectory corrections for up to 2500 ms as long as vision of the limb is visible (see also Heath, Rival & Binsted, 2004; for review see Heath et al. 2010). As such, the extant goal-directed grasping literature demonstrates that online vision serves as an important sensory source in supporting effective and efficient precision grasping.

1.2 Two streams visual processing

In the last 40 years, an important area of inquiry has been whether unitary or dissociable visual processing systems support the activities that we – and non-human primates - perform on a day-to-day basis. In an early demonstration of the importance of this issue, Mishkin and Ungerleider (1982) performed a lesion study in non-human primates (i.e., rhesus monkeys) and showed a dissociation of two ‘streams’ of neural projections from the primary visual cortex to inferotemporal (ventral visual pathway) and posterior parietal (dorsal visual pathway) cortices. In their work, a lesion to the ventral visual pathway impaired an object discrimination task, whereas a lesion to the dorsal visual pathway impaired performance on a visuospatial task. Based on these findings, Mishkin and Ungerleider proposed that the ventral pathway is responsible for processing visual information for object recognition, whereas the dorsal stream is responsible for processing visual information regarding the spatial relationship of an object (Mishkin & Ungerleider, 1982). Notably, Ungerleider and Mishkin’s model was – in part – used to develop a more contemporary view that separate pathways support vision for perceptions and vision for actions (i.e., the perception/action

model: Goodale & Milner, 1992). In particular, the PAM states that vision for perception is mediated via relative visual information laid down and maintained by the visuoperceptual networks of the ventral visual pathway (i.e., from the primary visual cortex to the inferotemporal cortex). In turn, vision for action is supported via absolute visual inputs mediated via dedicated visuomotor networks in the dorsal visual pathway (i.e., from the primary visual cortex to the posterior parietal cortex). Furthermore, the PAM asserts that the ventral and dorsal visual pathways process visual information in functionally distinct frames of reference. The PAM states that the ventral pathway computes target object properties in relation to other objects in the environment (i.e., allocentric frame of reference) (for review see Goodale, 2011). In turn, the PAM contends that the requirements of the dorsal pathway to process visual information on a moment-to-moment basis necessitate comparisons between an object of interest and the reaching/grasping limb (i.e., egocentric frame of reference).

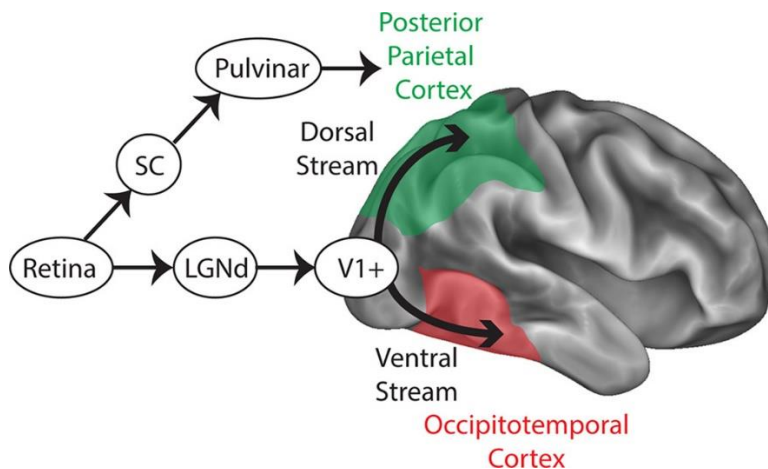


Figure 1. The anatomical location of the ventral and dorsal streams. Permission requested from Gallivan & Goodale, (2018), Handbook of Clinical Neurology

1.2.1 Evidence supporting PAM

Support for the PAM can be found in at least three lines of discovery: (1) clinical neuropsychology, (2) the pictorial illusions literature, and (3) the visually and memory-guided grasping literature. In the first case, Goodale and Milner studied a young woman (D.F.) with visual agnosia arising from bilateral lesions to the lateral occipital cortex of the ventral pathway (James et al., 2003). In an initial study, Goodale and Milner examined D.F.'s ability to: (1) orient a card so that it matched the opening of a 'slot', and (2) 'post' or 'mail' the

card through the slot (i.e., a task akin to placing an object in a mailbox). Results for the orienting task showed that D.F. was unable to correctly orient the card in relation to the slot and was a result attributed to the task's perceptual nature and D.F.'s impaired ventral pathway. In contrast, D.F. exhibited successful performance on the posting task and was a result attributed to her intact dorsal visual pathway. In a subsequent study, Goodale, Milner, Jakobson and Carey (1991) examined D.F.'s ability to manually estimate and grasp differently sized target objects. The manual estimation task required that D.F. separate her thumb and forefinger – without grasping – until she perceived it to match the size of the target object. Results showed that in the manual estimation task D.F. did not scale her grip aperture to the target objects; however, her PGAs in the grasping tasks scaled to target size and was commensurate with the performance of neurologically healthy controls. Once again, results indicate that DF's ventral stream lesions impair her perceptions but not actions.

In contrast to D.F., individuals with optic ataxia (i.e., resulting from lesions to the posterior parietal cortex of the dorsal pathway) exhibit a dissociable deficit for visually guided actions but not perceptions. For example Perenin and Vighetto (1988) had individuals with optic ataxia provide a verbal estimate of the absolute or relative position of different targets, and complete visually directed arm movements to the same targets. Results for the perceptual task showed that individuals with optic ataxia were able to report the location of the different targets. In contrast, results for the action task showed spatially inaccurate movements and poorly oriented hand positions. Based on these results, the authors concluded that damage to the dorsal pathway impairs the visual control of actions but does not influence perceptions – a conclusion supporting the theoretical tenets of the PAM. Moreover, Jeannerod, Decety and Michel (1994) examined the ability of optic ataxic patient A.T. to manually estimate and reach to grasp differently sized targets. Results showed that A.T. had intact manual estimation but was unable to metrically scale her grasping movements. Accordingly, Jeannerod concluded that damage to the dorsal stream impairs actions but not perceptions. Thus, evidence from the visual agnosia and optic ataxia literature demonstrates a double dissociation that provides extant support for the theoretical assertions of the PAM.

The pictorial illusions literature has also provided support for the PAM (but see Glover, 2004). For example, Aglioti, DeSouza & Goodale, (1995) employed the Titchener (Ebbinghaus) circles illusion (i.e., a central target disc surrounded by smaller or larger non-

targets) to examine a putative perception versus action dissociation. In that study, participants were instructed to manually estimate or grasp a target disc embedded in the Titchener circles illusion. Results for the manual estimation task indicated that responses were biased in a direction consistent with the perceptual effects of the illusion, whereas grasping PGAs were largely refractory to the illusion. In a subsequent study, Haffenden and Goodale (1998) had participants manually estimate the size of a target within the Titchener circles illusion and grasp the same target in conditions wherein vision of the hand and target was not available during the response (open-loop grasping). As expected, when participants were required to estimate the size of the central disk, they were influenced by the illusion, whereas PGAs for grasping were refractory to the illusion's effects. Based on these results Haffenden and Goodale concluded that grip aperture is calibrated to the veridical size of a target even when perception of an object is distorted by a pictorial illusion. In addition, Vishton et al., (1999) found that while perceptual judgements were affected by the horizontal-vertical illusion (i.e., where a vertical line is placed centrally along a horizontal line) associated grasping responses were refractory to the illusion's perceptual effects. Taken together, these findings suggest that pictorial illusions differentially influence perceptions and actions.

Westwood, Heath and Roy (2003) examined the degree to which a memory-delay impacts PGAs for an object embedded in a pictorial illusion (i.e., Mueller-Lyer figure). The basis for the question stemmed from the view that increasing the length of a visual delay may result in the motor system accessing a stable target representation laid down and maintained by the visuoperceptual networks of the ventral visual pathway. To examine this issue, Westwood et al., (2003) had participants complete grasps to a target embedded in the Mueller-Lyer illusion in visually guided, open-loop, and 3000 ms memory-delay conditions. As expected, PGAs in the visually guided condition were refractory to the illusion, whereas open-loop and 3000 ms delay conditions produced PGAs biased in a direction consistent with the illusion's perceptual effects. The authors concluded that such findings are consistent with the PAM (but see Westwood & Goodale, 2003). Notably, however, more recent findings by Westwood and Goodale (2003) suggest that open-loop grasps are not influenced by pictorial illusions because the dorsal system is able to access the metrical properties of a target when a response has been cued and only if the target is visible at the time of response cuing – a view

that has subsequently been referred to as the real-time component of the PAM (for review see Goodale, Westwood & Milner, 2004).

1.2.2 Evidence countering the PAM

In a previous section (1.2), I outlined that the proposed anatomical segregation between the ventral and dorsal visual streams was – in part – inspired by work examining patient D.F. Notably, however, Schenk (2006) has challenged Goodale and Milner's (1992) account of D.F.'s perceptual and motor abilities. In particular, Schenk compared the perceptual and visuomotor abilities of D.F. with those of ten healthy age-matched controls. However, unlike the previous research, D.F.'s perceptual and action performance was examined within an allocentric and egocentric coding framework. In one perceptual task, D.F. was required to indicate which of two targets to the left and the right of a reference target was closer (i.e., allocentric task) and in another D.F. indicated which of two targets was closer to her finger (i.e., egocentric task). Further, in an allocentric motor task D.F. was instructed to move her finger from a specified starting point until it matched the relative location of a 'dot' from a cross, whereas in an egocentric motor task D.F. was asked to move her finger from a start position to the location of the aforementioned 'dot'. Schenk (2006) found that independent of whether the task was perceptual or motor, D.F.'s performance on the allocentric tasks was impaired relative to that of healthy controls, whereas D.F.'s performance on the egocentric tasks was comparable to controls. Schenk concluded the possibility that D.F.'s deficit may not be related to an inability to perform perceptual tasks per se; rather, it may reflect an inability to exploit allocentric information (see also Schenk & Milner, 2006).

Hesse and Schenk (2014) examined D.F.'s behaviour in delayed and non-delayed conditions for a visuomotor (i.e., letter posting) and closed-loop pantomime task (i.e., a perceptual task). In particular, Hesse and Schenk varied the amount of visual feedback in four different conditions: closed-loop (i.e., vision of both the slot and hand during posting), open-loop move (i.e., vision of slot and hand occluded at movement onset), open-loop signal (i.e., vision of slot and hand occluded at movement cuing) and 3000 ms delay (i.e., vision of slot and hand occluded for 3000 ms prior to movement cuing). Results showed D.F. had no trouble posting the card in any of the visual conditions and that her performance on the closed-loop pantomime task was impaired relative to controls. Accordingly, the authors concluded that delayed visuomotor performance does not necessarily require ventral stream

input. Instead it seems that in some conditions visual information from the dorsal stream is sufficient to guide actions in both immediate and delayed conditions and the dissociation between D.F. and healthy controls in these tasks is driven by a difference in the ability to use environmental cues efficiently rather than by a difference in the ability to use online visual feedback.

The pictorial illusions literature is a point of debate regarding the separation of ventral and dorsal visual pathways. For example, Franz et al., (2000) proposed that previously reported differences between perceptual and grasping tasks reflect between-task attentional differences. In developing this assertion, Franz et al., (2000) employed the Titchener circles illusion in which one configuration of the illusion was presented at a time (i.e., a single array). This procedure differs from Aglioti et al.'s (1995) study wherein both small and large non-target arrays were concurrently presented. In a separate study, Franz, Hesse and Kollath (2009) had participants grasp an object embedded in the Müller-Lyer illusion in visually guided, open-loop (i.e. limb and target occluded at movement onset and during movement execution) and 5000 ms memory delay (i.e. limb and target occluded 5000 ms before movement cuing and throughout movement execution) conditions. Results showed a marginal illusory effect in the visually guided condition and a larger illusory effect in both open-loop conditions. Notably, Franz et al. argued that such a finding counters the PAM's prediction of a larger illusory effect following an increasing memory delay. Moreover, the authors argued that the extent to which an illusion influences action is dependent on the availability of vision during the response for online trajectory adjustments. To be certain, Franz et al.'s findings raise an interesting issue regarding the importance of online feedback in attenuating an illusory bias; however, Franz et al.'s conclusions are limiting by the fact that the study did not employ an immediate delay condition (i.e., 0 ms delay; for comparison see Heath 2005).

As outlined above, the real-time variant of the PAM asserts an immediate transition from dorsal to ventral processing when vision of the target is unavailable at the time of movement planning. In contrast to this view, Hesse and Franz, (2009) proposed an exponential decay of visual information as a function of the length of a visual delay. In particular, Franz et al. (2009) had participants grasp target objects in four different conditions: visually guided, open-loop with full vision until movement initiation (OL-Move), open-loop with full vision

until start-signal (OL-Signal) and a 5000 ms memory delay. Hesse and Franz (2009) found that the largest change in PGAs occurred between the CL and OL-Move, and the OL-Signal and 5000 ms delay produced only a small additional effect on PGA. The authors proposed that the observed changes in grasping kinematics following a delay are due to an exponential decay of visuomotor information over time and concluded that there are, “[...] no qualitative differences between movements executed after a delay and movements executed under full vision” (p. 1543).

1.3 Statistical summary representation

When we scan our visual environment, it is often cluttered and contains multiple objects that possess similar features (e.g., size). To account for the complexity of our environments and the limited resources of our visuoattentive system, it has been proposed that the visual system is capable of automatically "calculating" an average of a common property within a stimulus-set. For example, if an individual unfamiliar with Canadian monetary units was asked to identify the size of a specific coin (i.e., a dime) from a box containing many different coins (i.e., quarters, nickels, dimes, pennies), without having information about the specific size of each coin, their representation of size would likely be based on an average of the size of all coins included in the box. In other words, the perception of size is determined via a statistical summary representation (SSR). The notion of an SSR for visuoperceptual judgments was proposed by Ariely (2001) in a study wherein participants were presented with sets of 4, 8, 12, and 16 differently sized circles for 500 ms followed by a test circle. In Experiment 1, participants (N=2) were instructed to report whether the test circle was a member of the set (i.e., member-identification experiment), whereas in Experiment 2 participants (N=2) were instructed to report whether the test circle was larger or smaller than the mean of the set (i.e., mean-discrimination experiment). Experiment 1 showed that individuals were unable to accurately report whether the test circle was a member of the stimulus-set. In contrast, Experiment 2 demonstrated that participants were able to accurately determine whether the test circle was larger or smaller than the mean of the stimulus-set – a finding that was independent of the size of the stimulus-set. Accordingly, Ariely proposed

that "[...] the visual system represents the overall statistical, and not individual properties, of the [stimulus] set" (p. 157).

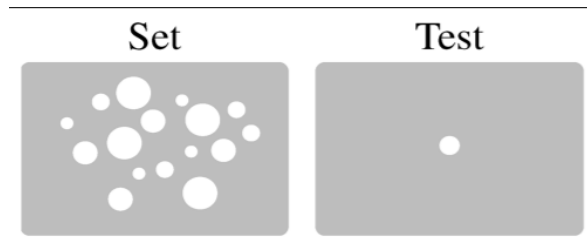


Figure 2. Schematic of the stimuli used in Ariely's (2001) study. The display on the left and right include the stimulus-set and the test circle, respectively. Permission requested from Ariely (2001), Psychological Science.

More recent work has shown that an SSR is immutable to the number, density, and complexity of stimuli and that an SSR representation is not influenced by attentional focus. For example, Chong and Treisman, (2003) examined the effect of stimulus-set complexity in the evocation of an SSR. In that study, participants were presented with homogeneous or heterogeneous stimulus-sets (i.e., differently sized circles) on the left and right side of their visual field concurrently or in serial presentation and results were compared to a control condition wherein only a single circle was presented in each visual field (see Figure 3). Chong and Treisman reported, "The results were surprising" (p. 400) as mean judgments for the heterogeneous display were as accurate as the single item display." The authors therefore proposed that the visual system automatically develops an SSR to economize on its limited capacity for perceiving and storing details related to a complex visual scene. In a follow up study, Chong and Treisman (2005a) examined whether attentional focus influences the instantiation of an SSR via a dual-task paradigm. Participants had to calculate the mean size of circles or report the size of a single object cued after the disappearance of a display. In both experiments, participants performed a secondary task to manipulate whether attention was focused or distributed. Results showed that it was easier for observers to extract the mean size of a stimulus-set when a simultaneous task required distributed versus focused attention. In contrast, participants were better at reporting the size of a single object when the manipulation required focused attention – a finding indicating that the development of an SSR does not require the sequential processing of each object in a stimulus-set.

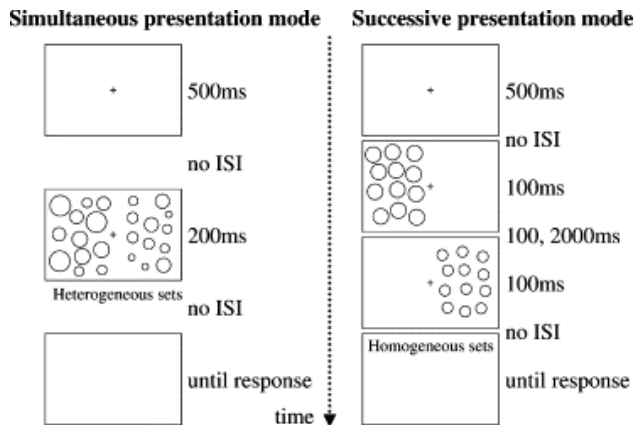


Figure 3. Chong & Treisman's (2003) experiment timeline. Example of simultaneous presentation (left panel) and example of successive presentation (right panel). Permission requested from Chong & Treisman (2003) Vision Research.

Further, Chong and Treisman (2005b) proposed that an SSR is not influenced by the density and color of stimuli. In that study, displays of red and green circles were presented and participants were asked to estimate the mean size of either the red or the green stimulus-set. In another experiment participants were presented displays of 8 circles in a dense ($0.139 \text{ circle/deg}^2$) or sparse array ($0.075 \text{ circle/deg}^2$). In both experiments, the colour and density of the stimulus-set did not influence participants use of ensemble averaging; that is, participants were able to accurately report the mean size of the stimulus-set.

More recently, an elegant study by Corbett, (2017) showed that an SSR is facilitated by Gestalt groupings. Here, stimulus-sets were presented in groups that varied as a function of four Gestalt principles: similarity (i.e., according to colour), proximity (i.e., according to location), connectedness (i.e., the presence of connecting lines between stimuli), and common region (i.e., stimuli were enclosed in a border). Participants were then asked to adjust the size of a presented test stimulus. Results showed that participants' error rates were more similar between the same rather than different Gestalt groups (i.e., adjusted test stimulus size was biased toward Gestalt-group-specific SSRs). Accordingly, Corbett concluded that the grouping of stimuli optimizes visual short-term memory by minimizing the variance of representations encoded by the visual system.

A growing body of work has shown that an SSR is not limited to the visual representation of object size. Indeed, an SSR has been observed for visuoperceptual judgments of orientation (Dakin & Watt, 1997), facial emotions (Haberman & Whitney,

2007), gist perception (Alvarez, 2011), and auditory processing (Piazza et al., 2013). For example, Haberman and Whitney, (2009) presented participants with pictures of faces with different expressions (i.e., sad to happy) and asked them to report the mean expression. Results showed that participants accurately identified the "facial mean" of the set and is a result demonstrating that an SSR governs multi-modality judgments.

Most of the SSR research has employed perceptual judgment tasks and there is therefore limited information regarding the influence of an SSR on action. To my knowledge, only Corbett and Song (2014) examined the role of an SSR on grasping. In that study, participants were presented with sets of computer-generated images (i.e., 14 dots arranged in concentric rings which were either small or large) for a 1-min adapting interval immediately followed by a 2000 ms "top-up" of the same display. Following the adapting interval, the stimulus-sets were replaced with a 'test dot.' The onset of the test dot cued participants to reach out and grasp it "[...] as if it were a real object" (p. 887). Results showed that participants made significantly larger grip apertures in the small relative to the large adapting condition during the early, but not later, stages of their reaching movements – a result demonstrating that visually guided reach-to-grasp actions were initially influenced by an SSR. Based on this finding Corbett and Song concluded that an SSR "[...] affects our physical interactions with objects in the external environment" (p. 890). However, an important feature of Corbett and Song's work is that targets were computer generated 2D stimuli; that is, they were not graspable. This is a notable issue because a number of behavioural studies have proposed that two-dimensional grasping is a perception-based task mediated by relative visual information (Ganel et al., 2020; Holmes et al., 2013; Hosang et al., 2016; Ozana et al., 2018). Hence, there remains no evidence to assert that an SSR influences *physical interactions* with objects. Therefore, Chapter Two of my thesis document explored whether an SSR influences not only visuoperceptual judgments, but also visually and memory-guided grasps to three-dimensional target objects.

References

- Aglioti, S., DeSouza, J. F., & Goodale, M. A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology: CB*, *5*(6), 679–685.
- Alvarez, G. A. (2011). Representing multiple objects as an ensemble enhances visual cognition. *Trends in Cognitive Sciences*, *15*(3), 122–131.
- Ariely, D. (2001). Seeing sets: Representation by statistical properties. *Psychological Science*, *12*(2), 157–162.
- Chong, S. C., & Treisman, A. (2003). Representation of statistical properties. *Vision Research*, *43*(4), 393–404.
- Chong, S. C., & Treisman, A. (2005a). Attentional spread in the statistical processing of visual displays. *Perception & Psychophysics*, *67*(1), 1–13.
- Chong, S. C., & Treisman, A. (2005b). Statistical processing: Computing the average size in perceptual groups. *Vision Research*, *45*(7), 891–900.
- Corbett, J. E. (2017). The whole warps the sum of its parts: Gestalt-defined-group mean size biases memory for individual objects. *Psychological Science*, *28*(1), 12–22.
- Corbett, J. E., & Song, J.-H. (2014). Statistical extraction affects visually guided action. *Visual Cognition*, *22*(7), 881–895.
- Dakin, S. C., & Watt, R. J. (1997). The computation of orientation statistics from visual texture. *Vision Research*, *37*(22), 3181–3192.
- Elliott, D., & Allard, F. (1985). The utilization of visual feedback information during rapid pointing movements. *The Quarterly Journal of Experimental Psychology A: Human Experimental Psychology*, *37A*(3), 407–425.
- Elliott, D., & Madalena, J. (1987). The influence of premovement visual information on manual aiming. *The Quarterly Journal of Experimental Psychology A: Human Experimental Psychology*, *39*(3, Sect A), 541–559.
- Franz, V. H., Gegenfurtner, K. R., Bühlhoff, H. H., & Fahle, M. (2000). Grasping visual illusions: No evidence for a dissociation between perception and action. *Psychological Science*, *11*(1), 20–25.
- Franz, V. H., Hesse, C., & Kollath, S. (2009). Visual illusions, delayed grasping, and memory: No shift from dorsal to ventral control. *Neuropsychologia*, *47*(6), 1518–1531.
- Gallivan, J. P., & Goodale, M. A. (2018). Chapter 23—The dorsal “action” pathway. In G. Vallar & H. B. Coslett (Eds.), *Handbook of Clinical Neurology* (Vol. 151, pp. 449–466). Elsevier.
- Ganel, T., Ozana, A., & Goodale, M. A. (2020). When perception intrudes on 2D grasping: Evidence from Garner interference. *Psychological Research*, *84*(8), 2138–2143.

- Gillen, C., & Heath, M. (2014). Perceptual averaging governs antisaccade endpoint bias. *Experimental Brain Research*, 232(10), 3201–3210.
- Glover, S. (2004). Separate visual representations in the planning and control of action. *The Behavioral and Brain Sciences*, 27(1), 3–24; discussion 24–78.
- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15(1), 20–25.
- Goodale, M. A., Milner, A. D., Jakobson, L. S., & Carey, D. P. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature*, 349(6305), 154–156.
- Goodale, Melvyn A. (2011). Transforming vision into action. *Vision Research*, 51(13), 1567–1587.
- Goodale, Melvyn A., Westwood, D. A., & Milner, A. D. (2004). Two distinct modes of control for object-directed action. *Progress in Brain Research*, 144, 131–144.
- Grafton, S. T. (2010). The cognitive neuroscience of prehension: Recent developments. *Experimental Brain Research*, 204(4), 475–491.
- Haberman, J., & Whitney, D. (2007). Rapid extraction of mean emotion and gender from sets of faces. *Current Biology: CB*, 17(17), R751–753.
- Haberman, J., & Whitney, D. (2009). Seeing the mean: Ensemble coding for sets of faces. *Journal of Experimental Psychology. Human Perception and Performance*, 35(3), 718–734.
- Haffenden, A. M., & Goodale, M. A. (1998). The effect of pictorial illusion on prehension and perception. *Journal of Cognitive Neuroscience*, 10(1), 122–136.
- Heath, M. (2005). Role of limb and target vision in the online control of memory-guided reaches. *Motor Control*, 9(3), 281–311.
- Heath, M., Rival, C., & Binsted, G. (2004). Can the motor system resolve a premovement bias in grip aperture? Online analysis of grasping the Müller-Lyer illusion. *Experimental Brain Research*, 158(3), 378–384.
- Heath, M., Rival, C., & Neely, K. (2006). Visual feedback schedules influence visuomotor resistance to the Müller-Lyer figures. *Experimental Brain Research*, 168(3), 348–356.
- Heath, Matthew & Neely, Kristina & Krigolson, Olav & Binsted, Gordon. (2010). Memory-guided reaching: What the visuomotor system knows and how long it knows it. *Vision and Goal-directed Movement: Neurobehavioral Perspectives*. 79–96.
- Hesse, C., & Franz, V. H. (2009). Memory mechanisms in grasping. *Neuropsychologia*, 47(6), 1532–1545.
- Holmes, S. A., Lohmus, J., McKinnon, S., Mulla, A., & Heath, M. (2013). Distinct visual cues mediate aperture shaping for grasping and pantomime-grasping tasks. *Journal of Motor Behavior*, 45(5), 431–439.

- 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(4), 945–954.
- Jackson, S. R., & Shaw, A. (2000). The Ponzo illusion affects grip-force but not grip-aperture scaling during prehension movements. *Journal of Experimental Psychology: Human Perception and Performance*, 26(1), 418–423.
- Jakobson, L. S., & Goodale, M. A. (1991). Factors affecting higher-order movement planning: A kinematic analysis of human prehension. *Experimental Brain Research*, 86(1).
- James, T. W., Culham, J., Humphrey, G. K., Milner, A. D., & Goodale, M. A. (2003). Ventral occipital lesions impair object recognition but not object-directed grasping: An fMRI study. *Brain: A Journal of Neurology*, 126(Pt 11), 2463–2475.
- Jeannerod, M. (1981). Specialized channels for cognitive responses. *Cognition*, 10(1–3), 135–137.
- Jeannerod, M. (1984). The timing of natural prehension movements. *Journal of Motor Behavior*, 16(3), 235–254.
- Jeannerod, M. (1999). Visuomotor channels: Their integration in goal-directed prehension. *Human Movement Science*, 18(2), 201–218.
- Jeannerod, M., Decety, J., & Michel, F. (1994). Impairment of grasping movements following a bilateral posterior parietal lesion. *Neuropsychologia*, 32(4), 369–380.
- Jeannerod, Marc. (1988). *The neural and behavioural organization of goal-directed movements* (pp. xii, 283). Clarendon Press/Oxford University Press.
- Khan, M. A., Elliot, D., Coull, J., Chua, R., & Lyons, J. (2002). Optimal control strategies under different feedback schedules: Kinematic evidence. *Journal of Motor Behavior*, 34(1), 45–57.
- Mishkin, M., & Ungerleider, L. G. (1982). Contribution of striate inputs to the visuospatial functions of parieto-preoccipital cortex in monkeys. *Behavioural Brain Research*, 6(1), 57–77.
- Neely, K. A., Tessmer, A., Binsted, G., & Heath, M. (2008). Goal-directed reaching: Movement strategies influence the weighting of allocentric and egocentric visual cues. *Experimental Brain Research*, 186(3), 375–384.
- Ozana, A., Berman, S., & Ganel, T. (2018). Grasping trajectories in a virtual environment adhere to Weber's law. *Experimental Brain Research*, 236(6), 1775–1787.
- Perenin, M. T., & Vighetto, A. (1988). Optic ataxia: A specific disruption in visuomotor mechanisms. I. Different aspects of the deficit in reaching for objects. *Brain: A Journal of Neurology*, 111 (Pt 3), 643–674.

- Piazza, E. A., Sweeny, T. D., Wessel, D., Silver, M. A., & Whitney, D. (2013). Humans use summary statistics to perceive auditory sequences. *Psychological Science*, *24*(8), 1389–1397.
- Schenk, T. (2006). An allocentric rather than perceptual deficit in patient D.F. *Nature Neuroscience*, *9*(11), 1369–1370.
- Schenk, T., & Milner, A. D. (2006). Concurrent visuomotor behaviour improves form discrimination in a patient with visual form agnosia. *The European Journal of Neuroscience*, *24*(5), 1495–1503.
- Smeets, J. B., & Brenner, E. (1999). A new view on grasping. *Motor Control*, *3*(3), 237–271.
- van de Kamp, C., & Zaal, F. T. J. M. (2007). Prehension is really reaching and grasping. *Experimental Brain Research*, *182*(1), 27–34.
- Vishton, P. M., Rea, J. G., Cutting, J. E., & Nuñez, L. N. (1999). Comparing effects of the horizontal-vertical illusion on grip scaling and judgment: Relative versus absolute, not perception versus action. *Journal of Experimental Psychology. Human Perception and Performance*, *25*(6), 1659–1672.
- Westwood, D. A., Heath, M., & Roy, E. A. (2001). The accuracy of reaching movements in brief delay conditions. *Canadian Journal of Experimental Psychology = Revue Canadienne De Psychologie Experimentale*, *55*(4), 304–310.
- Westwood, David A., & Goodale, M. A. (2003). Perceptual illusion and the real-time control of action. *Spatial Vision*, *16*(3–4), 243–254.
- Westwood, David A., Heath, M., & Roy, E. A. (2003). No evidence for accurate visuomotor memory: Systematic and variable error in memory-guided reaching. *Journal of Motor Behavior*, *35*(2), 127–133.
- Zaal, F. T. J. M., & Bongers, R. M. (2014). Movements of individual digits in bimanual prehension are coupled into a grasping component. *PloS One*, *9*(5), e97790.
- Zelaznik, H. Z., Hawkins, B., & Kisselburgh, L. (1983). Rapid visual feedback processing in single-aiming movements. *Journal of Motor Behavior*, *15*(3), 217–236.

Chapter 2

A Summary Statistical Representation Influences Perceptions but not Visually or Memory-Guided grasping

A version of this chapter has been published:

Hamidi, M., Giuffre, L & Heath, M. (2021). A summary statistical representation influences perception but not visually or memory-guided grasping. *Human Movement Science*, .

1. Introduction

A statistical summary representation (SSR) is a robust phenomenon wherein the property (e.g., size) of an object is represented as the average of a stimulus-set to which it belongs. In an elegant demonstration of this, Ariely (2001) displayed an array of differently sized circles for 500 ms and required participants to report whether a subsequent test circle: (1) was a member of the stimulus-set, or (2) was smaller or larger than the average size of the circles in the stimulus-set. Results showed that participants knew little about the individual items in a stimulus-set; however, they were markedly accurate in determining the stimulus-set's average size. Ariely proposed that the visual system encodes an SSR and discards information about individual items – a parsimonious strategy accounting for limited visuo-attentive resources. Subsequent work has shown that an SSR is associated with the presentation of simple (e.g., dots, Gabor patches, differently sized circles) and complex (e.g., facial expressions, sequences of different tones) stimuli, is immutable to the density, number and distribution of stimuli (Chong et al., 2008; Chong and Triesman 2003, 2005;), is associated with parallel or serial presentation (Corbett & Oriet, 2011; Im & Chong, 2009) and is facilitated by gestalt groupings (Corbett 2017; for reviews see Alvarez, 2011; Srinivasan, 2017).

The overwhelming majority of the SSR research has employed perceptual judgment tasks and it is therefore largely unclear whether an SSR influences movement. This represents a salient issue given the perception/action model's assertion that functionally and anatomically distinct visual pathways mediate perceptions and actions (Goodale & Milner, 1992). The perception/action model contends that perceptual judgments are mediated via the ventral pathway that encodes relative object properties in an allocentric frame of reference. Accordingly, the perception/action model predicts that an SSR influences perceptual judgments because the ventral pathway determines a target property in relation to the items contained in a stimulus-set. In turn, the perception/action model states that vision for action is mediated via the dedicated visuomotor networks of the dorsal pathway that process absolute target information in an egocentric frame of reference (see Hu & Goodale, 2000). As such, the perception/action model would predict that visually guided actions are refractory to an SSR due to the encoding of target features independent of context-dependent visual information (for review, see Goodale, 2011). To our knowledge, only one study examined the role of an SSR in grasping and that work offered a departure to the perception/action

model's prediction. Corbett and Song (2014) reported that an SSR influenced visually guided grasping in an adaptation paradigm wherein participants viewed two sets of computer-generated stimuli (i.e., 14 dots arranged in concentric rings) left and right of a central fixation for a 1-min interval prior to a block of trials. Subsequently, an additional 2000 ms "top-up" to the adapting stimuli was presented in advance of individual trials. One stimulus-set included dots ranging in diameter from 10.8 – 22.7 mm with an average of 17.7 mm (i.e., the 'small' stimulus-set), whereas the other ranged in diameter from 21.5 to 35.5 mm with an average of 28.5 mm (i.e., the 'large' stimulus-set). Following the adapting interval, the stimulus-sets were replaced with a test dot (diameter: 17.2 to 29.0 mm) and a non-test dot (i.e., with a diameter matching the mean of all dots in the adapting stimuli) located on opposite sides of the fixation. The onset of the test (and non-test) dot cued participants to reach out and grasp it "[...] as if it were a real object" (p. 887). Following the grasping response, participants provided a perceptual report of whether the test dot was smaller or larger than the non-test dot (i.e., perceptual judgment task). Grip apertures were computed at 101 spatially normalized points (i.e., 0% to 100% of traversed distance), and it was reported that values from ~12 to 45% of the response were larger (i.e., ~0.3 to 0.6 mm) for the 'small' as opposed to 'large' stimulus-set – a finding matching the perceptual judgment task (see also Corbett, Wurnitsch, Schwartz, & Whitney, 2012). In other words, early aperture shaping was inversely related to the average size of the adapting stimuli the test dot replaced. Corbett and Song proposed that for early aperture shaping, "...average size (of a stimulus-set) not only influences perceptual judgments but can also affect our physical interactions with objects in the external environment" (p. 890). As well, the author interpreted the early – but not later – effect of an SSR on aperture formation in line with Glover's (2004) contention that the early and late stages of grasping are supported by relative and absolute visual information, respectively (but see Goodale, 2011).

An important consideration of Corbett and Song's (2014) work is that target stimuli were computer-generated images and were not graspable. This is notable because a number of behavioural studies have proposed that 2D grasping is a perception-based task mediated by relative visual information (Ganel, Chajut & Algom, 2019; Holmes & Heath, 2013; Hosang, Chan, Davarpanah Jazi & Heath, 2016; Ozana, Berman & Ganel, 2018). For example, 2D grasps produce smaller apertures than their 3D counterparts and adhere to the psychophysical

principles of Weber's law during the early and late stages of aperture shaping (see Holmes & Heath, 2013). These behavioural results are supported by neuroimaging work reporting distinct activation patterns during the preparation of 2- and 3D grasps (Freud et al., 2018). In addition, 2D grasps do not provide terminal haptic feedback necessary to support an absolute visuo-haptic calibration for subsequent aperture shaping (Davarpanah Jazi & Heath, 2016; Davarpanah Jazi, Hosang & Heath, 2015; Davarpanah Jazi, Yau, Westwood & Heath, 2015; Schenk, 2012). As a result, there is insufficient evidence to support Corbett and Song's conclusion that an SSR influences *physical interactions* with objects.

In the present work participants completed a perceptual judgment task (i.e., method of adjustment) as well as visually and memory-guided grasps to differently sized 3D targets (i.e., 20, 30 and 40 mm in width, 10 mm in depth and height) presented within symmetrical (i.e., control) or asymmetrical (i.e., *small-target* and *large-target*) weighting conditions. Each trial involved the presentation of a single target and in the *control weighting* condition the differently sized targets were presented on an equal number of trials. In the *small-* and *large-target* weighting conditions the 20- and 40-mm targets were respectively presented five times as often as the other targets in the stimulus-sets. The use of separate target weightings was based on Alvarez's (2011) contention that an SSR is a rapidly developed percept that "[...] collapses across individual measurements to provide a single description of the set" (p. 122) and because in simultaneous, (Corbett & Song, 2011) and serial (Gillen & Heath, 2014a; 2014b; Heath, Gillen, & Weiler, 2015) target presentations, ensemble building has been shown to reflect total activations for the individual items included in a stimulus-set (Šetić, Švegar & Domijan, 2007). Moreover, Krügel and colleagues (Krügel, Rothkegel, & Engbert, 2020) showed that saccades directed to target eccentricities determined by a non-uniform Gaussian distribution render endpoint bias toward the distribution's mean; that is, prior knowledge governed the nature of the visual information supporting saccade endpoint error. For the method of adjustment task, a classic psychophysical method was used wherein participants altered the magnitude of a comparator stimulus (i.e., the width of a line appearing on a computer monitor) until they perceived it to match the width of a target object (Farell and Pelli 1999; Marks & Algom, 1998). For visually guided grasps, responses were completed with concurrent visual feedback of the movement environment (i.e., hand and target), whereas memory-guided grasps were completed without vision and were initiated

following 2000 ms of visual delay (e.g., Westwood, McEachern & Roy, 2001). In terms of research predictions, the left panels of **Figure 4** provide hypothesized percent frequency histograms for line width as a function of target size in the method of adjustment task and shows that *small-target* weighting condition responses underestimate line width compared to their *control weighting* condition counterparts, whereas in the *large-target* weighting condition responses overestimate compared to the *control weighting* condition. Put another way, the perceptual nature of the task is predicted to give rise to an SSR influenced by the more frequent activation of a specific target within a stimulus-set. The right panels of **Figure 4** provide hypothesized percent frequency histograms for peak grip aperture in visually guided grasps and shows responses are not biased in the direction of the most frequently presented target in the stimulus-set. Further, it is proposed that visually guided will operate independent of an SSR during the early and later stages of aperture formation – a prediction in line with the perception/action model's assertion that responses are governed by unitary and absolute visual information (Goodale, 2011). For memory-guided grasps, we provide competing predictions. The first is that aperture shaping will be biased in line with the method of adjustment task (see left panels of **Figure 4**). This prediction is based on the real-time variant of the perception/action model asserting that the visuomotor networks of the dorsal pathway support grasping only when vision is available at response cuing (Westwood & Goodale, 2003; see also Hu & Goodale, 2000) and work reporting that perceptual averaging is greatest when memory resources are taxed (Dubé & Sekuler, 2015). The second prediction is that the haptic feedback associated with the 3D target objects used here will support a visuo-haptic calibration and render unfolding aperture shaping independent of an SSR (Davaranah Jazi & Heath, 2016; Schenk, 2012) (see right panels of **Figure 4**).

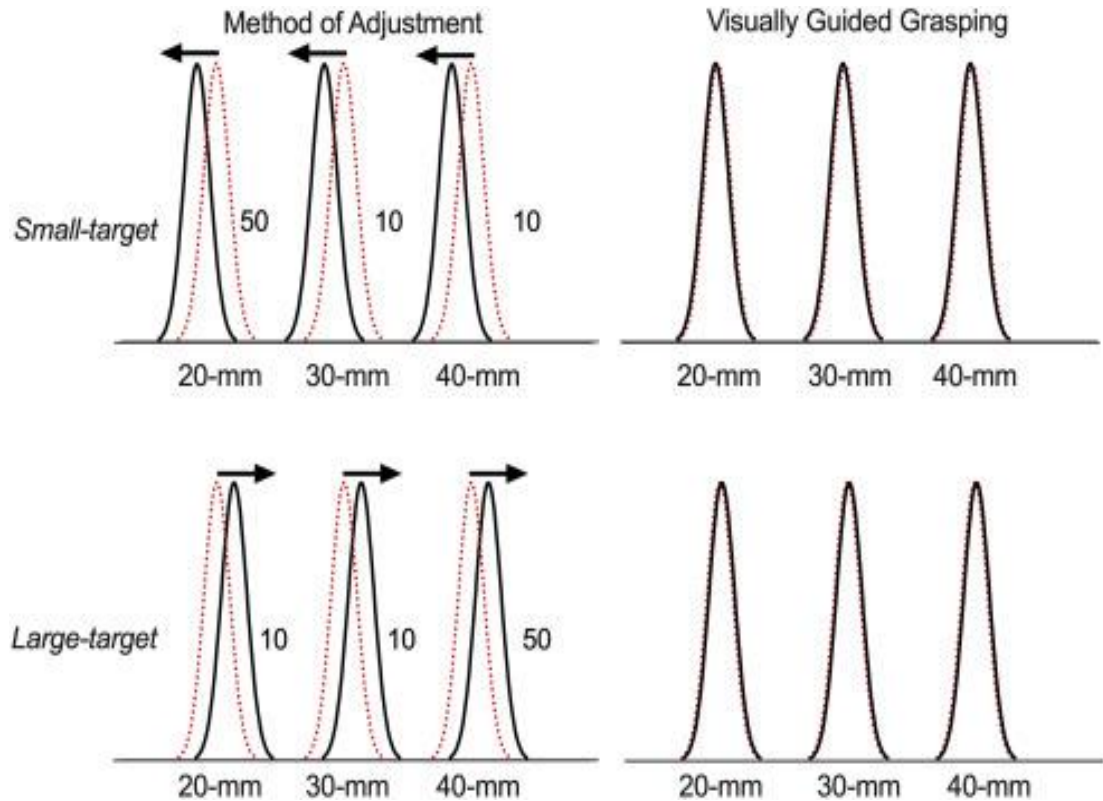


Figure 4. The solid black lines show hypothesized percent frequency histograms for line width (left panels) and peak grip aperture (right panels) as a function of target size (20, 30 and 40 mm) in method of adjustment and visually guided grasping tasks and for small and large-target weighting conditions. The text in each panel reports the frequency a target size was presented in the small- and large-target weighting conditions. The dotted red line in each panel depicts percent frequency histogram for the control weighting condition. For the method of adjustment task, small-target weighting condition distributions for each target size are shown as biased to the left of their control condition distribution (see leftward arrow), whereas large-target weighting condition distributions for each target are shown as biased to the right of their control condition distribution. Such findings would demonstrate a percept biasing target size in the direction of the most frequently presented target in a stimulus-set (i.e., an SSR). For visually guided grasps, peak grip aperture across weighting condition are shown to overlap because they are supported by absolute visual information independent of an SSR.

2. Methods

2.1. Participants

Twenty participants (15 female: age range 18-33 years) from the University of Western Ontario volunteered for this study. All reported normal or corrected-to-normal vision, self-declared right-hand dominance and being free of a current or previous neurological or upper-limb disorder. Prior to data collection, participants signed a consent form approved by the Non-Medical Research Ethics Board, University of Western Ontario, and this work was conducted according to the most recent iteration of the Declaration of Helsinki with the

exception that participants were not entered into a database. All participants completed the protocol; however, in post-processing it was determined that the infrared marker attached to one participant's wrist (i.e., a 22-year-old male) was not captured on greater than 40% of trials¹. For that reason, the analyses of visually and memory-guided grasps involve 19 participants.

2.2. Apparatus and procedures

Three tasks were completed: (1) method of adjustment, (2) visually guided grasping, and (3) memory-guided grasping. For each task, participants stood in front of a table (depth 760 mm; width = 1060 mm) with the height of the table adjusted to approximately 100 mm above navel level. This height allowed participants to rest their elbow on the table between trials and served to maximize comfort and reduce muscle fatigue. Targets were placed 75 mm to the right of midline and 500 mm in depth from the front edge of the table. Targets were vinyl, painted flat black and were 20 (i.e., small target), 30 (i.e., middle target) and 40 (i.e., large target) mm in width, and all were 10 mm in height and depth (i.e., 3D and physically graspable targets). Targets were secured to a laminated sheet of white paper (76 by 127 mm) and presented with their long-axis perpendicular to participants. Liquid-crystal shutter goggles (PLATO Translucent Technologies, Toronto, ON, Canada) (Milgram, 1987), MATLAB (R2018b, The MathWorks, Natick, MA, USA) and the Psychophysics Toolbox extensions (v 3.0) (Brainard, 1997; Kleiner, Brainard & Peli, 2007) were used to control visual, auditory and computer events.

Three conditions (*control*, *small-target* and *large-target* weighting) were completed in each task. In the *control* weighting condition, each target was presented 10 times. In the *small-target* weighting condition the 20 mm – or small – target was presented five times as often as the middle (i.e., 30 mm) and large (i.e., 40 mm) targets. In the *large-target* weighting condition, the large target was presented five times as often as the small and middle targets. Accordingly, in the *small-* and *large-target* weighting conditions the 'small' and 'large' targets were respectively presented on 50 trials, whereas the other targets were presented on 10 trials. The trial weighting manipulation matches Gillen and Heath's (2014b) examination of an SSR in pro- and antisaccade amplitudes. For all target weighting conditions, a randomization schedule determined the ordering of target object presentation. Each task required approximately 75-min to complete and were done in separate and

randomly ordered sessions separated by at least 24 h. As well, the order of target weighting condition within a task session was randomized.

2.3. Method of Adjustment Task

At the start of a trial the goggles were translucent while the experimenter placed a target on the tabletop. Once the target was positioned, the experimenter initiated a trial sequence wherein the goggles were set to their transparent state for 2000 ms (i.e., preview period) after which an auditory imperative (2900 Hz for 100 ms) was presented. The imperative cued participants to press a home switch (i.e., MFJ-550 telegraph key located 75 mm to the right of midline and 50 mm from the front edge of the table) with their right index finger to increase the horizontal width of a line appearing on a computer monitor (LG LCD monitor, 1024 × 768 pixels, 60 Hz; 25 ms response time) located 100 mm anterior to the target object. The initial height of the line was 10 mm with a width of 2 mm and the line was centered on the monitor screen. Participants pressed the switch until they perceived that the width of the line matched the width of the target object. The occlusion goggles remained transparent for the duration of a trial.

2.4. Visually and Memory-Guided grasping

The occlusion goggles were translucent in advance of each trial and during this time participants rested the palm of their right hand on the home switch. Once a target was placed the occlusion goggles were set to their transparent state for a 2000 ms preview. In the visually guided task, the auditory imperative immediately followed the preview and instructed participants to reach out and grasp – but not lift – the long-axis of the target via a precision grip (i.e., thumb and forefinger) "as quickly and accurately as possible". The occlusion goggles remained transparent until participants returned to the home switch. In the memory-guided task, the goggles were set to their translucent state following the preview and an auditory imperative was provided 2000 ms thereafter. Accordingly, participants planned and executed their response in the absence of online vision. For both tasks, participants were instructed to hold the target object for approximately 1000 ms before returning to the home switch.

2.5. Data collection, data reduction and statistical analyses

For the grasping tasks, the position of the right limb was measured via infrared emitting diodes (IREDs) placed on the lateral surface of the distal phalanx of the index finger, 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 (Northern Digital Inc., Waterloo, ON, Canada) for 1500 ms following response cuing. IRED position data were filtered offline via a second-order dual-pass Butterworth filter employing a low-pass cut-off frequency of 15 Hz. Subsequently, instantaneous velocities were computed from the position data via a five-point central finite difference algorithm. Movement onset was marked when participants released pressure from the start location and movement offset was determined when wrist velocity fell below a value of 50 mm/s for 20 consecutive frames (i.e., 50 ms). Dependent variables for grasping tasks included: reaction time (RT.: time from response cuing to movement onset), movement time (MT: time from movement onset to movement offset), peak grip aperture (PGA: maximum resultant distance between thumb and forefinger) and time to PGA (time from movement onset to PGA). In addition, we computed grip aperture at decile increments of normalized MT (i.e., 10%, 20%, ..., 90%, 100% of MT). For the method of adjustment task, we recorded the width (in mm) of the horizontal line generated on the computer monitor (henceforth referred to as line width).

For the method of adjustment task, line width was examined via 3 (weighting condition: *control*, *small-* and *large-target*) by 3 (target size: 20, 30 and 40 mm) fully repeated measures ANOVA. For the grasping tasks, dependent variables were examined via 2 (grasping task: visually guided, memory-guided) by 3 (weighting condition: *control*, *small-* and *large-target*) by 3 (target size: 20, 30 and 40 mm) fully repeated measures ANOVA. Main effects and interactions were decomposed via simple-effects and/or power polynomials (i.e., trend analysis) (Pedhazur, 1997). Where appropriate, two one-sided test statistics were used to determine if *small-* and *large-target* weighting conditions were within an equivalence boundary of the *control* weighting condition (for tutorial see Lakens, Scheel & Isager, 2018). Equivalence testing was completed via the TOSTER R package (Lakens, 2017).

3. Results

3.1. Method of Adjustment Task

Figure 5 presents an exemplar participant's trial-by-trial performance in the method of adjustment task. The figure shows that line width values for the *small-* and *large-target* weighting conditions were smaller and larger than the *control* weighting condition, respectively. In other words, responses were biased in the direction of the most frequently presented target in the stimulus-set.¹

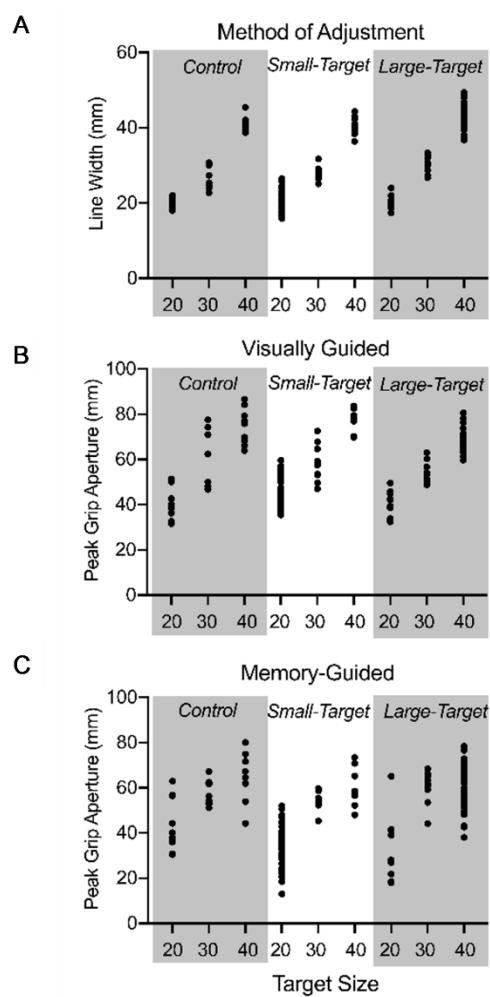


Figure 5. An exemplar participant's trial-by-trial line width for method of adjustment (A) and peak grip aperture for visually (B) and memory-guided (C) grasps as a function of target size and weighting condition.

ANOVA findings for line width produced main effects for target size and weighting condition, all $F(2,38)=864.34$ and 5.06 , $ps<.001$ and $=.001$, $\eta_p^2=.98$ and $.21$. The top panel in **Figure 6** shows that line width increased linearly with increasing target size (only linear effect significant: $F(1,19)=298.83$, $p<.001$). For the main effect of weighting condition, we computed participant-specific difference scores wherein line width for the *control* condition was subtracted from line width for the *small-* and *large-target* weighting conditions. The top offset panel in **Figure 6** presents group mean difference scores – and associated 95% between-participant confidence intervals – and demonstrates that line width for the *small-target* weighting condition was less than the *control* weighting condition, whereas line width for the *large-target* weighting condition was greater than the *control* weighting condition. Further, single-sample t-tests indicated that difference scores for *small-target* versus *control* ($t(19)=3.14$, $p=.005$, $d_z=0.92$) and *large-target* versus *control* ($t(19)=-2.86$, $p=.010$, $d_z=0.64$) weighting conditions differed from zero.

To determine whether sequential trial effects influences results, I identified *control-weighting* condition trials to the 30 mm target in which trial N-1 involved a target of the same, smaller, or larger target size. A subsequent one-way ANOVA for line width – as well as grip aperture at 30% of MT for visually and memory-guided grasps – did not elicit reliable effects, all $Fs<1.13$, $ps>.34$, all $\eta_p^2<.05$.

3.2. Visually and Memory-Guided Grasping

3.2.1. Transport kinematics

The top and middle panels of **Figure 7** present group mean RT and MT, respectively, for visually and memory-guided grasps as a function of target size and weighting condition. The figures show that visually guided grasps produced shorter RTs (304 ms, $SD=76$) and MTs (669 ms, $SD=103$) than memory-guided grasps (RT: 336 ms: $SD=105$; MT: 725 ms, $SD=148$), all $F(1,18)=4.96$ and 10.87 , $p=.039$ and $.004$, $\eta_p^2=.22$ and $.37$. RT and MT did not elicit main effects of weighting condition or higher-order interactions, all $F<1.17$, $ps>.33$, all $\eta_p^2<.06$. Two one-sided test statistics for RT and MT contrasting *small-* and *large-target* weighting conditions with the *control* condition were computed with an effect size derived

from the lower bound value in the method of adjustment task ($d_z=0.64$). Results indicated that contrasts were within an equivalence boundary, all $t(18)>1.86$, $p<.02$.

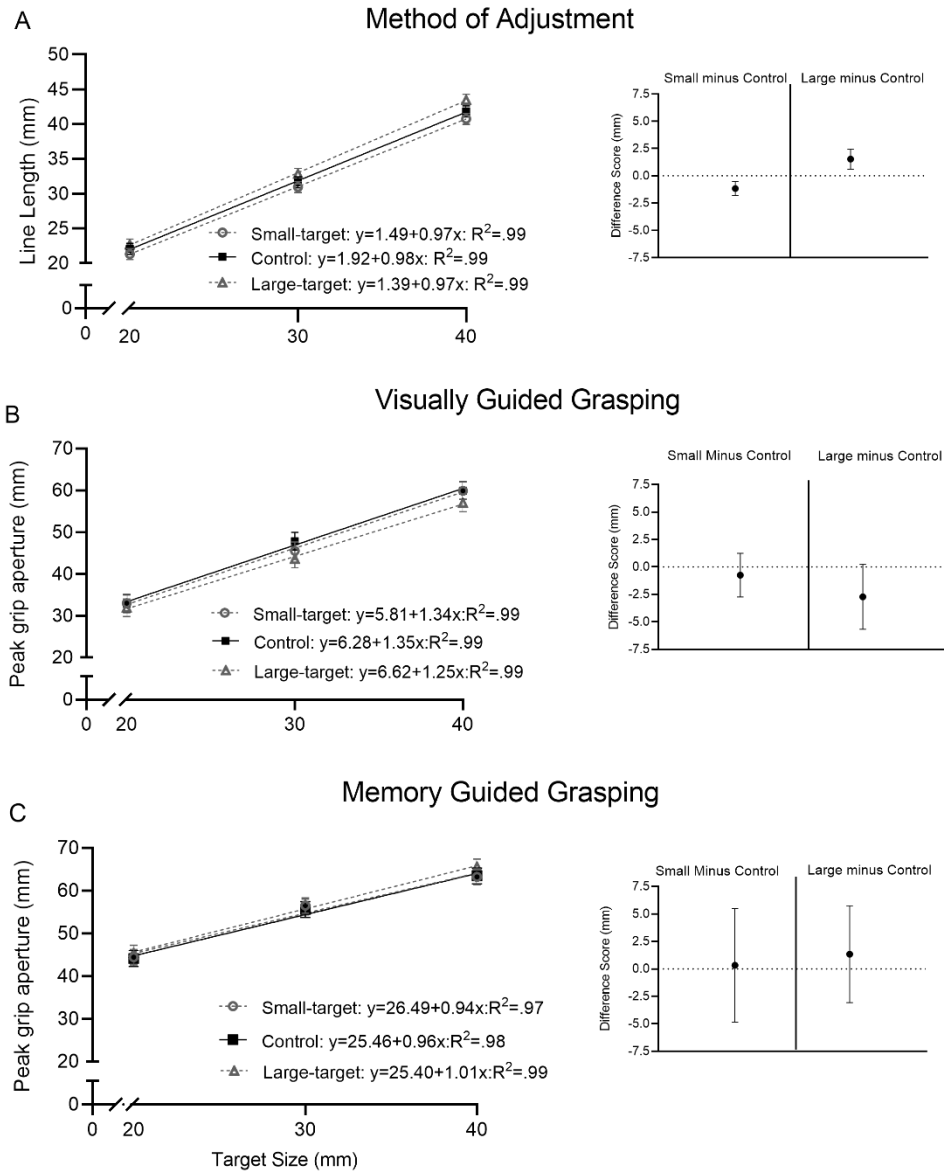


Figure 6 Group average line width for method of adjustment task (A) and peak grip aperture (PGA) for visually (B) and memory-guided grasps (C) as a function of target size and weighting condition. Error bars represents 95% within-participant confidence intervals. Each panel includes linear regression lines and associated regression equations. The offset panels represent weighting condition group mean difference scores computed wherein line

width and PGA values for the *control* condition were subtracted from the *small-* and *large-target* weighting conditions and are presented as means collapsed as function of target size. Error bars represent 95% between-participant confidence intervals and the absence of overlap between error bars and zero (i.e., the horizontal dotted line) represent a reliable difference inclusive to a test of the null hypothesis.

3.2.2. Grasping kinematics

The middle and bottom panels of **Figure 5** present an exemplar participant's trial-by-trial PGAs for visually and memory-guided grasps, respectively, and show that values did not systematically vary with weighting condition. Moreover, the figure demonstrates the expected finding that PGAs increased with target size and that values were smaller and less variable for visually than memory-guided grasps (Holmes et al. 2011).

Figure 8 shows group average grip aperture for visually (left panels) and memory-guided (right panels) grasps as a function of weighting condition at decile increments of MT. The small, middle, and large targets are presented in separate panels and in each panel the 95% between-participant confidence interval envelope is shown for the control weighting condition. The figure shows overlap between the error envelope for the *control* weighting condition and the mean grip aperture for the *small-* and *large-target* weighting conditions from 10% to 100% of MT. ANOVAs computed separately for each decile revealed main effects for target size from 10% to 100% of MT, all $F(2,36) > 13.90$, $ps < .001$, all $\eta_p^2 > .44$, such that values increased linearly with increasing target size (only significant linear effects: all $F(1,18) > 15.89$, $ps < .001$). The ANOVAs did not reveal significant main effects for grasping task from 10% to 30% of MT, all $F(1,18) < 2.16$, $ps > .15$, all $\eta_p^2 < .10$; however, from 40% to 100% of MT grip apertures were larger for visually than memory-guided grasps, all $F(1,18) > 8.76$, $ps < .01$, all $\eta_p^2 > .27$. The ANOVAs did not reveal reliable main effects for weighting condition, all $F(2,36) < 1.25$, $ps > .30$, all $\eta_p^2 < .03$, nor any higher-order interactions involving that variable, all $F < 1.53$, $ps > .23$, all $\eta_p^2 < .04$. In other words, the ANOVA findings coupled with the error envelopes provided in **Figure 7** indicate that an SSR did not influence aperture size from the early through late stages of visually and memory grasps.

ANOVA results for PGA produced main effects for target size, $F(2,36)=248.62$, $p<.001$, $\eta_p^2=.93$, grasping task $F(1,18)=13.64$, $p=.002$, $\eta_p^2=.43$, and their interaction, $F(2,36)=11.62$, $p<.001$, $\eta_p^2=.39$. The middle and bottom panels of **Figure 6** show that PGAs for visually and memory-guided grasps increased linearly with target size (only linear effects significant: $F(1,18)=530.80$ and 108.96 , $ps<.001$) and that values were smaller in the former condition (visually guided: 45 mm, $SD=17$; memory-guided: 54 mm, $SD=18$). Further, participant-specific PGA to target size slopes revealed a larger value for visually guided (1.31, $SD=.25$) than memory-guided (0.97, $SD=.40$) grasps, $t(18)=4.02$, $p=.001$, $d_z=0.92$. PGA did not elicit a main effect of weighting condition, $F(1,18)<1.0$, $p=.91$, $\eta_p^2<.01$, nor any higher-order interaction involving this variable, all $F(2,36)<1.18$, $ps>.23$, all $\eta_p^2<.06$. Two one-sided test statistics indicated that PGA for the *small-target* and *control* weighting conditions ($t(18)=2.68$, $p=.006$), and the *control* and *large-target* weighting conditions ($t(18)=2.47$, $p=.002$) were within an equivalence boundary.

Time to PGA did not produce main effects or interactions, all $F<2.49$, $ps>.103$, $\eta_p^2<.11$ (see bottom panel of **Figure 7**). In particular, weighting condition did not elicit a reliable main effect, $F(2,36)<1.0$, $p=.58$, $\eta_p^2=.03$, and two one-sided test statistics indicated that time to PGA for the *small-target* and *control* weighting conditions ($t(18)=2.24$, $p=.019$), and the *control* and *large-target* weighting conditions ($t(18)=2.48$, $p=.012$) were within an equivalence boundary.

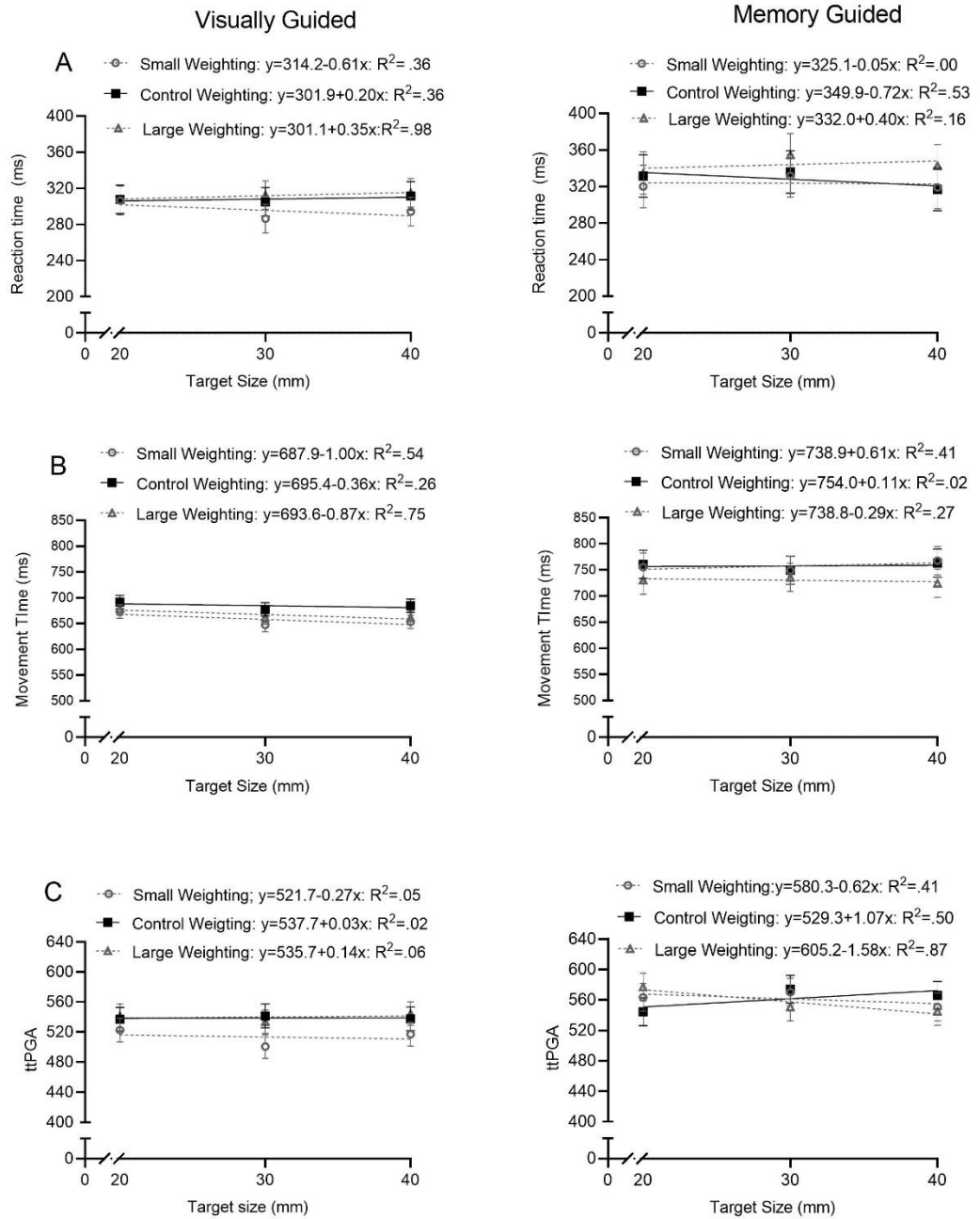


Figure 7 Group average reaction time (A), movement time (B), and time to peak grip aperture (C) for visually (left panels) and memory-guided (right panel) grasps as a function of target size and weighting condition. Error bars represent 95% within-participant confidence intervals and each panel depicts linear regression lines and associated regression equations.

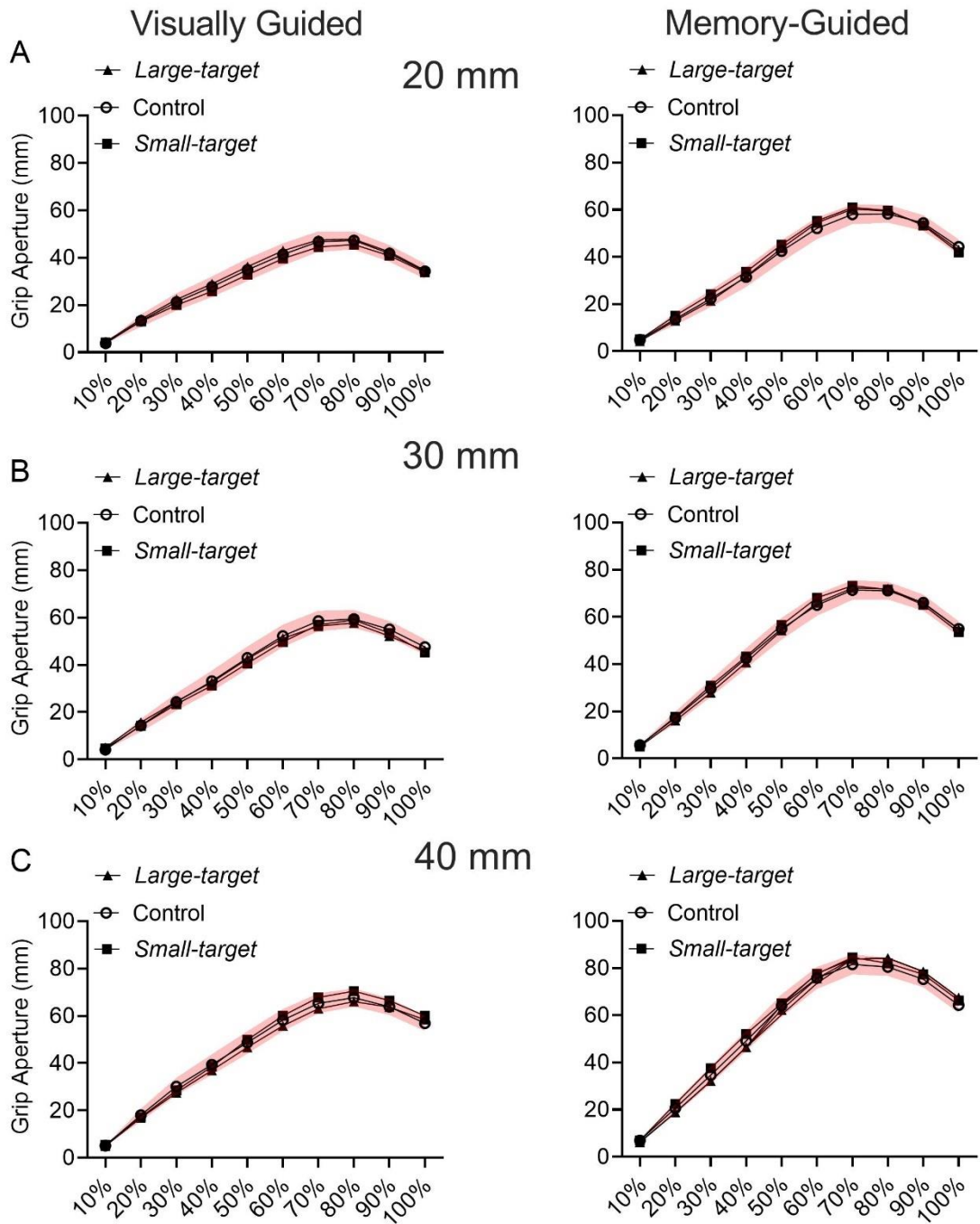


Figure 8 Group average aperture size at decile increments of normalized movement time for visually and memory-guided grasps as a function of target weighting conditions are shown

separately for the 20- (A), 30- (B) and 40-mm (C) target objects. The error envelope in each panel is the 95% between-participants confidence interval for the *control weighting* condition. We provide the confidence interval only for the *control weighting* condition because it graphically depicts that aperture size for the *small-* and *large-target weighting* conditions were within this envelope at each decile of the response. Include the labels A, B and C.

4. Discussion

We employed symmetrical and asymmetrical weighting conditions to determine whether visually and memory-guided grasps are influenced by an SSR. Further, a method of adjustment task was used to demonstrate that our target weighting conditions influenced perceptual judgments.

4.1. Summary statistics influence visuoperceptual judgments: evidence from the method of adjustment task

In the method of adjustment task participants adjusted the width of a line appearing on a computer monitor until they perceived it to match a target object – a task providing a classic measure of perceptual threshold discrimination (Farell & Peli, 1999; Marks & Algom, 1998). In this context, responses for the *small-* and *large-target weighting* conditions were smaller and larger than the *control weighting* condition, respectively; that is, responses were biased in the direction of the most frequently presented target. One interpretation of our findings can be drawn from the sequential trial effects literature wherein magnitude judgments on trial N are influenced by stimulus magnitude on trial N-1 (Jesteadt, Luce, & Green, 1977; for sequential effects in grasping and oculomotor control, see Dixon & Glover 2009; Weiler & Heath 2014). However, *a posteriori* analyses provide no evidence that sequential trial effects influenced perceptual judgments or grasping². Instead, we propose that our findings are consistent with the relative processing characteristic of the ventral pathway (Goodale & Milner, 1992) and supports the assertion that an SSR influences perceptions of the size of individual members in a stimulus-set."

The majority of SSR studies have examined perceptual judgments when a stimulus array is replaced by a test stimulus and this work demonstrates that participants extract an

SSR when all members of a stimulus-set are concurrently presented (Ariely, 2001; Chong & Treisman, 2003; Marchant & de Fockert, 2009; for review see Srinivasan, 2017). In addition, Corbett and Oriet (2011) showed that an SSR guides perception when the individual members of a stimulus-set are provided in a rapid serial presentation. Notably, the method of adjustment task used here did not entail concurrent or rapid serial presentation. As such, our results add to the general SSR literature in that they demonstrate that a summary statistic for a stimulus-set can be extracted even when individual members are presented across discrete and temporally unconstrained trials.

4.2. Summary statistics do not influence visually or memory-guided grasps

Before discussing whether grasps were influenced by target-weighting conditions we first outline the general differences between visually and memory-guided grasps. Visually guided grasps produced shorter RTs and MTs, smaller grip apertures from 40 to 100% of MT and including PGA, and an increased PGA/target size scaling than their memory-guided counterparts. The RT findings reflect that visually guided actions have shorter planning times because responses are implemented 'online' to advantage visual feedback during movement execution (Carlton, 1981; Elliott, 1988; Jakobson & Goodale, 1991, Neely, Tessmer, Binsted & Heath, 2008; Zelaznik, Hawkins & Kisselburgh, 1983). In contrast, memory-guided actions exhibit longer planning times due to an offline mode of control that increases the demands on central planning mechanisms operating prior to movement onset (e.g., Heath, 2005; for review, see Elliott et al. 2010). In addition, that memory-guided grasps produced longer MTs, larger grip apertures from 40 to 100% of MT (including PGA) and reduced PGA/target object scaling is a well-documented finding indicating that in the absence of visual feedback there is increased uncertainty about target size (and location) (Churchill, Hopkins, Rönqvist & Vogt, 2000; Hesse & Franz, 2009; Holmes, Mulla, Binsted & Heath, 2011; Jakobson & Goodale, 1991; Westwood et al. 2001) and results in apertures planned with a sufficiently large margin of error to prevent an early and unexpected 'collision' with the target (Whitwell, Ganel, Byrne & Goodale, 2015; Whitwell, Milner, Cavina-Pratesi, Barat & Goodale, 2015b).

In terms of our primary objective, visually guided grasps were not influenced by target-weighting conditions during any stage of the unfolding response. To underscore this point, **Figures 6** and **8** show that PGAs and apertures at decile increments of MT,

respectively, for *small*- and *large-target* weighting conditions did not differ from the *control* weighting condition. Moreover, two one-sided tests contrasting PGAs for the *small*- and *large-target* weighting conditions to the *control* weighting condition indicated that values were within an equivalence boundary. Thus, null and equivalence tests support the contention that an SSR does not influence visually guided grasps. This conclusion is consistent with our *a priori* prediction and the perception/action model's assertion that absolute unitary visual information mediated by dorsal visuomotor networks controls visually guided grasps (Goodale, 2011). In further support of the view that an SSR does not influence visually based actions, Gillen and Heath (2014) examined pro- (i.e., saccade to veridical target location) and antisaccade (i.e., saccade mirror-symmetrical to target location) amplitudes to target eccentricities (i.e., 10.5, 15.5 and 20.5°) in blocks wherein eccentricities were symmetrically and asymmetrically weighted (i.e., the same target-weighting used here) (see also Heath et al., 2015). Results showed that prosaccade amplitudes (see antisaccade results below) did not vary with target weighting and was a finding attributed to response output specified via direct (i.e., absolute) retinotopic projections in the superior colliculus (Wurtz & Albano, 1980). Of course, we recognize that the neural architecture of prosaccades and visually guided grasps is distinct (for review, see Rossetti, Pisella & Vighetto, 2003); however, the combined findings indicate that responses (i.e., oculomotor and grasping) supported by absolute visual information are refractory to ensemble averaging.

Memory-guided grasps (i.e., from 10 to 100% of MT and including PGA) were not influenced by target weighting and is a conclusion supported by null hypothesis and equivalence tests. At an initial level this represents an unexpected finding given work reporting that memory-guided grasps are cognitive and result in a size-scaling shift from absolute to relative visual information (i.e., a dorsal to ventral pathway transition) (Hu & Goodale, 2000; Westwood et al., 2001). As well, Gillen and Heath's (2014) oculomotor work described in the previous paragraph showed that antisaccade amplitudes were biased by the most frequently presented target in a stimulus-set – a result interpreted to reflect that the cognitive nature of antisaccades engenders the specification of target eccentricity via an SSR. In contrast, Hesse and Franz (2009) reported that memory-guided grasps are not associated with a perceptual representation and proposed that the kinematics of memory-guided grasps reflect a temporally based and exponential decay of visuomotor information (see also Elliott

& Madalena, 1987). Further, our group has shown that PGAs for memory-guided grasps violate Weber's law and indicated that absolute visual information is available for up to 5,000 ms of delay (Holmes et al., 2011; but see Ganel et al., 2008a; b). Part of the difference in the memory-guided literature might relate to the availability of terminal haptic feedback to support an absolute visuo-haptic calibration on subsequent trial performance (Davarnah Jazi & Heath, 2015; Schenk, 2012). Further, this interpretation serves to contextualize Gillen and Heath's findings given that antisaccades preclude the integration of visual or any other form of terminal feedback.

A final issue to address is the discrepancy between our results and Corbett and Song (2011). Recall Corbett and Song observed that the sustained exposure to an adapting array resulted in the early stages (i.e., ~12 to 45% of spatially normalized movement) of visually guided grasps being influenced by an SSR. In contrast, we employed discretely presented – and differently sized – target objects in different weighting conditions and did not observe an SSR effect across any stage of the unfolding aperture. It could be that our discrete target presentation did not entail a sufficiently complex environment to induce an SSR. That explanation, however, is countered by the method of adjustment task's demonstration of a reliable SSR for perceptual judgments (see *Summary statistics influence visuo-perceptual judgments: evidence from the method of adjustment task*). Instead, we propose the discrepancy – in part – relates to Corbett and Song's use of 2D targets. As indicated previously, convergent behavioural and neuroimaging evidence demonstrates that 2D grasps are perception-based and supported by relative visual information (Freud et al., 2018; Ganel, Ozana & Goodale, 2019; Holmes & Heath, 2013; Hosang et al., 2016; Ozana et al., 2018) and do not afford an absolute visuo-haptic calibration (Davarnah Jazi & Heath, 2015; Schenk, 2012). Accordingly, although an SSR may mediate the early stage of aperture formation for 2D grasps (see Corbett and Song, 2011), the present results provide no evidence that ensemble averaging underlies early or late stage aperture formation for grasps affording physical interactions with a target. It could also be the case that the adaptation paradigm used by Corbett and Song engenders a cognitive mode of control, permitting perceptual intrusions in early aperture shaping (Navon & Ganel, 2020).

5. Conclusions

Perceptual size judgments were biased in the direction of the most frequently presented target in a stimulus-set, whereas visually and memory-guided grasps were not. Based on these results, we propose that the visuomotor networks supporting naturalistic grasps specify target size independent of any contextual cue associated with the target's membership in a stimulus-set.

Footnote

1. The present sample included more female than male participants. This represents a potential limitation given work reporting sex differences in online trajectory control (Hansen & Elliott, 2008). Hence, it could be argued that sex differences influenced the method of adjustment and/or grasping performance in the current investigation. Accordingly, we computed participant-specific slopes relating line width and PGA (separately for visually and memory-guided grasps) to target size. Subsequently, we computed z-scores contrasting the slopes for individual male participants to the group mean for female participants. The resulting values across male participants and tasks ranged from -0.77 and 0.69 – a result evincing that sexual dimorphism did not influence perceptual or grasping responses (see also Sundström Poromaa &Gingnell, 2014).
2. We used grip aperture at 30% of MT because Dixon and Glover (2009) reported that this stage of grasping elicits the largest magnitude sequential trial effects. Further, we note that our study was not purpose-designed to examine sequential trial effects given that target size in each weighting condition was randomized, and as a result our retrospective analyses did not include an equal number of trials wherein trial N was preceded by a trial that was the same, smaller or larger size.

References

- Alvarez, G. A. (2011). Representing multiple objects as an ensemble enhances visual cognition. *Trends in Cognitive Sciences*, *15*, 122–131.
- Ariely, D. (2001). Seeing sets: Representation by statistical properties. *Psychological Science*, *12*, 157-162.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433-436.
- Carlton, L. G. (1981). Visual information: the control of aiming movements. *The Quarterly Journal of Experimental Psychology A*, *33*, 87-93.
- Chong, S. C., Joo, S.J., Emmanouil T-A., & Triesman, A. (2008). Statistical processing: Not so implausible after all. *Perception and Psychophysics*, *70*, 1327-1334.
- Chong, S. C., & Treisman, A. (2003). Representation of statistical properties. *Vision Research*, *43*, 393-404.
- Chong, S. C., & Treisman, A. (2005). Attentional spread in the statistical processing of visual displays. *Perception & Psychophysics*, *67*, 1-13.
- Churchill, A., Hopkins, B., Rönqvist, L., & Vogt, S. (2000). Vision of the hand and environmental context in human prehension. *Experimental Brain Research*, *134*, 81-89.
- Corbett, J. E. (2017). The whole warps the sum of its parts: Gestalt-defined-group mean size biases memory for individual objects. *Psychological Science*, *28*, 12-22.
- Corbett, J. E., & Oriet, C. (2011). The whole is indeed more than the sum of its parts: Perceptual averaging in the absence of individual item representation. *Acta Psychologica*, *138*, 289-301.
- Corbett, J. E., & Song, J. H. (2014). Statistical extraction affects visually guided action. *Visual Cognition*, *22*, 881-895.
- 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.
- Davarpanah Jazi, S. D., 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. D., 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*, 2029-2040.
- Dixon, P., & Glover, S. (2009). Perseveration and contrast effects in grasping. *Neuropsychologia*, *47*,

1578-1584.

Dubé, C., & Sekuler, R. (2015). Obligatory and adaptive averaging in visual short-term memory. *Journal of Vision*. 15, 13-13.

Elliott, D., & Madalena, J. (1987). The influence of premovement visual information on manual aiming. *The Quarterly Journal of Experimental Psychology*. 39, 541-559.

Elliott, D. (1988). The influence of visual target and limb information on manual aiming. *Canadian Journal of Psychology*. 42, 57-68.

Elliott, D., Hansen, S., Grierson, L. E., Lyons, J., Bennett, S. J., & Hayes, S. J. (2010). Goal-directed aiming: two components but multiple processes. *Psychological Bulletin*. 136, 1023-1044.

Farell, B., & Pelli, D. G. (1999). Psychophysical methods, or how to measure a threshold and why, in: Carpenter, R.H.S. & Robson, J.G. (Eds.), *Vision Research: A Practical Guide to Laboratory Methods*. Oxford University Press, New York, pp. 129-136.

Freud, E., Macdonald, S. N., Chen, J., Quinlan, D. J., Goodale, M. A., & Culham, J. C. (2018). Getting a grip on reality: Grasping movements directed to real objects and images rely on dissociable neural representations. *Cortex*. 98, 34-48.

Ganel, T., Chajut, E., & Algom, D. (2008a). Visual coding for action violates fundamental psychophysical principles. *Current Biology*. 18, R599-R601.

Ganel, T., Chajut, E., Tanzer, M., & Algom, D. (2008b). Response: When does grasping escape Weber's law? *Current Biology*. 18, R1090-R1091.

Ganel, T., Ozana, A., & Goodale, M. A. (2019). When perception intrudes on 2D grasping: evidence from Garner interference. *Psychological Research*. Manuscript accepted for publication. doi: 10.1007/s00426-019-01216-z.

Gillen, C., & Heath, M. (2014a). Perceptual averaging governs antisaccade endpoint bias. *Experimental Brain Research*. 232, 3201–3210.

Gillen, C., & Heath, M. (2014b). Target frequency influences antisaccade endpoint bias: Evidence for perceptual averaging. *Vision Research*. 105, 151– 158.

Glover, S. (2004). Separate visual representations in the planning and control of action. *Behavioral Brain Sciences*. 27, 3–78.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neuroscience*. 15, 20-25.

- Goodale, M. A. (2011). Transforming vision into action. *Vision Research*. 51, 1567-1587.
- Hansen, S., & Elliott, D. (2010). Three-dimensional manual responses to unexpected target perturbations during rapid aiming. *Journal of Motor Behavior*. 41, 16-29.
- Heath, M. (2005). Role of limb and target vision in the online control of memory-guided reaches. *Motor Control*. 9, 281-309.
- Heath, M., Gillen, C., & Weiler, J. (2015). The antisaccade task: Vector inversion contributes to a statistical summary representation of target eccentricities. *Journal of Vision*. 15, 4.
- Hesse, C., & Franz, V. H. (2009). Memory mechanisms in grasping. *Neuropsychologia*. 47, 1532-1545.
- Holmes, S.A., Mulla, A., Binsted, G., & Heath, M. (2011) Visually and memory-guided grasping: aperture shaping exhibits a time-dependent scaling to Weber's law. *Vision Research*. 51. 1941–1948
- Holmes, S. A., & Heath, M. (2013). Goal-directed grasping: The dimensional properties of an object influence the nature of the visual information mediating aperture shaping. *Brain and Cognition*. 82, 18-24.
- Hosang, S., Chan, J., Jazi, S. D., & Heath, M. (2016). Grasping a 2D object: terminal haptic feedback supports an absolute visuo-haptic calibration. *Experimental Brain Research*. 234, 945-954.
- Hu, Y., & Goodale, M. A. (2000). Grasping after a delay shifts size-scaling from absolute to relative metrics. *Journal of Cognitive Neuroscience*. 12, 856-868.
- Im, H. Y., & Chong, S. C. (2009). Computation of mean size is based on perceived size. *Attention, Perception, & Psychophysics*. 71, 375-384.
- Jakobson, L. S., & Goodale, M. A. (1991). Factors affecting higher-order movement planning: a kinematic analysis of human prehension. *Experimental Brain Research*. 86, 199-208.
- Jesteadt, W., Luce, R. D., & Green, D. M. (1977). Sequential effects in judgments of loudness. *Journal of Experimental Psychology: Human Perception and Performance*. 3, 921-944.
- Kleiner, M., Brainard, D., & Pelli, D. (2007) What's new in Psychtoolbox-3? *Perception*. 36, ECVF Abstract Supplement.
- Krügel, A., Rothkegel, L., & Engbert, R. (2020). No exception from Bayes' rule: The presence and absence of the range-effect for saccades explained. *Journal of Vision*. Manuscript accepted for publication.
- Lakens, D., Scheel, A. M., & Isager, P. M. (2018). Equivalence testing for psychological research: a

- tutorial. *Advances in Methods and Practices in Psychological Science*. 1, 259-269.
- Lakens, D. (2017). Equivalence tests: a practical primer for t-tests, correlations, and meta-analyses. *Social Psychological and Personality Science*. 8, 355-362.
- Marchant, A. P., & de Fockert, J. W. (2009). Priming by the mean representation of a set. *Quarterly Journal of Experimental Psychology*. 62, 1889-1895.
- Marks, L.E., & Algom, D. (1998). Psychophysical scaling. In: Birnbaum MH (ed) Measurement, judgment, and decision making. *Academic Press, San Diego*, pp 81-178.
- Milgram, P. (1987). A spectacle-mounted liquid-crystal tachistoscope. *Behavioral Research Methods, Instruments and Computers*. 19: 449–456.
- Navon, G., & Ganel, T. (2020). Consciously monitored grasping is vulnerable to perceptual intrusions. *Consciousness and Cognition*. 85, 103019.
- Neely, K. A., Tessmer, A., Binsted, G., & Heath, M. (2008). Goal-directed reaching: movement strategies influence the weighting of allocentric and egocentric visual cues. *Experimental Brain Research*. 186, 375-384.
- Ozana, A., Berman, S., & Ganel, T. (2018). Grasping trajectories in a virtual environment adhere to Weber's law. *Experimental Brain Research*. 236, 1775-1787.
- Pedhazur, E. J. (1997). *Multiple Regression in Behavioral Research: Explanation and Prediction* (3rd ed.). Orlando: Harcourt Brace College Publishers.
- Rossetti, Y., Pisella, L., & Vighetto, A. (2003). Optic ataxia revisited: visually guided action versus immediate visuomotor control. *Experimental Brain Research*. 153, 171-179.
- Schenk, T. (2012). No dissociation between perception and action in patient D.F. when haptic feedback is withdrawn. *Journal of Neuroscience*. 32, 2013–2017.
- Šetić, M., Švegar, D., & Domijan, D. (2007). Modelling the statistical processing of visual information. *Neurocomputing*. 70, 1080-1812.
- Srinivasan, N. (2017). Statistical summary perception in vision. *Journal of the Indian Institute of Science*. 97, 435-442.
- Sundström Poromaa, I., & Gingnell, M. (2014). Menstrual cycle influence on cognitive function and emotion processing-from a reproductive perspective. *Frontiers in Neuroscience*. 8, 380.
- Weiler, J., & Heath, M. (2014). Oculomotor task-switching: alternating from a nonstandard to a standard response yields the unidirectional prosaccade switch-cost. *Journal of Neurophysiology*. 112,

2175-2184.

Westwood, D. A., McEachern, T., & Roy, E. A. (2001). Delayed grasping of a Müller-Lyer figure. *Experimental Brain Research*. 141, 166-173.

Westwood, D., & Goodale, M. (2003). Perceptual illusion and the real-time control of action. *Spatial Vision*. 16, 243-254.

Whitwell, R. L., Ganel, T., Byrne, C. M., & Goodale, M. A. (2015). Real-time vision, tactile cues, and visual form agnosia: removing haptic feedback from a "natural" grasping task induces pantomime-like grasps. *Frontiers in Human Neuroscience*. 9, 216.

Whitwell, R. L., Milner, A. D., Cavina-Pratesi, C., Barat, M., & Goodale, M. A. (2015). Patient DF's visual brain in action: Visual feedforward control in visual form agnosia. *Vision Research*. 110, 265-276.

Wurtz, R. H., & Albano, J. E. (1980). Visual-motor function of the primate superior colliculus. *Annual Review of Neuroscience*. 3, 189-226.

Zelaznik, H. N., Hawkins, B., & Kisselburgh, L. (1983). Rapid visual feedback processing in single-aiming movements. *Journal of Motor Behavior*. 15, 217-23

Appendices



Date: 5 September 2019

To: Dr. Matthew Heath

Project ID: 114358

Study Title: Statistical Summary Representation in Visually and Memory-Guided Grasping

Short Title: Statistical Summary Representation in Action

Application Type: NMREB Initial Application

Review Type: Delegated

Full Board Reporting Date: 04/Oct/2019

Date Approval Issued: 05/Sep/2019 14:56

REB Approval Expiry Date: 05/Sep/2020

Dear Dr. Matthew Heath,

The Western University Non-Medical Research Ethics Board (NMREB) has reviewed and approved the WREM application form for the above mentioned study, as of the date noted above. NMREB approval for this study remains valid until the expiry date noted above, conditional to timely submission and acceptance of NMREB Continuing Ethics Review.

This research study is to be conducted by the investigator noted above. All other required institutional approvals must also be obtained prior to the conduct of the study.

Documents Approved:

Document Name	Document Type	Document Date	Document Version
Age-Collection Form	Other Data Collection Instruments	03/Sep/2019	V1
LOI-2(mlh)	Written Consent/Assent	07/Aug/2019	v2
Optotrak Certus tool	Other Data Collection Instruments	03/Jul/2019	V1
Participants advertisement#2	Recruitment Materials	08/Aug/2019	v3

No deviations from, or changes to the protocol should be initiated without prior written approval from the NMREB, except when necessary to eliminate immediate hazard(s) to study participants or when the change(s) involves only administrative or logistical aspects of the trial.

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. The NMREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000941.

Please do not hesitate to contact us if you have any questions.

Sincerely,

Katelyn Harris, Research Ethics Officer on behalf of Dr. Randal Graham, NMREB Chair

Note: This correspondence includes an electronic signature (validation and approval via an online system that is compliant with all regulations).

ELSEVIER LICENSE
TERMS AND CONDITIONS

Dec 29, 2020

This Agreement between Western University -- Maryam Hamidi ("You") and Elsevier ("Elsevier") consists of your license details and the terms and conditions provided by Elsevier and Copyright Clearance Center.

License Number	4978270759259
License date	Dec 29, 2020
Licensed Content Publisher	Elsevier
Licensed Content Publication	Vision Research
Licensed Content Title	Representation of statistical properties
Licensed Content Author	Sang Chul Chong, Anne Treisman
Licensed Content Date	Feb 1, 2003
Licensed Content Volume	43
Licensed Content Issue	4
Licensed Content Pages	12
Start Page	393
End Page	404
Type of Use	reuse in a thesis/dissertation

Appendix A 2. License for reuse figure 3, form Elsevier publisher.

ELSEVIER LICENSE
TERMS AND CONDITIONS

Dec 29, 2020

This Agreement between Western University -- Maryam Hamidi ("You") and Elsevier ("Elsevier") consists of your license details and the terms and conditions provided by Elsevier and Copyright Clearance Center.

License Number	4978280178511
License date	Dec 29, 2020
Licensed Content Publisher	Elsevier
Licensed Content Publication	Elsevier Books
Licensed Content Title	Handbook of Clinical Neurology
Licensed Content Author	Jason P. Gallivan,Melvyn A. Goodale
Licensed Content Date	Jan 1, 2018
Licensed Content Pages	18
Start Page	449
End Page	466
Type of Use	reuse in a thesis/dissertation
Portion	figures/tables/illustrations
Number of figures/tables/illustrations	1

<https://s100.copyright.com/AppDispatchServlet>

1/7

Appendix A 3. License for reuse figure 1, from Elsevier Books publisher.

Curriculum Vitae

Name:

Maryam Hamidi

Post-secondary Education and Degrees:

M.Sc. of Neuroscience, The University of Western, London, Ontario, Canada, 2019- present

B.Sc. of Cellular and Molecular Biology, University of Damghan, Semnan, Iran, 2014-2018

Honours and Awards:

Western Graduate Research Scholarship, 2019-2020

Graduate Research Assistantship, 2019

Related Work Experience:

Teaching Assistant, School of kinesiology, University of Western, 2019-2020

TA for KIN1080b – Introduction to Psychomotor Behavior – an undergraduate course averaging 400 students per semester

TA for KIN 1070 – Psychology of Human Movement Science – an undergraduate course averaging 400 students per semester

Publications:

Hamidi, M., Giuffre, L & Heath, M. (2021). A summary statistical representation influences perception but not visually or memory-guided grasping. *Human Movement Science*,