The dynamic interplay between target size perception and visually-guided action

By Christine M. Gamble
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This dissertation by Christine M. Gamble is accepted in its present form by the Department of Cognitive, Linguistic, and Psychological Sciences as satisfying the dissertation requirement for the degree of Doctor of Philosophy.

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May 2011-June 2013

HONORS AND AWARDS

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PUBLICATIONS

Gamble, C. M., & Song, J. H. (2017). Dynamic modulation of illusory and physical target size on separate and coordinated eye and hand movements. *Journal of Vision,* 17(3), 23-23.

Gamble, C. M., & Song, J. H. Modulation of visually-guided action by the image size and known size of real-world objects. *In preparation.*

CONFERENCE PRESENTATIONS

Gamble, C. M. & Song, J. H. Congruency between perceptual and conceptual object size modulates visually-guided action. Poster to be presented at International Psychonomic Society Meeting, Amsterdam, The Netherlands, May 2018

Gamble, C. M. & Song, J. H. Congruency between perceptual and conceptual object size modulates visually-guided action. Talk given at Vision Sciences Society, St. Pete Beach FL, May 2017

McCarthy, J. D., **Gamble, C.**, Moher, J., & Song, J. H. Salient distractors attract visual attention but attenuate action-related interference: Corroborating evidence from EEG and fMRI. Poster presented at at Society for the Neural Control of Movement, Dublin IE, May 2017

McCarthy, J. D., **Gamble, C.** & Song, J. H. Distinct prefrontal responses to salient distractors during perception and goal-directed action. Poster presented at Cognitive Neuroscience Society, San Francisco CA, March 2017

Gamble, C. M. & Song, J. H. Impact of conscious versus unconscious distractors in pop-out visual search. Talk given at Vision Sciences Society, St. Pete Beach FL, May 2016

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Gamble, C. M. & Song, J. H. Distinct influences of size-contrast illusion on action preparation and execution. Poster presented at Vision Sciences Society, St. Pete Beach FL, May 2015

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SKILLS

- Behavioral methods: eye tracking, pointing and grasping hand-movement tracking, visual masking and continuous flash suppression
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TEACHING EXPERIENCE

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Teaching Assistant, Perception and Mind, Brown University
September – December 2014
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Undergraduate Assistant, Principles of Neuroscience, Boston University
September – December 2011
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OUTREACH

Brown University symposium organizer, "Communicating Science to Society"
September 2016
- Recipient of Friedman Family Lecture grant ($7000) to coordinate multi-speaker conference for Brown faculty, students, and the general public on topics of scientific communication and science literacy

Brown University Sci-Toons consultant, "How does your brain see the world?"
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New England Girl Scout Leadership Conference invited lecturer, "The Amazing Brain"
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The research presented here represents a small fraction of my work during my graduate studies at Brown University, absolutely none of which would have been possible without support from several key sources.

I can't thank my research advisor, Joo-Hyun Song, enough for bringing me to Brown and for guiding me every step of the way. She pushed me hard to succeed, but never without personally providing the knowledge and encouragement I needed to do so. I wouldn't be where I am today without her high expectations, or without her kind words and chocolates when I was feeling discouraged.

Furthermore, as a young woman just beginning to navigate the worlds of science and academia, having a brilliant, successful woman scientist as an advisor has been invaluable. God willing this will be less noteworthy in the future.

The other members of my dissertation committee, Bill Warren and Takeo Watanabe similarly provided invaluable guidance and support. Both gave me feedback on my dissertation, but perhaps more importantly as the professors of two of my favorite classes here at Brown, they shaped my thinking in regards to my research and the field in general.

I owe by far the most thanks though to my parents—Bob and Debi Gamble. For their support in this endeavor, and every endeavor I've ever attempted or even considered, I am truly grateful. At no moment in my life have I doubted their love, their pride, or their willingness to sacrifice for me. Not the smallest of these sacrifices was my mom's decision to work multiple jobs in order to send me to a better school than the one she had attended in her youth. Or my dad's willingness to drop everything and travel cross-country to simply be with me when that was what I needed to get through a difficult time.

Despite their intense commitment to my success, my parents never pushed me in any direction against my will—a particular extracurricular, class, field of study, etc. They always listened to what I wanted, and supported me in it. When I said I wanted to be a magician they watched me put on magic shows in the living room. When I said I wanted to pursue my PhD they jokingly asked why on earth I'd want to…then sincerely asked what I would need from them in order to do so.

Because of them, I was the first in my family to go to college, let alone pursue a doctorate. Thank you, Mom and Dad.

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Introduction

Vision can largely be stated to serve two major functions: making sense of the world around us, and facilitating interaction with it. We perform both tasks extremely efficiently—with only a glance we can both identify an object as a cup of tea, and precisely guide our hand to reach out and pick it up. Despite their subjective ease though neither task is trivial, and each relies on a complex network of brain regions and myriad component perceptual processes.

Converging neurological and behavioral research has shown that after initial processing in primary visual cortex (V1), two structurally and functionally distinct visual processing streams begin to diverge (Mishkin, Ungerleider, & Macko, 1983a). The ventral visual processing stream is critical for conscious visual perception and object identification. For this reason it is commonly referred to as the "what pathway" producing "vision for perception." The dorsal pathway is responsible for "vision for action," and has been called both the "where pathway" due to processing spatial information about where a target is (Ungerleider & Haxby, 1994), and the "how pathway" for its role in planning and executing visually-guided action (Mishkin, Ungerleider, & Macko, 1983; Milner & Goodale).

The ventral visual stream is further divided into a functional hierarchy of perceptual processing mechanisms, leading to increasingly complex visual feature processing and representation (Barbur, Wolf, & Lennie, 1998; Riesenhuber & Poggio, 1999). "Low level" features like image size and spatial frequency are processed early in the course of this processing, in V1 or earlier (DeValois & DeValois, 1991), mid-

level features like shape and 3D depth cues are processed in V2-V4 (Peirce, 2015), and high-level features like object identity are processed in category-specific regions of inferotemporal cortex (Barbur et al., 1998; Bell, Pessoa, Tootell, & Ungerleider, 2012; Downing, Chan, Peelen, Dodds, & Kanwisher, 2006; Groen, Silson, & Baker, 2017; Martin, Wiggs, Ungerleider, & Haxby, 1996; Saxe, Brett, & Kanwisher, 2006). For example, human neuroimaging techniques have identified specific cortical regions dedicated to perceiving faces (Nancy Kanwisher & Yovel, 2006; Tong, Nakayama, Moscovitch, Weinrib, & Kanwisher, 2000), tools (Beauchamp, Lee, Haxby, & Martin, 2003; Chao, Haxby, & Martin, 1999; Chao & Martin, 2000), places (Dilks, Julian, Paunov, & Kanwisher, 2013; Epstein, Harris, Stanley, & Kanwisher, 1999; Nancy Kanwisher & Yovel, 2006; Spiridon, Fischl, & Kanwisher, 2006) and animate versus inanimate objects (Caramazza & Shelton, 1998; Konkle & Caramazza, 2013). Recently, the dorsal stream has similarly been subdivided into regions responsible for specific aspects of vision for action and its motor programming is implicated in the perception of tools in addition to ventral stream processing (Chao & Martin, 2000).

As both visual processing streams become increasingly well characterized, one of the most researched and most hotly debated questions in the perception and action literature is this: though they are to some degree structurally and functionally distinct, *when*, *how*, and *to what degree* do perception and action interact?

Low-level features like physical object size have long been known to modulate visually-guided action in a straightforward manner—for example, there is an inverse relationship between target size and goal-directed reaching speed (Fitts,

1954a). However, the relationship between more complex features and action is less straightforward and well characterized.

In the present work we investigate the relationship between visually-guided hand movements, and a range of visual features representing a corresponding range in perceptual processing complexity. Specifically, in both Chapter 1 and Chapter 2 we manipulated the sizes of visual objects. Object size was selected to examine perception/action interactions as size is one of the key features constraining how to perform appropriate interactions with objects, and because size perception can be broken into low, mid, and high level processes.

In the following studies I refer to three aspects of object size. *Image size* refers to the physical size an object appears in a given visual array in terms of retinal image or space occupied on a screen, and is a low-level feature. *Illusory size* refers to the size an object appears to be in a given presentation based on an illusory context. For example, the integration of a stimulus with 3D depth cues in the Ponzo illusion creates a larger *illusory size* than another stimulus outside of the illusion context with the same veridical *image size.* Finally, *familiar size* refers to the sizes of objects as they exist in the real world, which is a high-level visual feature requiring object identification and prior knowledge. Thus, all three aspects of visual size are dissociable, and represent different levels of perceptual and cognitive processing which can be integrated with visually-guided action.

In Chapter 1, we investigate two of the most common forms of visually-guided action—saccadic eye movements and reaching hand movements—and their responses to the *image* and *illusory* sizes of objects. Specifically, we investigate how

quickly and accurately movements are made to simple targets of varying image and illusory sizes. As mentioned earlier, Fitts' Law states that the larger the image size of an object is, the faster goal-directed movements to it can be made without sacrificing accuracy. This effect has been demonstrated both in hand movements and saccadic eye movements. However, this law refers to the feature we are calling *image size;* Chapter 1 examines if larger *illusory* size additionally leads to faster movements.

Interactions between size-contrast illusions and visually-guided action have long been used to examine the relationship between the dorsal and ventral visual processing streams in healthy normal human populations. It has been argued that because size contrast illusions rely on ventral visual stream processes, they are separate from visually-guided action processing in the dorsal stream, and thus illusions "deceive the eye but not the hand" (Aglioti, DeSouza, & Goodale, 1995).

However, accumulating evidence shows that at least some aspects of visually-guided action are susceptible to size-contrast illusion, such as the trajectory of pointing movements (Gentilucci, Chieffi, Daprati, Saetti, & Toni, 1996; for review, Bruno et al.), grip force (Brenner & Smeets, 1996), saccade amplitude (Bruno, Knox, & de Grave, 2010; de Brouwer, Brenner, Medendorp, & Smeets, 2014), and movement preparation (Glover, 2002, 2004a). The original Aglioti et al. (1995) findings additionally may be due in part to insufficiently matched perception and action measures (Franz, Gegenfurtner, Bülthoff, & Fahle, 2000; Franz, 2001; Pavani, Boscagli, Benvenuti, Rabuffetti, & Farnè, 1999).

Simultaneous with these studies, findings supporting some degree of perception/action dissociation in illusion paradigms continued to emerge (Ganel,

Tanzer, & Goodale, 2008; Milner & Goodale, 2008). However, on both sides of the debate, hand and eye movements were largely studied independently as opposed to being coordinated naturalistically, and hand movement paradigms failed to control for simultaneous eye movements. Further, movement *timing* as opposed to measures like amplitude, grip aperture, etc. was largely ignored. Chapter 1 responds to these gaps in the literature, and shows evidence for dynamic modulation of both hand and eye movements by illusory size in addition to image size.

Chapter 2 goes on to investigate if and how action is modulated by an even higher-level visual feature, *familiar size*. Previous behavioral research has established interactions between the high-level feature familiar size and the low-level feature image size. Konkle & Oliva (2012) designed as Stroop-like task in which participants made judgments based on the *image* sizes of objects, when the relative *familiar* sizes were congruent or incongruent.

As in the classic Stroop task, incongruency between the task-relevant feature and the task-irrelevant feature led to slower reaction times in selecting the correct response. However, this study only looked at the unidirectional influence of familiar size on image size, as opposed to bidirectional influence from familiar on image size and image on familiar size. The authors hypothesize that image size would interfere with familiar size judgments as well, but we know nothing about the relative strength of each feature—if the interference would be symmetrical or one would exert greater influence on the other.

Furthermore, it is unknown if action would respond similarly to discrete perceptual responses based on familiar size and its congruence with image size.

Previous literature has found that continuous action measures produce different patterns of results compared to discrete button-press measures in otherwise similar visual perceptual tasks (Jeff Moher, Anderson, & Song, 2015).

Finally, in this prior study the authors grouped familiar size into "large" and "small" categories as opposed to a more systematic graded manipulation. Thus, we know that image size and familiar size interact, but not if or how this interaction is modulated by size magnitude. Further, if familiar size does interact with action, it is reasonable to expect that different magnitudes of familiar size might impact action to different degrees or in different ways.

It bears emphasizing that investigations of visually-guided action are useful not only for determining perception's influences on action. Action paradigms are valuable tools for investigating perceptual and cognitive processes in a way that other behavioral paradigms cannot. For example, visually-guided reaching and pointing movements produce continuous as opposed to binary data and unfold over a longer timescale compared with button-press tasks. Thus in any decision-making task, while both button-press and reach-to-touch paradigms can provide information on a participant's choice and their reaction time, the latter also provides information on how the decision unfolds. Specifically, continuous hand trajectory information can reveal choice conflict, changes of mind, and a more nuanced timecourse of the decision-making process (Erb, Moher, Sobel, & Song, 2016; McKinstry, Dale, & Spivey, 2008; J.-H. Song & Nakayama, 2009; Spivey & Dale, 2006).

For example, when subjects are instructed to reach and touch a cued object, but the cue is ambiguous until after the reaching movement has begun, the position of

the hand reflects the state space of the decision (McKinstry et al., 2008; Spivey & Dale, 2006). Before the decision is made the hand begins moving, but only veers off toward one of the two options after enough information accumulates that the correct target becomes clear (Spivey & Dale, 2006). Similarly, the degree of curvature in reaching movements has been shown to correspond to the degree to which other potential targets attract attention (Erb et al., 2016; Moher et al., 2015; Song, 2017). Thus, in both Chapter 1 and Chapter 2, action is not investigated for its own sake, but rather for the insight it can provide into each task's underlying cognitive and perceptual processes.

In Chapter 1, I examine the responses of pointing hand movements and saccadic eye movements to objects that vary in their veridical *image* sizes and their perceptual *illusory* sizes. Though these two action types are different in their effectors and timescales, they both can be broken into movement preparation and movement execution phases, which provide insight into unique perceptual and cognitive processes (Glover, 2002, 2004b). Further, any discrepancies between participants' explicit judgments of illusory size and implicit action measures can be investigated. In Chapter 2 I examine the interactions between action and both *image size* and *familiar size* in a more cognitively demanding Stroop task. Stroop tasks involve overcoming an automatic response to an irrelevant feature in order to accurately respond to a relevant feature. One previous study investigating a classic Stroop task with a continuous pointing measure found that curvature toward the incorrect response was greater during incongruent trials compared to congruent trials, suggesting co-activation of both potential choices (Erb et al., 2016). Thus our online

hand movement paradigm can provide a wealth of information into the conflict between *image size* and *familiar size,* and the relationship of each with action, particularly in terms of the temporal dynamics of the conflict between the two (Erb et al., 2016; Jeff Moher et al., 2015; Sullivan, Hutcherson, Harris, & Rangel, 2015).

Overall, the following studies attempt to address gaps in the literature regarding interactions between visual perception and action, across levels of visual processing complexity. Specifically we characterize the ways in which image size, illusory size, and familiar size all modulate action, and what our continuous action measures reveal about perceptual decision-making involving these features.

Chapter 1:

Modulation of separate and coordinated eye and hand movements by the illusory and image sizes of targets

In everyday behavior two of the most common visually-guided actions—eye and hand movements—can be performed independently, but are often synergistically coupled. In this study, we examine whether the same visual representation is used for different stages of saccades and pointing, namely movement preparation and execution, and whether this usage is consistent between independent, and naturalistic coordinated eye and hand movements. To address these questions, we used the Ponzo illusion to dissociate the veridical image sizes and the illusory sizes of visual targets and measured the effects on movement preparation and execution for independent and coordinated saccades and pointing. During independent movements, we demonstrated that targets with larger image sizes and larger illusory sizes both produced faster preparation for both effectors. Furthermore, participants who showed a greater influence of illusion on saccade preparation also showed a greater influence on pointing preparation, suggesting that a shared mechanism involved in preparation across effectors is influenced by illusion. However, only image size and not illusory target size influenced saccade and pointing execution. When pointing was coordinated with saccades, we observed different dynamics: pointing no longer showed illusion modulation, while saccades showed modulation by illusory size for both preparation and execution. Interestingly, in independent and coordinated movements, illusion modulated saccade preparation more than pointing preparation,

with this effect more pronounced during coordination. These results suggest that a shared mechanism, dominated by the eyes, may underlie visually-guided action preparation across effectors. Furthermore, illusion's influence on action may operate within such a mechanism, leading to dynamic interactions between action modalities based on task demands.

Introduction

In many complex real-world behaviors such as making tea or grocery shopping, eye and hand movements are closely coupled. To guide hand movements, individuals constantly make saccadic eye movements toward relevant objects in the field of view (e.g., a kettle or fruit, respectively), with very few fixations on non-essential loci (Hayhoe, Shrivastava, Mruczek, & Pelz, 2003; M. F. Land & Lee, 1994; M F Land & Hayhoe, 2001; M F Land & McLeod, 2000; Patla & Vickers, 2003). In general, eye and hand movements are spatially and temporally coordinated for selecting a relevant goal (Bekkering, Abrams, & Pratt, 1995; Carey, Coleman, & Della Sala, 1997; Fisk & Goodale, 1985; Gielen, van den Heuvel, & van Gisbergen, 1984; Jackson, Newport, Mort, & Husain, 2005; Johansson, Westling, Bäckström, & Flanagan, 2001; S. F. Neggers & Bekkering, 2000; S. F. W. Neggers & Bekkering, 2001; Sailer, Eggert, Ditterich, & Straube, 2000; J.-H. Song & McPeek, 2009; Vercher & Gauthier, 1988). This eye-hand coordination is observed even when targets are not presently visible (Foerster, Carbone, Koesling, & Schneider, 2012). Studies investigating synergic effects of eye-hand coordination in both humans and non-human primates have shown that actions performed simultaneously often differ from those performed in isolation. For example, the peak velocity of saccades is typically considered an invariant function of saccade amplitude. However, saccades to the same goal show significantly higher peak velocities when they are accompanied by pointing movements (Epelboim et al., 1997; Snyder, Calton,

Dickinson, & Lawrence, 2002), and the trajectories of saccades can be influenced by reaching movements (Tipper, 2005).

Considering the ubiquitous close coupling between eye and hand movements, and their demonstrated interactions, it is important to understand whether the visual representation used for guiding coordinated eye-hand movements is the same or different from that used for separate actions. For over two decades, research has extensively characterized the relation between the visual representations used for perception and goal-directed action in the normal population using contextual size illusions such as the Ebbinghaus, Ponzo, and Müller-Lyer illusions. Such illusions provide tools to effectively dissociate the veridical image sizes of objects, and the perceptual sizes induced by the illusions (N. Bruno, 2001; N. Bruno & Bernardis, 2002; Volker H Franz, 2001; Glover & Dixon, 2002; Milner & Goodale, 2008). For example, a seminal paper by (Aglioti, DeSouza, & Goodale (1995) claimed that grasp aperture is modulated by the image sizes of objects, not by their illusory sizes within the Ebbinghaus illusion, in accord with the dual-streams hypothesis proposing that vision for perception and vision for action are dissociated (M. a. Goodale & Milner, 1992; Milner & Goodale, 2008).

Although the majority of these investigations have focused on the effect of visual illusions on a single-effector action—mostly reaching to grasp an object, previous studies have also extended this investigation into other types of action such as saccades and pointing and their coordination (e.g., Bernardis, Knox, & Bruno, 2005; Binsted & Elliott, 1999; de Grave, Franz, & Gegenfurtner, 2006). For instance, when performing separate saccadic eye movements and pointing movements toward

the Müller–Lyer illusion, Bernardis et al. (2005) found that saccades are more susceptible to illusion than pointing movements, concluding that different representations are used for the eye and the hand. Yet, by directly comparing separate and concurrent saccades and pointing movements in the Bretano illusion, de Grave et al. (2006) instead showed that both effectors were modulated by the illusion, but eye movements showed greater illusion modulation when coordinated with hand movements as opposed to being performed independently.

Extending prior work, the current study seeks to understand how objects of varying illusory/perceptual and physical/image sizes modulate different component phases, namely movement *preparation* and *execution,* of separate and simultaneous goal-directed pointing and saccadic eye movements. Past studies have shown that these phases display differing responses to perceptual illusion when examined independently. For example, Glover and colleagues (Glover, 2004b; Glover & Dixon, 2004) claim that perceptual size illusions affect only the planning and not the control of actions.

To address these questions, we employed a goal-directed saccade and pointing paradigm within a variation of the Ponzo illusion (Figure 1A), which dissociates the illusory and image sizes of targets. By presenting identical illusions for both saccade and pointing tasks we were able to directly compare the modulation of illusory and image size for each effector, both during movement planning and execution (Exp. 1). We additionally examined how this modulation is changed by the naturalistic coordination of eye and hand movements in the form of simultaneous free saccadic eye movements and goal-directed pointing (Exp. 2). Furthermore, we compared the

results in the movement preparation and execution phases between isolated (Exp. 1) and coordinated movements (Exp. 2). Taken together, the current study provides an opportunity to directly compare the impact of size-contrast illusions on the planning and execution of independent and coordinated saccades and pointing movements.

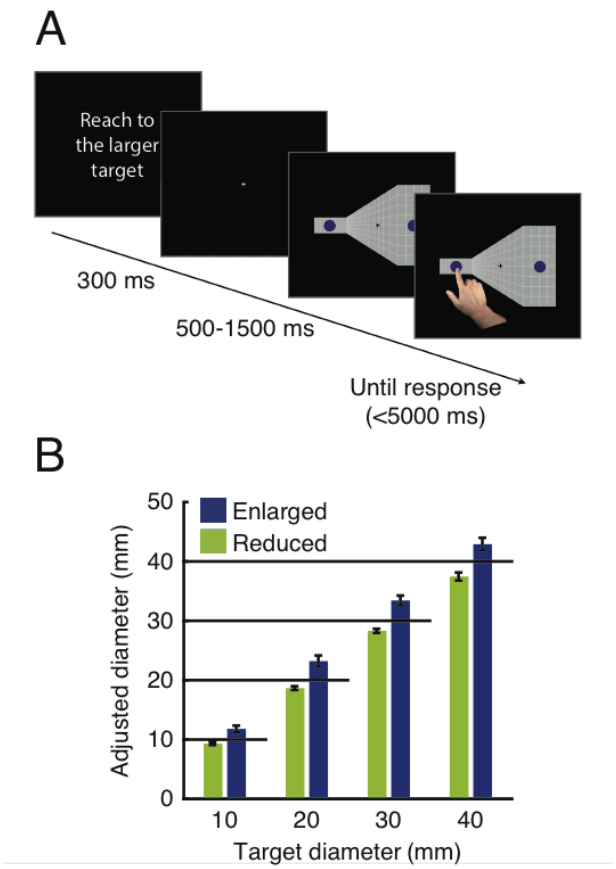

Figure 1 Experimental paradigm and illusion performance. **A.** Illusion and pointing trial diagram. Within the illusion configuration shown, the circle on the left ("enlarged") is perceived as being farther away from the viewer, and therefore larger than the circle on the right ("reduced"). Trial timing and components are identical for the saccade experiment, with eye movements replacing hand movements. **B.** Perceived sizes of visual stimuli. Circles that were adjusted outside of the illusion with circles within each illusion condition as a reference reveal that circles were perceived as significantly larger than their image sizes in the "enlarged" conditions, and significantly smaller in the "reduced" conditions, across all image sizes. Errorbars represent between-subjects standard error.

Experiment 1: Effects of illusory and image size on separate pointing and eye movements

The execution of goal-directed pointing movements has long been known to be modulated by the image size and distance of targets. Fitts' Law states that the higher the index of difficulty (ID)—the smaller or father away a target is—the slower the movement time to hit the target (Fitts, 1954). Furthermore, studies have demonstrated that ID similarly affects movement preparation, measured by reaction time (Sidaway, Christina, & Shea, 1988). Although the effect of image size on action execution has been extended to include illusory size as well (Lee & Van Donkelaar, 2002; Van Donkelaar, 1999), it is less known how the preparation of pointing movements is affected by illusory size.

Recently, saccadic eye movements were also shown to respect Fitts' Law in that overall movement time, incorporating corrective saccades, increases as target image size decreases (Wu, Kwon, & Kowler, 2010). The effect of illusory rather than image size on saccade execution in the form of movement time has yet to be examined, though previous studies have shown that some aspects of saccadic eye movement execution are influenced by illusion (for review see Bruno, Knox, and de Grave, 2010). For example, McCarley, Kramer, & DiGirolamo (2003), and DiGirolamo, McCarley, Kramer, & Griffin (2008) showed that the amplitudes of both voluntary and reflexive saccades were scaled with the illusory lengths of lines that were the same image size. Thus, in Exp. 1, we addressed how pointing and saccades are individually modulated by illusory target size in contrast to target image size, both

in their preparation and execution. Since we used the same display and paradigm for pointing and saccades, we were able to directly compare the effect of illusion on these two goal-directed action effectors.

Methods

Similar hand and eye tracking techniques, including apparatus and data analysis procedures, have been implemented in our previous work (J. Moher & Song, 2013; Jeff Moher & Song, 2014). All experimental protocols were approved by the Institutional Review Board at Brown University. Participants were compensated monetarily ($8/hour) or with course credit.

Participants

17 right-handed participants (11 female, mean age 24) with normal color vision, and normal or corrected-to-normal visual acuity performed both visually-guided action tasks: pointing and saccadic eye movements. Of these, three participants were excluded from both tasks due to high rates (>20% of trials for either task) of incorrect responses (i.e. selecting the object inconsistent with instructions for relative illusory target size). Thus, data from 14 total participants were included in the analysis.

Apparatus

Stimuli were presented on an upright Plexiglas display facing the seated participant at a distance of approximately 55 cm. A projector behind the display

projected a screen measuring 44.1 by 33 cm onto the Plexiglas, which participants viewed binocularly. Stimulus presentation was conducted using custom software designed with MATLAB (Mathworks) and Psychtoolbox (Brainard, 1997). Three-dimensional hand position was recorded with an electromagnetic position and orientation recording system (Liberty, Polhemus) at a rate of 160 Hz with a measuring error of .3 mm root mean square. A motion-tracking marker was fastened to the tip of each participant's right index finger using a Velcro strap. A foam starting block placed 27 cm in front of the participant, between the participant and the display, served as the starting position on which the index finger rested at the beginning of each trial. Eye position was monitored online with an Eyelink II (SR Research) and recorded at a rate of approximately 250 HZ.

Stimuli

All stimuli were presented on a black background. A white fixation cross measuring 7 mm x 7 mm (0.7˚ of visual angle) appeared at the center of the screen before each trial. As shown in Figure 1A, two dark blue circles of equal sizes (10 mm: 1.09º, 20 mm: 2.17º, 30 mm: 3.26º, or 40 mm: 4.34º) in diameter were presented at a distance of 12.5 cm (12.37º) to each side of the fixation cross, measured from fixation to target center. The background on which the stimuli were presented was designed in Adobe Illustrator and comprised a white and grey grid simulating a wall receding into the distance, similar to stimuli used in prior studies (Ganel et al., 2008; Gonzalez, Ganel, & Goodale, 2006). Consistent with the Ponzo illusion and similar size-contrast illusions, the circles appearing to be farther away were perceived as

larger than their veridical image size. Thus, presenting targets in the perceptually farther position was referred to as the *enlarged* condition. Circles appearing perceptually closer in the illusion were perceived as smaller than their veridical image size, and are referred to as the *reduced* condition (Figure 1A).

Prior to conducting the main visually-guided action experiments, we confirmed that this size-contrast illusion manipulation resulted in a robust difference in illusory size. A separate group of 14 participants (8 female, mean age 21) was presented with the illusion (Figure 1A) with one circle in either the *enlarged* or *reduced* condition, and another 10.5 cm (9.22º) above fixation and thereby outside of the illusion environment. Subjects used a keyboard to adjust the size of the circle *outside* of the illusion to perceptually match the size of circle presented *inside* the illusion, with trials for both the *enlarged* and *reduced* conditions. Figure 1B shows that participants adjusted the outside circle to be 29.5% larger on average when matching the *enlarged* targets than when matching the *reduced* targets. A 2x4 repeated measures ANOVA with factors of illusion condition (*enlarged* vs. *reduced*) and target image size (10 mm, 20 mm, 30 mm, and 40 mm), revealed main effects of illusion condition ($F(1,13) = 4.789$, $p = .048$, $\eta_p^2 = .269$), and image size ($F(3,39) = 912.3$, $p < .001$, $\eta_p^2 = .986$), and no interaction ($F(3,39) = 2.25$, $p = .098$, $\eta_p^2 = .148$). Together, this indicates that the illusion was effective and participants perceived the *enlarged* condition as significantly larger than the *reduced* condition, consistent across target image sizes. Thus, we used this size-contrast illusion manipulation for all our subsequent experiments.

Procedure

Participants performed the pointing and saccade tasks on two separate days, with the order of the two tasks counterbalanced across participants. At the beginning of each pointing experiment, and each block of the saccade experiment, nine-point calibration and validation were conducted. Participants also completed a practice block of 48 trials of the relevant pointing or saccade task before data collection.

Each experiment contained eight blocks (48 trials/block) with each block containing targets of only one of the four image sizes (2 blocks/size). All participants completed all blocks and were presented with all image and illusory size conditions. Each block was broken into two sub-blocks (24 trials/sub-block) in which the targets were consistently either the perceptually *enlarged* or perceptually *reduced* targets only. Thus each illusion condition of each image size was repeated 48 times, for 384 trials per experiment. Target selection instructions appeared in white at the beginning of each sub-block (e.g. "Point to the larger target"). The order of the blocks was randomized with sub-block order counterbalanced. For instance, for a given image size condition, participants might be instructed to select the perceptually smaller targets for the first sub-block and then the perceptually larger for the second sub-block. This sub-block order would be reversed for the second block of the same target image sizes. Within sub-blocks, trials were counterbalanced for target presentation on the left or the right side of the screen, and background illusion oriented with the perceptually *enlarged* condition on the left or the right side of the screen.

An example trial of the pointing task is diagrammed in Figure 1A. At the beginning of each sub-block, instructions indicated the type of action required

(pointing or saccade) and which circle would be the target: the perceptually smaller circle for the *reduced* target condition or to the perceptually larger circle for the *enlarged* target condition. In both pointing and saccade trials, an initial fixation cross was presented for a variable amount of time (500-1500 ms) and drift correction was conducted. This was followed by the stimulus display. In the pointing task, participants were instructed to hold eye fixation throughout the trial and execute a goal-directed pointing movement to the target. If at any time eye position extended outside of a 54 mm x 54 mm (4.97º x 4.97º) box surrounding fixation, a warning was presented on the screen reminding participants to maintain fixation, and the trial was excluded from data analysis. In the saccade task, participants were instructed to make a saccade to a target while holding their index finger on the starting block. In both tasks, the display was presented until the relevant action was performed, or for a maximum of 5000 ms. A feedback beep was played either indicating the selection of a circle, or that the time limit had been reached.

Data analysis

Using custom MATLAB (Mathworks), we conducted off-line data analysis on the pointing and saccade data. An algorithm using velocity criteria relevant to the task effector detected the beginning and end of pointing and saccadic movements, and the algorithm's identification of these movements was visually inspected to verify its accuracy for every trial (Moher & Song, 2013, 2014). Pointing and saccadic eye movements were classified as correct responses if they ultimately landed within target boundaries (10, 20, 30, or 40 mm diameter depending on condition) in the x- and y-

dimensions. Similar movements landing within the non-target circle were marked as incorrect. For pointing movements, participants heard a beep to indicate that a circle had been selected when their finger came within 5 mm of the screen (the z-dimension) and within the x- and y-dimension boundaries of either the target or non-target circle. This feedback was unrelated to selection accuracy.

Pointing task: Movement velocity was calculated from the 3D position traces after filtering with a low-pass filter (cutoff frequency of 10 Hz). The beginning and end of pointing movements were detected using a velocity criterion of 10 cm/sec. *Initiation latency (IL)* was defined as the time elapsed between stimulus onset and movement onset. *Movement time (MT)* was defined as the time elapsed between movement onset and movement offset/target landing. *Peak velocity* was calculated as the highest velocity achieved over the course of the reach, between movement initiation and target landing. A measure of the *constant error* of pointing movements was calculated from the average distance between the landing position of the pointing movement and the center of the target in the x dimension.

Saccade task: An algorithm using a similar velocity criterion of 100º/sec detected the beginning and end of saccades. Velocity was calculated after filtering with a low-pass filter with a cutoff frequency of 50 Hz. If the primary above-threshold saccade failed to reach the target, and a lower amplitude corrective saccade with the same velocity criterion of 100º visual angle/sec was performed successfully hitting the target, this was defined as a *corrective saccade*. Saccadic *initiation latency*

(IL) was defined as the time elapsed between stimulus onset and initial saccade onset. As in Wu et al. (2010), *movement time (MT)* was defined as the in-flight time of the initial saccade, and any corrective saccades. As in the pointing task, *peak velocity* was calculated as the maximum velocity achieved during this movement time, and constant error was calculated as the distance from the target center to the final landing position of saccades in the x dimension.

Results

Overall, participants were accurate in illusion-consistent target selection (e.g. choosing the perceptually *enlarged* target when instructed to point/saccade to the larger circle) for the pointing and saccade tasks: 97.12% (± .80%), and 93.14% (± 2.13%), respectively. These accuracy rates were consistent across conditions for both tasks. ~10% trials were excluded from data analysis from each task due to technical issues (e.g. sampling drop), blinking, erratic movements, or lack of proper eye fixation in the pointing task. Thus, the total number of trials included in data analysis was 86.1% (± 2.4%) for the pointing task and 87.17 (± 3.2%) for the saccade task. All subsequent data analyses were restricted to non-rejected correct (illusion-consistent) pointing and saccadic eye movements. Only illusion-consistent responses were included to ensure that analyzed trials involved the dissociation between image and illusory size necessary to reveal any dissociation between perception and action.

Effect of illusory and image sizes on pointing task

Pointing preparation. In order to examine how size-contrast illusions affect preparation for pointing movements across various target sizes, we first analyzed initiation latency (IL). Figure 2A shows that IL was faster overall when targets of the same size were enlarged by the illusion (green line) than when they were reduced (blue line), consistent across target image sizes. All analyses follow this convention, with the perceptually *enlarged* condition shown in green, and the perceptually *reduced* condition in blue. We similarly observed faster IL across both illusion conditions as the target image size increased from 10 mm to 40 mm. These observations were supported by a 2x4 repeated measures ANOVA with factors of illusion condition (*enlarged* targets vs. *reduced* targets) and stimulus size (10, 20, 30, and 40 mm), which revealed a main effect of illusion condition, $F(1,13) = 5.99$, $p = .029$, $\eta_p^2 = .316$, a main effect of stimulus size, $F(3,39) = 8.81$, $p < .001$, $\eta_p^2 = .404$, and no interaction $F(3,39) = 1.82$, $p = .159$, $\eta_p^2 = .123$. Thus, both the illusory and image sizes of targets modulated the initiation latency for pointing movements.

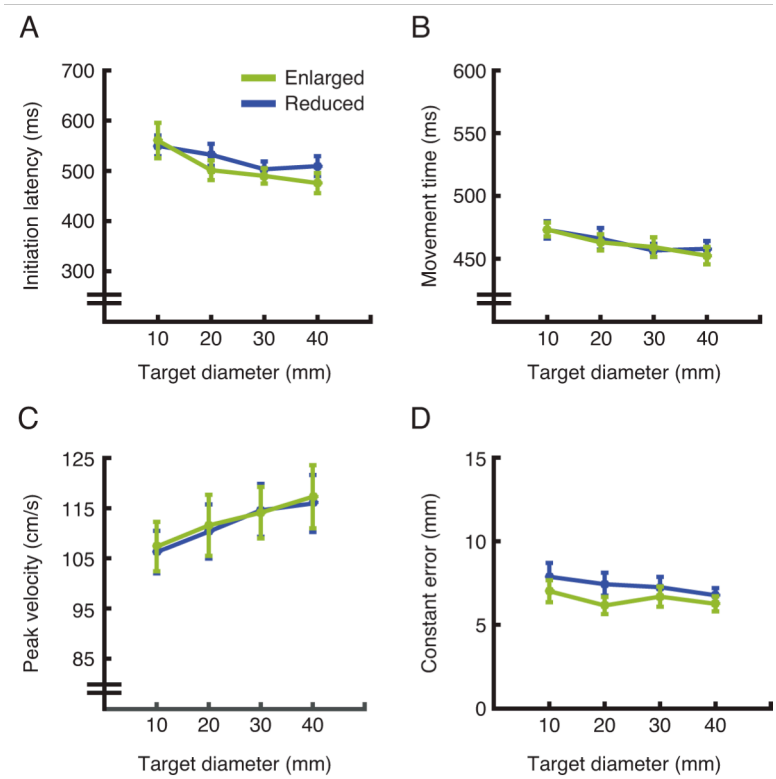

Figure 2 Independently performed pointing measures (Exp. 1). All errorbars represent between-subjects standard error. **A.** Pointing initiation latency. IL was faster when targets were either perceived as larger due to the illusion, or had larger image sizes. **B.** Pointing movement time. MT was faster when image sizes were larger, but not when targets were perceived as larger due to the illusion. **C.** Pointing peak velocity. The peak velocity reached over the course of the movements was faster when image sizes were larger, but not when targets were perceived as larger due to the illusion. **D.** Pointing constant error. The distance between the landing position and target center is larger for the perceptually smaller than the perceptually larger targets, but no difference was seen based on image size.

Pointing execution. To examine the impact of the size-contrast illusion on the execution of pointing movements across the four target image sizes and two illusion conditions, we analyzed the pattern of movement time (MT). Figure 2B shows no difference in MT between the enlarged (green) and reduced (blue) illusion conditions. However, like initiation latency, MT was modulated by image size such that

movements were faster to the targets with larger image sizes and slower to targets with smaller image sizes across subjects, consistent with Fitts' Law (Fitts, 1954).

A 2x4 repeated measures ANOVA with factors of illusion condition and target diameter here revealed no effect of illusion, $F(1,13) = .493$, $p = .495$, $\eta_p{}^2 = .037$, a significant main effect of target diameter, $F(3,39) = 6.34$, $p = .001$, $\eta_p^2 = .328$, and no interaction $F(3,39) = .644$, $p = .591$, $\eta_p^2 = .047$. Thus, in contrast to pointing preparation, this result suggests that manipulating image size alone modulates the speed of executing pointing movements, with no modulation based on illusory size. Movements were no faster to targets only perceived as larger, despite the fact that movements were faster to targets with larger image sizes in accord with Fitts' Law. This is consistent with a dissociation between visual perception and visually-guided action as proposed in prior work for the *execution* of hand movements specifically (for review, see Goodale, 2014).

Additionally, we analyzed the peak velocity across image and illusory size conditions as another measure of movement *execution.* Figure 2C shows that peak velocity increased as target diameter increased, with no differences between the perceptually enlarged (green) and reduced (blue) conditions. This observation was supported by a 2x4 repeated measures ANOVA which revealed no significant effect of illusion, $F(1,13) = 1.13$, $p = .307$, $\eta_p^2 = .080$), a significant effect of target size, $F(3,39) = 10.51$, $p < .001$, $\eta_p^2 = .447$, and no interaction $F(3,39) = .468$, $p = .706$, $\eta_p^2 = .035$. This is consistent with our other measure of movement execution, movement time, which also showed impact based on target image size but not illusion

condition. Thus, both movement *execution* measures are modulated by the image sizes of targets, but were immune to the illusion.

By examining constant error, measuring the distance of target landing from target center across illusion conditions and image sizes, we confirmed that participants overall performed the pointing task accurately across all conditions. As shown in Figure 2D, constant error was modulated by image and illusory size during pointing. Pointing movements more precisely landed on the centers of their targets as both the image sizes increased, and when the targets were perceived as larger (green) compared to smaller (blue). This was supported by a significant main effect of illusion, $F(1,13) = 9.31$, $p = .009$, $\eta_p^2 = .417$ and stimulus size, $F(3,39) = 4.92$, $p = .005$, $\eta_p^2 = .274$, and no interaction $F(3,39) = 2.03$, $p = .125$, $\eta_p^2 = .135$.

Effect of illusory and image sizes on saccade task

Saccade preparation. To determine the role of illusory target size in saccadic eye movement preparation, we compared the initiation latencies of saccades between perceptually *enlarged* and *reduced* targets across the four target image sizes. As seen in Figure 3A, participants were faster to initiate saccades to enlarged targets (green) than to reduced targets (blue), indicating modulation based on illusory size. Initiation latency was also faster for the larger target diameters, indicating modulation based on image size. A 2x4 ANOVA with factors of illusion condition and stimulus size supported these observations, with a significant main effect for illusion condition $F(1,13) = 5.83$, $p = .031$, $\eta_p^2 = .310$ and a significant main effect for image size $F(3,11) = 4.391$, $p = .032$, $\eta_p^2 = .568$. No interaction was observed $F(3,39) = 1.28$, $p =$

.296, η_p^2 = .089. This modulation of saccadic eye movement preparation based on both illusory and image size (Fig. 3A) is consistent with the results seen in pointing movement preparation (Fig 2A).

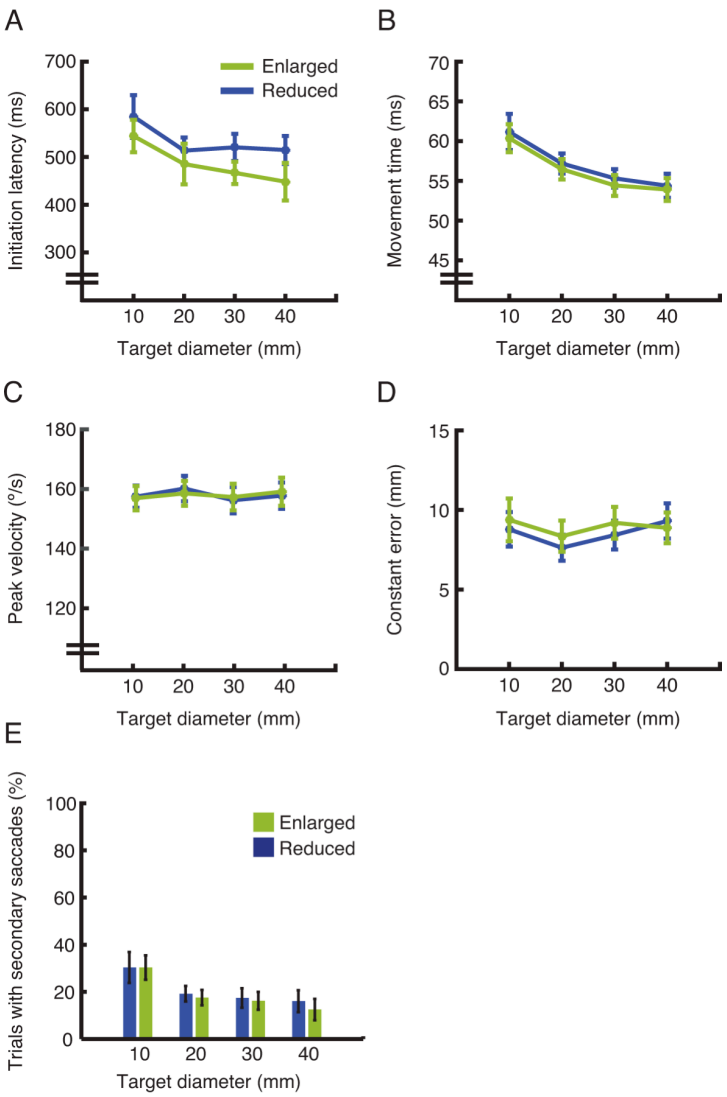

Figure 3 Independently performed saccade measures (Exp. 1). All errorbars represent between-subjects standard error. **A.** Saccade initiation latency. IL was faster when targets were either perceived as larger due to the illusion, or had larger image sizes. **B.** Saccade total MT. MT was faster when image sizes were larger, but not when targets were perceived as larger due to the illusion. **C.** Saccade peak velocity. There was no difference in the peak saccadic velocities reached based on either image or perceptual illusory size. **D.** Saccade constant error. There was no difference in distances between the saccadic landing position and target center based on either image or perceptual illusory size.

Saccade execution. We also examined the modulation of saccadic eye movement *execution* by image and illusory size by analyzing saccadic movement time (MT). Figure 3B shows that MT decreased as image size increased, indicating that the total time required between saccade initiation and landing within the intended target was modulated by image size in a manner similar to hand movements (Figure 2B). As in pointing MT, there was no difference between the two illusion conditions for MT (enlarged shown in green, reduced in blue), indicating a lack of impact of illusion size on saccadic eye movement execution.

Here we found no main effect of illusion condition $F(1,13) = 2.51$, $p = 0.137$, $\eta_p^2 = .162$, a main effect of target diameter $F(3,39) = 15.38$, $p < .001$, $\eta_p^2 = .542$, and no interaction $F(3,39) = .098$, $p = .961$, $\eta_p^2 = .007$ for total MT. Again, these findings suggest dissociation between perception and action for saccadic eye movement execution, as was seen in pointing execution. Additionally, the modulation of saccadic MT by image size is consistent with prior evidence of Fitts' Law or a broader speed/accuracy trade-off for saccade execution (Wu et al., 2010).

In examining saccadic peak velocity, we found no effect of image or illusory size (Figure 3C); unlike with hand movements (Fig. 2C), saccades in all conditions showed approximately the same velocity profile. Thus there was no effect of illusion, $F(1,13) = .004$, $p = .95$, $\eta_p^2 < .001$, no effect of stimulus size, $F(3,39) = .996$, $p = .405$, $\eta_p^2 = .071$, and no interaction $F(3,39) = 1.30$, $p = .289$, $\eta_p^2 = .091$. Similarly, Figure 3D shows no difference in constant error based on target diameter or illusion condition, indicating that saccadic landing was consistent across conditions and was not influenced by illusory or image size; there was no main effect of illusion, $F(1,13)$

= 1.12, p = .309 η_p^2 =.079, no effect of stimulus size, $F(3,39) = 1.74$, p = .175, η_p^2 = .118, and no interaction $F(3,39) = .688$, p = .565, η_p^2 = .050.

Interestingly, we also noticed a higher prevalence of corrective saccades in trials with smaller image sizes than trials with larger targets (Figure 3E), supported by a 2x4 ANOVA with no main effect of illusion condition $F(1,13) = 2.25$, p = .157, η_p^2= .148, a main effect of image size $F(3,39) = 9.35$, $p < .001$, η_p^2=.418, and no interaction $F(3,39) = .419$, p = .740, η_p^2 = .031. This is consistent with the prior finding that smaller targets result in a higher prevalence of corrective saccades, and that it is this manifestation of a speed/accuracy trade-off that parallels Fitts' Law (Wu et al., 2010). However, this difference appears to reflect the image sizes of targets only, as there is no difference in the number of corrective saccades performed based on illusory size.

Taken together, we have shown that illusion influences the preparation, as measured by IL, but not the execution, measured by MT and peak velocity, of both pointing and saccadic eye movements. However, there was some influence of illusion on pointing constant error at the end of movement execution, consistent with past research (for review, see Bruno et al., 2010). Given the similarity in IL and MT responses to image and illusory size manipulation observed in pointing and saccades, we were able to compare the findings from these two effectors directly, and examine the potential for shared underlying mechanisms.

Correlations of illusion effect for pointing and saccades

As shown in Figures 2A and 3A, both pointing and saccades showed modulation based on target illusory and image sizes for IL, and modulation based on image size alone for MT. Crucially, both pointing and saccade IL were modulated by the size-contrast illusion. To directly compare the extent to which the illusion modulated pointing and saccadic preparation, we calculated a normalized initiation latency index for each participant, as follows:

$$\text{Illusion index}_{\text{IL}} = \frac{\text{Mean IL}_{\text{reduced}} - \text{Mean IL}_{\text{enlarged}}}{\text{Mean IL}_{\text{reduced}} + \text{Mean IL}_{\text{enlarged}}} \qquad \text{Eq (1)}$$

where Mean $IL_{reduced}$ and Mean $IL_{enlarged}$ indicate the mean initiation latency of all reduced and enlarged conditions, respectively by collapsing across target image size conditions.

As seen in Figure 4A, correlating the illusion index for the initiation latency of pointing and saccades across individual participants revealed that participants who showed larger differences between initiation latency for the *reduced* and *enlarged* illusion conditions in the pointing task also showed larger differences in the saccade task. A significant correlation between the illusion indices for pointing and saccades supports this observation, $r = .66$, $p = .01$. The least-squares regression line (solid) demonstrates this trend. The unity line (dotted) indicates equal modulation based on illusion for both pointing and saccades. The majority of participants' data points fell below the unity line (dotted), indicating that saccades were more affected by illusory

size than pointing movements were $t(13) = 2.18$, $p = .048$, $d = .58$. Thus, the illusion affected the preparation of eye movements more than hand movements overall.

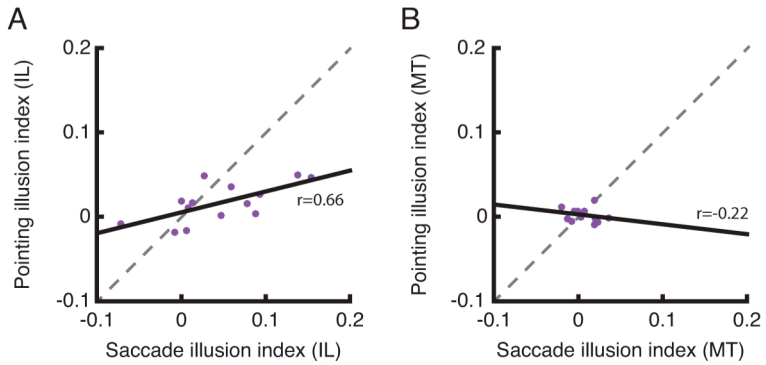

Figure 4 Correlations between illusion impact on independent pointing and saccades (Exp. 1) **A.** Correlation in illusion's impact on initiation latency. The effect of illusion on the initiation latency of both pointing and saccades was positively correlated such that subjects with more of an influence of illusion on pointing IL also had a larger influence for saccadic IL. **B.** Correlation in illusion's impact on movement time. There was no relation between the influence of illusion on pointing and saccadic initiation latency.

We also calculated a similar index for the influence of the illusion on movement time (MT) for pointing and saccadic eye movements:

$$\text{Illusion index}_{\text{MT}} = \frac{\text{Mean MT}_{\text{reduced}} - \text{Mean MT}_{\text{enlarged}}}{\text{Mean MT}_{\text{reduced}} + \text{Mean MT}_{\text{enlarged}}} \qquad \text{Eq (2)}$$

As expected, given that we saw no effect of illusion on movement time in pointing (Figure 2B) or saccades (Figure 3B), we saw no relation between the impact of illusion on pointing MT and saccadic total MT across subjects, as shown in Figure 4B. This was supported by a correlation which failed to reach significance $r = -.22$, $p = .44$, again shown by the least-squares regression line (solid). Comparing the data

points to the unity line (dotted) here reveals no systematic bias, suggesting that both pointing and saccade movement time are impacted by illusion to a similar degree, consistent with neither showing a significant effect of illusion, $t(13) = .76$, $p = .46$, $d = .20$. Overall, Figure 4 displays a significant correlation between how the illusion affects the preparation, but not the execution, of pointing and saccades, and suggests that saccadic preparation is more impacted by illusion than pointing preparation.

Summary

Overall, Exp. 1 demonstrated that when goal-directed pointing and saccadic eye movements are performed independently, both respond to perceptual size illusion in similar ways. Namely, the perceived illusory sizes of targets affected the preparation portion of pointing and saccadic eye movements, measured by initiation latency, but not their execution, measured by movement time. This distinction between phases has not previously been investigated in the context of illusion and action. Thus these findings, particularly that illusion can and does influence some aspects of action, provides new insight for the perception/action dissociation literature. Interestingly, we also demonstrated that while the influence of illusion on pointing and saccade preparation was positively correlated, saccades were more susceptible to illusion overall than pointing. This provides insights into the mechanisms of pointing and eye movements, and raises questions about the relationship between the two coordinated actions addressed in Experiment 2.

Experiment 2: Effects of illusory and image size on eye-hand coordination

Exp. 2 had two primary goals: to examine how size-contrast illusion modulates goal-directed action in a more naturalistic, real-world context; and to examine whether illusory size continues to affect saccades more strongly than pointing as seen in Exp. 1. In order to answer these questions, we asked participants to perform the same pointing task as in Exp. 1, but without constraining eye movements. The resulting coordinated eye-hand movements within an otherwise identical paradigm to Exp. 1 enabled us to directly compare whether illusory size modulates independent and coordinated eye and hand movements differently.

Methods

Participants

17 right-handed participants (13 female, mean age 23) with normal color vision, and normal or corrected-to-normal visual acuity performed the combined pointing and saccade task. Of these, three participants were excluded from analysis for both tasks due to high error rates (> 20% of trials) in the pointing task, high rates of unreadable eye movement data, or both. Thus, a total of 14 participants were included for data analysis.

Apparatus and Stimuli

The same apparatus and stimuli were used as in Exp. 1.

Procedure

The task performed in Exp. 2 was the same as the *pointing* task in Exp. 1, except that participants were allowed to make free eye movements instead of fixating

at the screen center. Nine-point calibration and validation were conducted for hand movements at the beginning of the experiment, and for eye movements at the beginning of each block. Participants completed a practice block of 48 trials of the combined pointing and saccade task before data collection.

Data analysis

Pointing movements: Pointing movements were defined and analyzed as in Exp. 1.

Saccadic eye movements: The same algorithm as in Exp. 1 was used to define the beginning and end of saccades. Among these sequential saccades, we defined the *target saccade* as the first saccade to land within the boundaries of the target + 1.8 degrees on either side. Our primary analysis to characterize the effects of illusory size on unconstrained saccades was focused on these target saccades. *Target saccade initiation latency (TIL)* was defined as the time between stimulus onset and the onset of the target saccade. *Movement time* of the target saccade (MT) was defined as the time elapsed between target saccade onset and landing including the in-flight time of corrective saccades as in Exp. 1.

Results

Overall illusion-consistent target selection accuracy for the pointing task was 98.96% (± 1.34%), which was consistent across conditions. As in Exp. 1, we confined our pointing analyses to correct trials (i.e. when target selection based on relative size was illusion-consistent). Furthermore, ~10% trials were excluded from data analysis from each task due to technical issues (e.g., sampling drop), erratic movements, etc. Thus, the total percent of trials included in data analysis across subjects was 92.3% (±

1.5%). We first report the results from the pointing aspect of the experiment, then the results from the free saccadic eye movements.

Effects of illusory and image size on pointing with unconstrained saccades

Pointing preparation. Figure 5A compares the initiation latency of pointing performed alongside free saccades as a function of image size in the perceptually *enlarged* (green) and *reduced* (blue) conditions. We found that the illusion did not result in a significant pointing initiation latency (IL) difference, $F(1,13) = 1.91$, $p = .190$, $\eta_p^2 = .128$. This differs from what we observed in the pointing movements performed alongside eye fixation in Exp. 1, where pointing IL was faster in the *enlarged* than the *reduced* condition (Figure 2A). However, as in Exp. 1, IL was also faster for targets with larger image sizes compared to smaller image sizes $F(3,39) = 9.82$, $p < .001$, $\eta_p^2 = .430$. There was no significant interaction between effects of illusory and image sizes on IL, $F(3,39) = .767$, $p = .519$, $\eta_p^2 = .056$. Thus, this result shows that only the image size and not the illusory target size influences the preparation of pointing movements that were paired with natural eye movements.

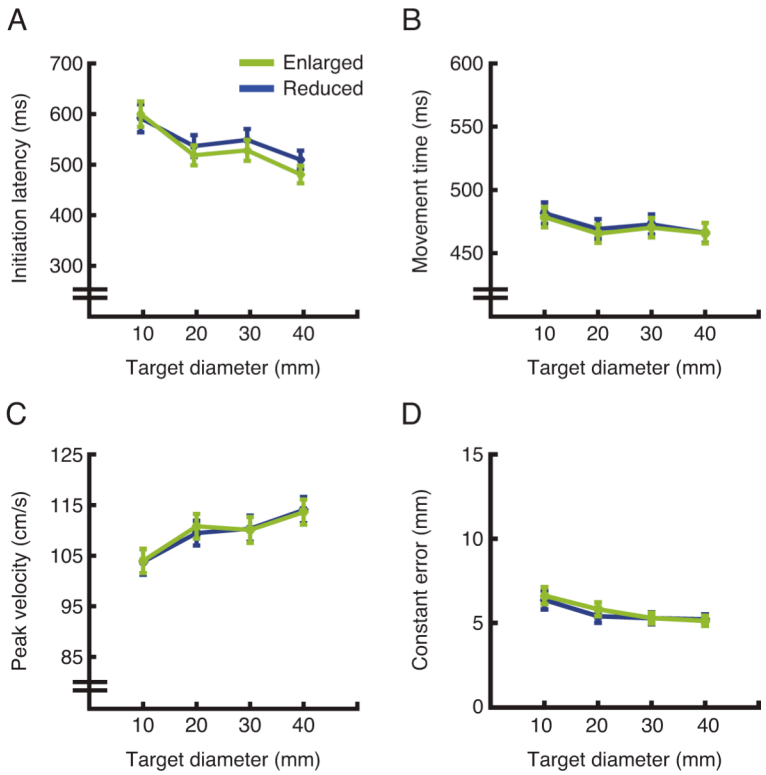

Figure 5 Pointing measures when performed in coordination with saccades (Exp. 2). All errorbars represent between-subjects standard error. **A.** Pointing initiation latency. IL was faster when image sizes were larger, but not when targets were perceived as larger due to the illusion. **B.** Pointing movement time. MT was faster when target image sizes were larger, but not when targets were perceived as larger due to the illusion. **C.** Pointing peak velocity. The peak velocity reached over the course of the movements was faster when target images sizes were larger, but not when targets were perceived as larger due to the illusion. **D.** Pointing constant error. There was no difference in distances between the saccadic landing position and target center based on either image or illusory size.

Pointing execution. Figure 5B depicts the impact of illusion on the execution of pointing movements. We found no significant difference in movement time (MT) based on illusory size, $F(1,13) = 1.90$, $p = .191$, $\eta_p^2 = .127$, while larger image sizes facilitated MT marginally, $F(3,39) = 2.60$, $p = .066$, $\eta_p^2 = .167$. There was no significant interaction between illusory and image size conditions, $F(3,39) = .066$, $p = .978$, $\eta_p^2 = .005$. This is consistent with the pointing movements performed with eye

fixation in Exp. 1 (Fig 2B), where image size but not illusory size modulated pointing movement execution.

We also examined the peak velocity of pointing movements, as in Exp. 1, as another measure of *movement execution*. Figure 5C shows that there was no difference in peak velocity between the perceptually *enlarged* (green) and *reduced* (blue) conditions $F(1,13) = .871$, $p = .368$, $\eta_p^2 = .063$, but peak velocity was higher for targets with larger image sizes, $F(3,39) = 7.70$, $p < .001$, $\eta_p^2 = .372$. There was no interaction effect, $F(3,39) = .698$, $p = .559$, $\eta_p^2 = .059$. This is also consistent with the pattern observed with eye fixation in Exp. 1, where image size but not perceived illusory size modulated the peak velocity reached over the course of pointing movement execution. As shown in Figure 5D, there was no effect of illusory target size on constant error, $F(1,13) = .299$, $p = .594$, $\eta_p^2 = .022$, a marginally significant effect of image size, $F(3,39) = 2.58$, $p = .067$, $\eta_p^2 = .166$, and no interaction, $F(3,39) = 1.23$, $p = .311$, $\eta_p^2 = .087$. Thus constant error was consistent, suggesting that pointing movements were performed consistently across illusion conditions. Overall then, image size but not illusory size influenced both the preparation and execution of pointing movements that were paired with unconstrained eye movements.

Unconstrained eye movements

In contrast to Exp. 1, here eye movements were unconstrained and were not a task requirement. Trials with unreadable eye movements due to excessive head movements, blinking, or erratic saccades were excluded from saccade analysis (27.20 ± 4.00% total excluded). Although unconstrained eye movements were allowed, we

observed that participants made only a very small number of targeted saccades (1.70 ± .55 per trial) and acquired the target within 1.38 saccades on average (± .24) (Figure 6A). Thus, in a typical trial, participants looked directly at the target, though some trials involved looking at both the target and non-target circles once, and some involved multiple landings on each circle. This overall efficient pattern of unconstrained saccades is consistent with previous studies demonstrating that saccades are made purposefully in both humans and monkeys (e.g., Rothkopf, Ballard, & Hayhoe, 2007; Song & McPeek, 2009).

Figure 6A compares the number of saccades made per trial as a function of target size between the two illusion conditions. There was no significant difference between the perceptually *enlarged* (green bars) and perceptually *reduced* (blue bars) illusion conditions, $F(1,13) = 1.49$, $p = .243$, $\eta_p^2 = .103$, though significantly fewer saccades were made as image size increased from 10mm to 40mm, $F(3,39) = 13.52$, $p < .001$, $\eta_p^2 = .510$. There was no interaction effect, $F(3,39) = .255$, $p = .857$, $\eta_p^2 = .019$. In Figure 6B, similarly, we compared the number of saccades made until the target was acquired. We demonstrated that the larger the illusory size ($F(1,13) = 16.50$, $p < .001$, $\eta_p^2 = .559$), or image size ($F(3,39) = 5.08$, $p = .005$, $\eta_p^2 = .281$), the fewer saccades were needed to hit the target. There was no interaction between illusory and image sizes, $F(3,39) = 2.01$, $p = .129$, $\eta_p^2 = .134$. This suggests that as illusory or image target size increases, participants more efficiently land their eyes on the target with fewer saccades.

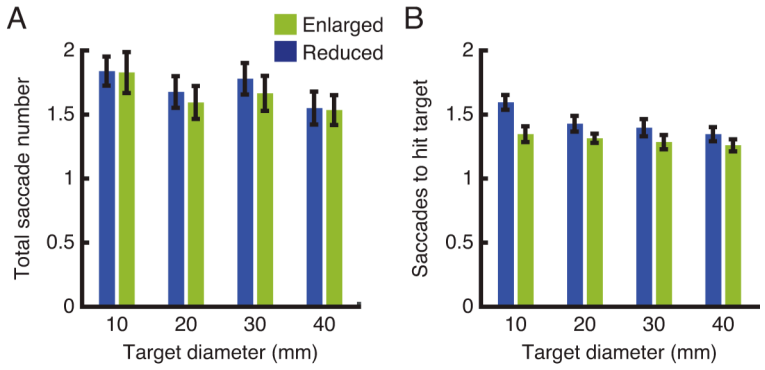

Figure 6 Patterns of free saccadic eye movements performed in coordination with pointing (Exp. 2). All errorbars represent between-subjects standard error. **A.** Total saccade number. Overall more free saccadic eye movements were made per trial when target images sizes were smaller, but not when they appeared smaller based on the illusion. **B.** Saccades necessary to hit target. The number of free eye movements performed leading up to and ultimately landing on the target was greater when image size or illusory size was smaller.

Preparation of target saccade. We examined how perceptual illusion affects freely coordinated eye movements towards a pointing target by comparing the target saccade initiation latency (TIL) (see Methods) across conditions. As shown in Figure 7A, TIL was faster in the perceptually *enlarged* (green) than in the perceptually *reduced* (blue) conditions. Similarly, TILs were faster the larger the target image size. These observations were supported by a 2x4 repeated-measures ANOVA which showed a significant main effect for illusion condition $F(1,13) = 34.29$, $p < .001$, $\eta_p^2 = .725$ and target image size $F(3,39) = 3.57$, $p = .022$, $\eta_p^2 = .216$, and no interaction, $F(3,39) = .754$, $p = .527$, $\eta_p^2 = .055$. Thus, the movement preparation of unconstrained saccadic eye movements that were coordinated with pointing movements was modulated both by the illusory and image sizes of targets. This is consistent with the pattern of illusion's influence on the initiation latency of separate

goal-directed saccades seen in Exp. 1 (Figure 3A), though these two indices are not identical.

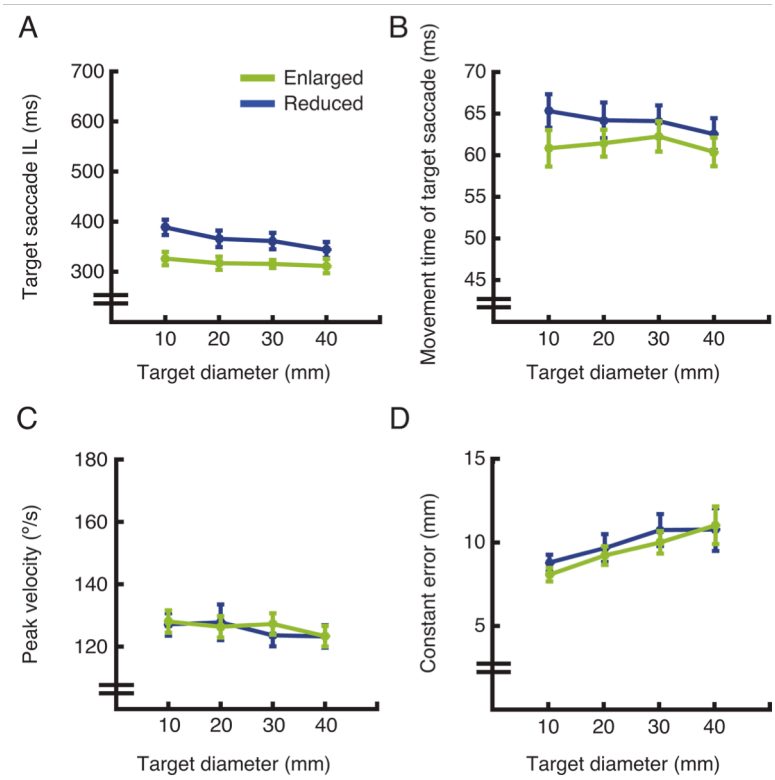

Figure 7 Free saccadic eye movement measures when performed in coordination with pointing (Exp. 2). All errorbars represent between-subjects standard error. **A.** Target saccade initiation latency. The latency to the onset of the target saccade was faster when targets were either perceived as larger due to the illusion, or had larger image sizes. **B.** Saccade total movement time. Total MT was faster when target illusory size or image size was larger. **C.** Saccade peak velocity. The peak velocity reached over the course of the movements was faster when image sizes were larger, but not when targets were perceived as larger due to the illusion; however there was an interaction between illusory and image size. **D.** Saccade constant error. The distance between the landing position and target center is larger for the perceptually smaller than the perceptually larger targets, but no difference was seen based on image size.

Execution of target saccade As seen in Figure 7B, target saccade movement time was faster for perceptually *enlarged* compared to perceptually *reduced* targets, and for larger compared to smaller image sizes. This was supported by an ANOVA

showing a main effect of illusory size, $F(1,13) = 27.39$, $p < .001$, $\eta_p^2 = .678$, a main effect of image size $F(3,39) = 3.83$, $p = .017$, $\eta_p^2 = .227$, and no interaction, $F(3,39) = 1.53$, $p = .221$, $\eta_p^2 = .106$. Thus, the execution of unconstrained target saccades was modulated by both illusory and image size. Overall then, the execution of unconstrained saccades (Exp. 2) differed from that of constrained goal-directed saccades (Exp. 1) in that here saccade execution was influenced by the image and illusory sizes of targets, as opposed to image size alone.

As seen in Figure 7C, we found no difference in peak velocity based on illusory size, $F(1,13) = 1.34$, $p = .268$, $\eta_p^2 = .093$, a marginally significant effect of target image size $F(3,39) = 2.81$, $p = .052$, $\eta_p^2 = .178$, and no interaction, $F(3,39) = 1.40$, $p = .259$, $\eta_p^2 = .097$, suggesting that saccadic eye movements, like hand movements, were faster for larger image but not illusory target sizes.

Finally, as seen in figure 7D larger image sizes resulted in larger constant errors, with no difference based on illusory size. An ANOVA revealed no main effect of illusion condition $F(1,13) = .392$, $p = .542$, $\eta_p^2 = .029$, a main effect of image size $F(3,39) = 5.80$, $p = .002$, $\eta_p^2 = .309$, and no interaction $F(3,39) = .456$, $p = .715$, $\eta_p^2 = .034$. However, overall there was no clear systematic pattern of illusory or image size modulating landing position across experiments and effectors.

Uncorrelated illusion modulation for coordinated pointing and saccades.

Unlike in Exp. 1 where both pointing and saccade movement preparation (initiation latency) were modulated by illusion, in Exp. 2 illusory size modulated the initiation latency measure for saccades but not for pointing. Nevertheless, as in Exp. 1

(Fig. 4) we calculated an illusion index as a measure of the influence of the illusion on each movement preparation measure. Because unconstrained eye movements were allowed in Exp. 2, in Eq. (1), we replaced Illusion Index_{IL} with Illusion Index_{TIL} using target saccade initiation latency (TIL) (see Methods) to estimate the effect of illusion on saccadic preparation.

$$\text{Illusion index}_{TIL} = \frac{\text{Mean TIL}_{reduced} - \text{Mean TIL}_{enlarged}}{\text{Mean TIL}_{reduced} + \text{Mean TIL}_{enlarged}} \qquad \text{Eq (3)}$$

Illusion Index_{MT} was calculated as in Exp. 1 (Eq. 2). Thus, we were able to compare how the illusion affected eye and hand movements when they are freely coordinated, as we did for independent movements in Exp. 1.

As anticipated given that there was only a measurable effect of illusion on saccade preparation and not pointing preparation, there was no significant correlation between the Illusion Index_{TIL} (Eq. 3) for saccades and Illusion Index_{IL} (Eq. 1) for pointing ($r = .29$, $p = .31$), as seen in Figure 8A. However, as in Figure 4A, we again used a unity line to indicate equal illusion index for both pointing and saccades. As in Exp. 1, we found that the illusion influenced the saccade task far more than pointing, resulting in higher illusion indices across subjects, and the data falling below unity on average. This was supported by a paired t-test which showed significantly higher illusion index values for saccades than for pointing across subjects $t(13) = 4.98$, $p < .001$, $d = 1.33$.

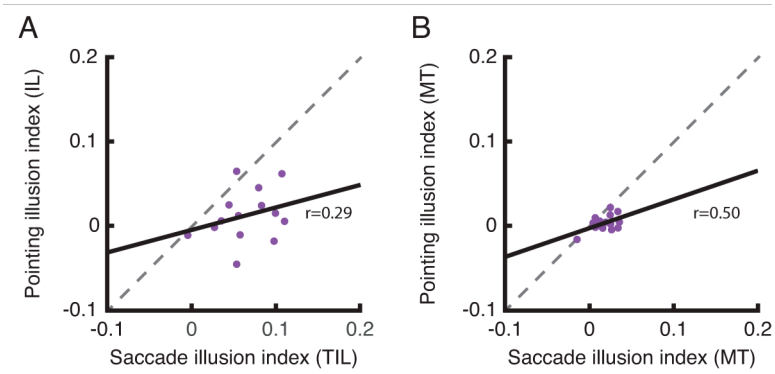

Figure 8 Correlations between illusion impact on coordinated pointing and saccades (Exp. 2) **A.** Correlation in illusion's impact on initiation latency. There was no relation between the influence of illusion on coordinated pointing and saccadic initiation latency. **B.** Correlation in illusion's impact on movement time. There was no relation between the influence of illusion on coordinated pointing and saccadic initiation latency.

As shown in Figure 8B, there was no correlation between Illusion Index$_{MT}$ for pointing and saccades (r = .50, p = .07), again, not surprisingly given that a significant illusion modulation was seen only for saccade and not for pointing execution. However, in contrast to the MT correlation in Exp. 1, here there was a shift below unity, indicating that saccadic MT was significantly more impacted by the illusion than pointing MT $t(13) = 4.79$, $p < .001$, $d = 1.28$.

Thus, when eye and hand movements are naturally coordinated as in Exp. 2, the illusion no longer influences both in the same way, resulting in the lack of an illusion index correlation. Instead, the illusion impacts saccades exclusively. Unlike for isolated saccades, this influence is seen both for preparation and execution. Furthermore, unconstrained eye movements display greater overall illusion modulation compared to constrained eye movements, and to hand movements overall.

Stronger illusion modulation for saccades than for pointing preparation in both separate and coordinated eye and hand movements.

Given the overall stronger effect of illusion on saccade compared to pointing movement preparation, and the different patterns of illusion influence seen in Exp. 1 and Exp. 2, we compared the illusion indices for movement preparation between hand and eye movements in both Exps. 1 and 2. Figure 9 shows the mean Illusion $Index_{IL}$ and Illusion $Index_{TIL}$ (i.e. the degree to which illusion modulated movement preparation) for both effectors and experiments. Again, the pointing task was identical in Exps. 1 and 2. The saccades performed in Exp. 1 were goal-directed like the pointing movements in both experiments, and independent like the pointing movements in Exp. 1. In contrast, the saccades performed in Exp. 2 were naturalistic and performed in coordination with the pointing movements. Thus, the illusion indices for each type of saccadic eye movements are not identical, but are parallel in their measures of the influence of illusion on the preparation of each respective saccade type.

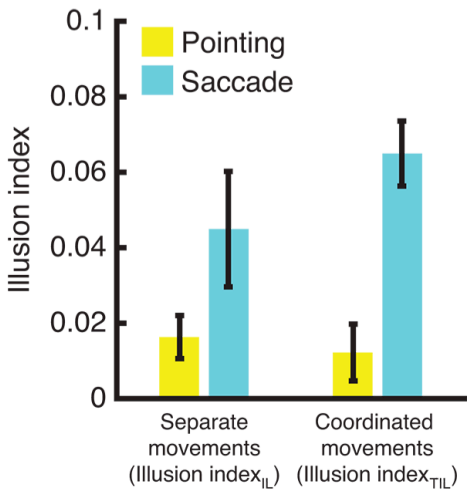

Figure 9 Relative illusion impacts on movement preparation between task conditions and effectors. All errorbars represent between-subjects standard error. Saccadic initiation latencies were overall more influenced by illusion than pointing initiation latencies. Overall, coordinated movement ILs (Exp. 2) were more influenced by illusion than separate movement ILs (Exp. 1), primarily due to the larger illusion index for free saccades coordinated with pointing in Exp. 2. The difference between saccade and pointing illusion index was more pronounced for coordinated movements (Exp. 2) than when movements were separate (Exp. 1).

In both experiments, saccadic preparation showed larger illusion indices than pointing movements, with Exp. 2 showing this effect more strongly than Exp. 1. A 2x2 ANOVA with a within-subjects factor of movement effector (saccade vs. pointing), and a between-subjects factor of experiment (Exp. 1 vs. Exp. 2) revealed a significant main effect of effector, $F(1,26) = 10.60$, $p < .001$, $\eta_p^2 = .290$, and a significant main effect of experiment $F(1,26) = 4.70$, $p = .040$, $\eta_p^2 = .153$. This suggests that eye movements are overall more susceptible to the illusion than pointing movements, and that modulation by illusion was higher overall in Exp. 2 than in Exp. 1. This effect of experiment is driven by the increase in saccade illusion index across the two experiments; there is no difference in pointing illusion index between Exp. 1 and Exp. 2. Thus, the difference between pointing and saccades in terms of

susceptibility to illusion appears to be more robust with coordinated, naturalistic movements (Exp. 2) compared to independent (Exp. 1) eye and hand movements. This observation is supported by a marginally significant interaction effect between effector and experiment, $F(1,26) = 3.90$, $p = .059$, $\eta_p^2 = .130$.

Summary

Taken together, in Exp. 2, we showed that both the image and illusory sizes of targets affected when saccades were initiated towards the target (movement preparation) and the duration of target saccades (movement execution). In contrast, only image size modulated pointing initiation latency and movement time. This is in contrast with the pattern seen in Exp. 1, where both pointing and saccade *preparation* were modulated by both illusory and image size, and both saccade and pointing *execution* were modulated by image size only. Overall then we observe that coordinating eye and hand movements changes their behavior compared to isolated pointing and saccades, and that the two effectors do not respond in the same way to illusion when they are coordinated. Furthermore, as in Exp. 1 we found that saccades overall were more susceptible to illusion modulation than pointing, with this modulation even stronger for the saccades accompanying pointing movements (Exp. 2) than isolated saccades (Exp. 1). These differences could reflect inherent differences between isolated versus coordinated naturalistic hand and eye movements, as well as inherent differences between pointing and saccades.

Discussion

In the present study we dissociated the illusory and image sizes of visual stimuli using a variation of the Ponzo illusion, and investigated the resulting impact on separate pointing and saccadic eye movements and the coordination between the two. We observed that when pointing and saccades were generated separately, image size consistently modulated movement preparation, measured by initiation latency, and movement execution, measured by movement time, for both effectors. However, for both effectors illusory size affected primarily *movement preparation* and not *movement execution* measures, with some illusion modulation also observed in pointing constant error. We also showed that although the impact of illusion on the preparation of independent saccades and pointing movements was positively correlated, the magnitude of illusory size modulation was much larger for saccades than for pointing.

Furthermore, we also demonstrated that performing naturally coordinated eye-hand movements altered the weights of the information used for each effector. Specifically, while target image size continuously modulated movement time for both effectors, illusory target size modulated the initiation latency and movement time of saccades only. Thus, even if the same pointing movements were planned and executed towards identical visual targets, whether or not the movements were accompanied by unconstrained saccades influenced the effect of the illusion on pointing movement preparation. As a result, during natural eye-hand coordination, illusory object size modulated saccades much more strongly than pointing, to an even larger degree than seen when the two movements were independent. Taken together,

these results provide a picture of how various visual representations continuously guide goal-directed actions in natural environments.

Common influence of perceived illusory size on target selection for saccades and pointing

When saccade and pointing movements were performed individually, we observed that those participants who showed more influence of illusion on pointing preparation also showed more influence of illusion on saccade preparation (Fig. 4A). Thus, the impact of illusion on movement preparation was correlated between pointing and saccadic eye movements, though the impact of image size on the two effectors was not. Additionally, there was no relation between the illusion's impact on pointing and saccadic *execution* as opposed to *preparation* (Fig. 4B). These results suggest that despite the fact that low-level motor-related metrics must be computed and implemented by separate brain network for the two effectors (Andersen, Snyder, Bradley, & Xing, 1997; Schall, 1995), a common process involved in the motor *preparation* for both eye and hand movements (e.g. target selection) could be affected by representations of illusory sizes.

Prior work in both humans and non-human primates has demonstrated common target selection characteristics for saccades and pointing movements (Song, Rafal, & McPeek, 2011; Song & McPeek, 2015). For instance, in visual search, as the number of distractors increases, target selection is facilitated for saccades (Arai & Keller, 2005; McPeek & Keller, 2001; McPeek, Maljkovic, & Nakayama, 1999; McSorley & Findlay, 2003) as well as for pointing movements (Song & Nakayama

2006, 2008). Furthermore, the effects of color priming such as faster target selection when the target color is repeated on consecutive trials as opposed to switched, have been commonly reported for both saccades (N P Bichot & Schall, 1999; Narcisse P Bichot & Schall, 2002; McPeek & Keller, 2001; McPeek et al., 1999) and pointing (Song & Nakayama, 2006; Moher & Song, 2013). Song and McPeek (2009) also showed that, during coordinated eye and hand movements, target selection for pointing and saccades was highly correlated, with hand and eye movements landing near the same stimulus both for correct reaches to the target and for incorrect reaches to a distractor. In addition, Moher and Song (2016) recently reported a direct transfer in facilitation of target selection by color priming and suppression by distractor previewing across saccades and pointing, further supporting a shared target selection mechanism for the two effectors.

Although the aforementioned behavioral studies are consistent with a shared target selection mechanism, they do not completely rule out the possibility that two separate but parallel target selection processes could exist (Sailer, Eggert, Ditterich, & Straube, 2002). However, recent temporary focal inactivation and single-unit recordings in non-human primates support the existence of a shared neural mechanism for target selection in eye and arm movements (Mcpeek & Keller, 2014; Song et al., 2011; Song & McPeek, 2015). Song et al. (2011) recently found that the superior colliculus (SC), which lies near the output of the saccadic eye movement system, plays a causal role in target selection during reaching tasks. Specifically, this study demonstrated that temporary focal inactivation of the SC causes monkeys to be biased against selecting a reaching target located in the inactivated part of the visual

field, and that this effect cannot be explained as a simple visual or motor impairment. This result supports the idea that the SC is part of a general-purpose, as opposed to effector-specific, target selection system (Nummela & Krauzlis 2010; Song et al. 2011). In a subsequent single-unit recording study, Song & McPeek (2015) further confirmed that the majority of intermediate-layer SC cells discriminate a reach target from distractors, consistent with the idea that the SC contains a priority map used for effector-independent target selection.

Based on the common behavioral characteristics and neural underpinnings of target selection for saccades and pointing, we speculate that visual illusions might affect the target selection process for both effectors, resulting in the correlated modulation of movement preparation based on illusory size for saccade and pointing movements.

Dominant illusion modulation for saccade over pointing preparation

While we found in Exp. 1 that the impact of illusory size on initiation latency for separate saccades and pointing was correlated, illusion much more strongly modulated saccade preparation compared to pointing preparation. Furthermore, we demonstrated that during natural eye-hand coordination, saccade preparation became *more* affected by the illusory target size, while pointing preparation became *less* affected by it. Though the current study is not sufficient to determine at what point in time the cognitive processes for saccadic and manual target selection differ, this discrepancy in the degree of illusion modulation between the two is noteworthy. This difference could be because target selection during coordinated actions is typically

dominated by saccades as has been demonstrated in both humans and non-human primates (e.g. Bekkering & Neggers, 2002; Frens & Erkelens, 1991; Horstmann & Hoffmann, 2005; Johansson, Westling, Backstrom, & Flanagan, 2001; Land & Hayhoe, 2001; Land & McLeod, 2000; S. F. Neggers & Bekkering, 2000; S. F. W. Neggers & Bekkering, 2001; Scherberger, Goodale, Andersen, Goodale, & Richard, 2003; Soechting, Engel, & Flanders, 2001; Zelinsky, Rao, Hayhoe, & Ballard, 1997). Furthermore, the same is also true for attention allocation in the preparation of eye and hand movements. For instance, Khan, Song, and McPeek (2011) showed that perceptual discrimination performance was consistently better for an eye goal than a corresponding hand goal, suggesting that shared attentional resources are allocated predominantly to the eyes. Thus, we conjecture that eye and hand movement preparation—specifically target selection—may rely on the same mechanism, but that this mechanism may be allocated preferentially to eye movements.

Because the current study relied on closed-loop control of movement execution, we could not fully evaluate the extent to which the greater illusion effect seen in saccades compared to pointing might be explained by greater online visual feedback available for the latter compared to the former. Indeed, it has been shown that continuous vision of the hand over the course of a movement can influence the degree of illusion modulation on action (e.g. Bartelt & Darling, 2002; Binsted & Elliott, 1999; A. Bruno & Morrone, 2007; V.H. Franz, Hesse, & Kollath, 2009; Haffenden & Goodale, 1998; Pavani, Boscagli, Benvenuti, Rabuffetti, & Farnè, 1999; Van Donkelaar, 1999). For instance, Binsted & Elliott (1999) demonstrated that while the Müller–Lyer illusion consistently modulated saccadic amplitude, a pointing bias

only occurred in trials with concurrent eye movements and the elimination of retinal target information on pointing movement initiation. Franz et al. (2009) also reported that reduced effects of visual illusions on hand movements could often be attributed to corrections based on online visual feedback.

Yet, it is worth noting that our result can not be fully explained by the presence of visual feedback for pointing or a lack of feedback for saccades. For instance, we observed an increased modulation by the illusion on saccades and reduced modulation on pointing when unconstrained eye movements were allowed, making longer visual feedback available for both effectors. In addition, in accord with a prior study demonstrating that saccades respect Fitts' Law when secondary corrective saccades are considered (Wu et al., 2010), we included corrective saccades to evaluate the impact of illusory size, allowing some extent of correction, for saccades analogous to the correction available for pointing.

Relation to prior work on the dual visual stream hypothesis for perception and action

There is an extensive literature regarding the existence of two parallel, independent cortical streams for the visual processes that allow us to make sense of the world, and those that facilitate interaction with it (Goodale & Milner, 1992; Milner & Goodale, 1995, 2008; Mishkin, Ungerleider, & Macko, 1983). Studies of neuropsychological patients support the division of the visual system into separate pathways for processing visual perception/identification (the "what" pathway) in the ventral stream, and spatial-motor action (the "how" pathway) in the dorsal stream (Goodale & Milner, 1992; Milner & Goodale, 1995). Patients with ventral lesions,

such as cortically blind patients (Stoerig & Cowey, 1997) and DF, an apperceptive agnosic (Goodale & Milner, 1992; Milner & Goodale, 1995), can still perform appropriate motor actions such as reaching and grasping for objects, even when they cannot see or recognize them. A recent neuroimaging study has also confirmed that DF's intact visually guided grasping is accompanied by robust brain activation in the anterior part of the intraparietal sulcus (hAIP) in the dorsal stream, as in healthy participants (James, Culham, Humphrey, Milner, & Goodale, 2003).

For decades, behavioral studies in healthy normal participants have also evaluated whether vision for perception and vision for action are dissociated using size contrast illusions. Since the pioneering work of Aglioti et al. (1995) providing converging evidence for perception-action dissociation, many other studies have shown evidence for action's immunity to illusion (Ganel et al., 2008; A M Haffenden & Goodale, 1998; Angela M. Haffenden, Schiff, & Goodale, 2001; McCarley et al., 2003; Shmuelof & Zohary, 2005).

In Aglioti et al. (1995) and number of these other studies, hand movements (typically grasping) have typically been performed in the presence of natural eye movements which are used to compare the hand performing the action to the visual stimuli. Our results showed that when eye and hand movements were performed simultaneously, hand movements became completely independent of illusion. This appears to be consistent with prior studies on grasping, and the resulting perception-action dissociation model (for review, see Goodale, 2014). However, we observed a significant impact of illusion on the saccades performed in coordination with these hand movements—a measure absent in the majority of perception/action studies.

Furthermore, this effect was not seen for independently performed saccades, or for independent pointing movements. Thus, when hand movements are performed in the presence of naturalistic eye movements, we speculate that the illusion effect dominates in the unmeasured eye movements, with hand movements showing less modulation as seen in Exp. 2. Therefore, we speculate that the degree to which perceived object size modulates goal-directed actions could be altered by task demands, particularly in terms of the relative degree of separation or naturalistic coordination across effectors.

However, it is also worth noting that the characteristics of aiming movements such as pointing differ from grasping, which could also contribute to the differences between our results and those from prior grasping studies that support a perception/action dissociation (e.g. Aglioti at al. 1995, Ganel et al., 2008). For example, Carnahan, Goodale, & Marteniuk (1993) showed that when changes in target position were introduced, amending movements occurred much earlier for grasping compared to pointing movements, suggesting the differential use of online visual feedback between the two tasks. A difference in visual coding between pointing and grasping has been also observed in unilateral neglect patients: the degree of neglect was attenuated when grasping rather than pointing was required (Edwards & Humphreys, 1999; Robertson, Nico, & Hood, 1995). Furthermore, Tang, Whitwell, & Goodale (2015) directly examined the equivalence between pointing to targets and grasping them, by measuring the carry-over effect between these two tasks. This study took advantage of the well-established effect that during a reach-to-grasp movement, when vision is not available (visual open loop) participants show a larger

peak grip aperture compared to when vision is available throughout the movement (visual closed loop) (for review see Fukui, Takemura, & Inui, 2006; Smeets & Brenner, 1999). Tang et al. (2015) demonstrated that the difference in peak grip aperture between closed- and open-loop trials was smaller when these trials were intermixed ('homogenization'). However, this carry-over effect of homogenization did not occur when an open-loop pointing movement was alternated with a closed-loop grasping movement (or vice versa). Thus, the authors suggest that pointing and grasping are not equivalent and result in separate motor or sensorimotor memory traces.

In addition, functional specialization in the brain for pointing and grasping has been demonstrated (for review, Filimon, 2010). For example, fMRI and PET studies showed stronger activation in the anterior intraparietal sulcus (aIPS) for grasping than pointing (Culham et al., 2003; Grafton, Arbib, Fadiga, & Rizzolatti, 1996) and TMS to aIPS also disrupted grasping but not pointing (Rice, Tunik, & Grafton, 2006). Therefore, future studies investigating the relation between hand and eye movements might further consider the specific characteristics of distinct forms of action such as pointing, grasping, and other hand/arm movements.

Dynamic influence of illusory size on the planning and control of actions

In addition to the perception-action dissociation model (for review, see Goodale, 2014), a series of alternative models examining the effects of illusions on action have also emerged over time. For instance, some have proposed that a common visual representation is used for perception and action, based on observations that

grasp aperture *can* be adjusted to the illusory sizes of objects rather than their veridical image sizes in contrast with a strict interpretation of the perception-action dissociation (Franz, Fahle, Bulthoff, & Gegenfurtner, 2001; Franz, Gegenfurtner, Bülthoff, & Fahle, 2000; Pavani et al., 1999). Furthermore, multiple studies have shown that measures other than grasp aperture are susceptible to visual illusion, such as movement amplitude (de Grave, Brenner, and Smeets, 2004), or how the object is lifted or gripped (Brenner & Smeets, 1996; Jackson & Shaw, 2000). Several studies have shown that both saccadic and pointing movements are susceptible to the Müller-Lyer illusion such that when lines are perceived as longer, movements to their perceived endpoints have longer amplitudes (for review, Bruno et al., 2010). Thus, it is argued, illusory perception does have an effect on some aspects of action.

Glover and colleagues (Glover, 2004; Glover & Dixon, 2001, 2002) proposed another model, which posits that illusions induced by objects' contexts affect only the planning, and not the control of actions. This planning-control model predicts that perceptual errors associated with movement planning will be corrected during the execution phase of a movement. On the surface, our results demonstrating an impact of illusion on initiation latency but not movement time seem to support this. However, multiple studies have found contradictory results. van Donkelaar and colleagues (Lee & van Donkelaar, 2001; van Donkelaar, 1999), though they did not measure movement preparation, did find that movement time was affected by the illusory sizes of targets in the Ebbinghaus illusion. Furthermore, Handlovsky, Hansen, Lee, & Elliott (2004) demonstrated that participants' aiming was affected more by target configuration when it was visible during movement execution than

when it was visible during movement planning. (Meegan, Glazebrook, Dhillon, Tremblay, Welsh, and Elliott (2004) found that illusion affected both the planning and the control of the pointing movements within the Müller-Lyer illusion such that movement amplitude was impacted by the illusion, particularly when pointing was performed without vision of the hand.

We speculate that these seemingly contradictory results might be driven by multiple factors that shift the relative contribution of planning and control along a continuum between the two. Therefore, as the reliance on preparation as opposed to execution mechanisms increases, given that preparation is more susceptible to illusion as shown in the present study, illusory modulation of goal-directed action would correspondingly increase. For instance in open-loop paradigms, where participants must necessarily rely on planning mechanisms in the absence of online vision of the hand during control, an influence of illusion could manifest in control/execution measures as well (e.g. Bartelt & Darling 2002; Bruno et al. 2007; Haffenden & Goodale, 1998; Pavani et al., 1999). Similarly, in rapid pointing and saccade tasks where movements are more ballistic, the movement amplitudes and end points may rely on preparation mechanisms more so than movements that have the opportunity to be corrected on-line, particularly in pointing movements when subjects are deprived of visual feedback of the hand. This, we conjecture, could explain the influence of illusion on action seen in a number of studies (e.g. Binsted & Elliott, 1999; Franz et al., 2008; Meegan et al., 2004).

Conclusions

By examining the modulation of illusion during the preparation and execution of both separately and simultaneously generated saccade and pointing movements, the present study can contribute to a more complete picture of how illusion modulation dynamically changes across the phases of goal-directed actions (planning vs. execution), effectors (eye vs. hand), and the nature of the movements (separate vs. coordinated). Direct comparisons between isolated eye and hand movements may suggest a common mechanism for the preparation of visually-guided actions shared across effectors, and such a mechanism may be responsible when illusion modulates visually-guided action. Though we conjecture that this mechanism modulates hand and eye movements in a similar manner when each is performed in isolation, when the two are coordinated saccades show increased modulation by the illusion while hand movements show decreased modulation. This suggests that the mechanism impacted by illusion might favor the eyes over the hands. Thus, these results could reconcile discrepancies within the perception and action literature.

Specifically, the present study sheds light on two potential causes of disagreements between studies on the relation between the representations used for perception and action. If movement preparation and execution do consistently behave differently in their responses to illusion—the former showing modulation based on illusory size and the latter showing none—the relative degree of preparation versus execution mechanisms in the measure used could account for differences in perception-action dissociation across studies. Similarly, the presence or absence of free saccadic eye movements alongside hand movements such as grasping may

influence the degree to which the illusion is reflected in the hand-based measure of "action," if the extant influence of illusion is expressed preferentially in the eye movements. The current study alone is insufficient to provide conclusive evidence regarding a singular cause for the influence of illusion on action, or its on underlying mechanisms. Further investigations are needed to identify the mechanism or mechanisms responsible for the influence of perceptual illusion on movement preparation, and how it may modulate other forms of visually guided action.

Chapter 2:

Modulation of visually-guided action by the image and familiar sizes of real-world objects

In daily life, the size of objects in our environment is critical to how we interact with them. Here we investigated two aspects of real-world object size perception: *image size* is the size an object appears visually, and *familiar size* is the size we know objects are in the real world based on past experience. Typically in the real world these features and their processing is confounded. However, by manipulating the relationship between the two we can disentangle how each is processed, and furthermore how they modulate action. Here, we manipulated image and familiar size in displays of paired real-world objects. Paired objects were presented with both congruent and incongruent size arrangements (e.g. a rubber duck presented as smaller and larger than a boat, respectively). Participants were instructed to reach to touch selected objects based on image size in one task, and familiar size in another.

We observed that when pointing to target objects in the *incongruent* conditions, participants' movements were slower and were more curved towards the incorrect object (e.g. a rubber duck presented with a larger *image size* when the task is to choose the object with a larger *familiar size*). Both image size and familiar size influenced action in this way even when task-irrelevant, indicating that both are processed automatically (Konkle & Oliva, 2012a). Image size however showed

influence earlier in the course of movements and more robustly overall than familiar size.

We additionally found that the greater the familiar size difference between paired objects, the *less* image size interfered in the familiar size task. Similarly, the greater the familiar size difference, the *more* familiar size interfered in the image size task. Thus, greater relative familiar size differences led to more robust processing of familiar size. Overall, our data suggest that image and familiar size perception interact both with each other and with visually-guided action, but that the relative contributions of each are unequal and vary based on task demands.

Introduction

In 2007 an art installation appeared floating in the harbor of Saint-Nazaire, a small town in Western France. "Rubber Duck" by Florentijn Hofman quickly gained international recognition due to the unexpected scene created by a toy that typically measures 5.5 cm in height dwarfing nearby boats at 32 m. The *familiar size* of a rubber duck, the size that we know it typically would be based on past experience, and the *image size* of "Rubber Duck," the size the piece appeared visually to viewers, were dramatically in conflict.

In normal daily life, objects' *familiar size* and *image size* are highly correlated. When presented in the same context, real-world objects like rubber ducks that we know to be relatively small in the real world typically appear smaller than objects like boats which we know to be larger. Even when the sizes of objects on the retina vary, they are integrated with their environment via size constancy

mechanisms. Thus, given size constancy into account, in the real world the two are very rarely in conflict, and their processing is highly confounded—when we see an object and its image size and familiar size are congruent, how each factor affects us is difficult to disambiguate.

Attempts have recently been made to disentangle image size and familiar size perception. Konkle & Oliva (2012a) demonstrated that incongruence between familiar size and image size (e.g. a rubber duck presented with a larger image size than a boat) results in a "familiar size Stroop effect," impairing performance on an image size judgment task. This combined with evidence for familiar size representations in temporoparietal cortex from functional MRI suggests that these two highly different aspects of real-world object size, *image* size and *familiar* size, are both processed automatically, and with distinct neural representations (Konkle & Oliva, 2011, 2012c).

However, despite disambiguating the two to some degree, this study only examined the unidirectional influence of familiar size on image size, as opposed to the bidirectional influence of each on the other. Furthermore, binary categories were used for large and small image sizes, and large and small familiar sizes, though both exist on a continuum in the real world. Therefore, the relative contributions of each type of object size on perception, and other visual processes, bear further investigation.

The size of objects is a key component of vision for *action* in addition to vision for *perception,* as size constrains how we interact with the objects in our environment. For example, image size modulates the speed of goal-directed pointing

movements (Fitts, 1954b), and grip aperture scales to the physical sizes of objects (Jeannerod, 1984). However, less is known about how aspects of object size other than image size influence action. Image size is a low-level visual feature—it is represented retinally and in V1, one of the earliest visual processing regions (Murray, Boyaci, & Kersten, 2006). In contrast, familiar size is a high-level visual feature requiring object identification and the recruitment of memory, and is represented in a later visual processing region in the temporoparietal cortex (Konkle & Oliva, 2012c).

Though conflict between image and familiar size was demonstrated in the aforementioned paper using a discrete behavioral response paradigm, it is not known how action would respond to conflict between the two, again given that such scenarios are highly uncommon in the real world. It has been shown that discrete behavioral responses and action measures can produce different results for the same perceptual decision-making task. For example low salience distractors influence button-press tasks *less* than high salience distractors, but influence action *more* than high salience distractors, potentially due to response suppression mechanisms in the action measure that do not exist for discrete behavioral responses (Jeff Moher et al., 2015). Furthermore, the continuous nature of visually-guided action measures has been shown to reveal a wealth of information about underlying cognitive processes. Because decision-making processes often unfold over the course of a movement, the timing and curvature of movement trajectories can reflect multiple aspects of the conflict between potential targets (Erb, Moher, Sobel, & Song, 2016; McKinstry, Dale, & Spivey, 2008; Song, 2017; Song & Nakayama, 2009). Such a methodology

can therefore provide insight into the timing of both image size and familiar size, and the conflict these perceptual features.

Overall, gaps in the literature we seek to address in the present study are the influence of the higher-level visual feature of familiar size on action, how it compares to the influence of the lower-level visual feature of image size on action, and what further insight online continuous action measures can provide into the conflict between the two. In order to address these questions, we employed a similar paradigm to Konkle & Oliva's 2012 study, with the addition of A) a familiar size judgment task in which image size was the conflicting task-irrelevant feature, B) parametrically varied familiar object sizes and C) action as opposed to discrete behavioral responses.

In Experiment 1 we sought to investigate the relative magnitude and timing of *image* size, *familiar* size, and their influences on pointing movements. In this experiment, we found evidence that image size exerts a stronger influence than familiar size, and we therefore sought to examine how different familiar size magnitudes might strengthen or weaken this effect. Thus, in Experiment 2 we systematically varied the magnitude of the familiar size differences in object pairs to investigate dynamic interactions between image and familiar size.

Experiment 1: Congruency between target image and familiar size in visually-guided action

Methods

Participants

Thirteen right-handed participants (8 women; mean age 25.7 years) with normal color vision, and normal or corrected-to-normal visual acuity completed both tasks within Experiment 1. The experimental protocol was approved by the Brown University Institutional Review Board in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki) for experiments involving humans. Participants were compensated monetarily ($10 per hour) or with course credit.

Apparatus

Stimuli were presented on an upright Plexiglas display facing the seated participant at a distance of approximately 55 cm. A projector behind the display projected a screen measuring 44.1 × 33.0 cm (43.7º × 33.4º visual angle), which participants viewed binocularly. Stimulus presentation was conducted using custom software designed with MATLAB (MathWorks, Natick, MA) and Psychtoolbox (Brainard, 1997). Three-dimensional hand position was recorded with an electromagnetic position and orientation recording system (Liberty; Polhemus, Colchester, VT) at a rate of 160 Hz with a measuring error of 0.3 mm root mean square. A motion-tracking marker was fastened to the tip of each participant's right

index finger using a Velcro strap. A foam starting block placed 27 cm in front of the participant, between the participant and the display, served as the starting position on which the index finger rested at the beginning of each trial.

Stimuli

Stimuli were adapted from Konkle & Oliva's "Object Size Stroop" database (Konkle & Oliva, 2012b). All stimuli were presented on a white background. A black fixation cross, measuring 7 × 7 mm (0.73° of visual angle) appeared at the center of the screen before each trial. As shown in Figure 1A two real world objects were displayed, one to each side of fixation (5.6 cm or 5.8º measured from fixation to target center). Sixteen unique object pairs were used each for the image size and familiar size tasks, and two unique object pairs used for the practice blocks. Thus, 34 total object pairs were used, with each object being assigned to only one other object. Example object pairs are shown in Figure 1B.

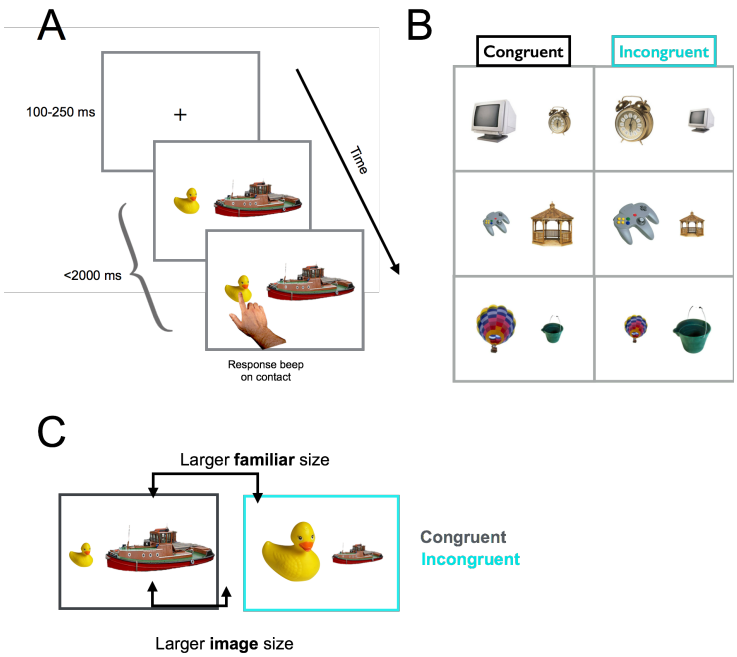

Figure 1. Representative figures and trial diagram. **A.** Trials began with hand and eye fixation for a variable period between 100 and 150 ms. Once stimuli were presented participants had up to 2000 ms to complete the hand movement indicating their choice. **B.** The objects' *image size* and *familiar size* could be presented as congruent (e.g the left image where the rubber duck has a smaller image size than a boat) or incongruent (e.g the right image where the rubber duck has a larger image size than a boat). Additionally, objects were counterbalanced such that the larger and smaller image size and familiar sizes were presented in both left and right positions. **C.** Examples of paired objects. The left column shows examples of incongruent conditions and the right side congruent conditions.

In each object pair, one object had a larger relative familiar size and the other a smaller relative familiar size (see Figure 1C). Familiar sizes of objects ranged from 3 cm (a die) to 8776 cm (a cathedral) diagonally, as reported by Konkle & Oliva (2012a). In every trial, one object was presented with a larger image size and one was presented with a smaller image size. Image sizes, as reported by Konkle and Oliza (2012a), were designed such that the objects with "small" image sizes were bounded by a rectangle with a diagonal equal to 17.5% of our screen height (5.8 cm or 6.0º) and objects with "large" image sizes were bounded by a rectangle with a diagonal

equal to 30% of our screen height (9.9 cm or 10.3º). This method was selected to account for the variations in real-world objects' aspect ratios (Konkle & Oliva, 2011, 2012b; Kosslyn, 1978).

In congruent trials, the object with the larger *familiar* size was presented with a larger *image* size and the object with the smaller *familiar* size was presented with a smaller *image* size. For example, in a congruent trial a rubber duck would be presented as 5.8 cm diagonally and a boat as 9.9 cm diagonally. In an incongruent trial, a rubber duck would be presented as 9.9 cm diagonally and a boat as 5.8 cm diagonally.

Procedure

Two blocks of each task (image or familiar size judgment) were performed in an ABBA order, with image and familiar size tasks assigned as A or B randomly. Task instructions appeared at the beginning of each block ("Make your selections based on the sizes you know the objects are in the real world" for the familiar size task, and ("Make your selections based on the sizes of the objects on the screen" for the image size task).

Each block was broken into two sequential sub-blocks, which each contained all trials with the same task instructions ("Choose the object that is larger/smaller"). For example, in an image size task block, for the first sub-block participants would select the object with the larger image size, and in the second sub-block, the object with the smaller image size. The order of these sub-blocks was randomly determined (i.e. large-small or small-large), and reversed in the second block of the relevant

experimental task (e.g. the first image size block would begin with selecting the object with the larger image size, and the second image size block would begin with selecting the object with the smaller image size.) In total each of the 32 experimental object pairs was repeated eight times (congruent x incongruent configurations, left x right presentation side and left x right side pointing target) for a total of 128 trials per experimental task.

At the beginning of each participant's session, nine-point calibration was conducted for the tracker. Participants also completed a practice block of 16 trials of the relevant size-judgment task before the first experimental block of that task. In both experimental tasks each trial began with an initial fixation cross presented for a variable amount of time (100–250 ms). This was followed by the presentation of the object pair. Participants were instructed to make their decisions as quickly and accurately as possible, by reaching out and touching the selected object on the screen. In both tasks, the display was presented for a maximum of 2000 ms. A feedback beep was played indicating that the correct object had been selected, the incorrect objects had been selected, or that the time limit had been reached. An example trial of the task is diagrammed in Figure 1b.

Data analysis

Data analysis procedures were largely adapted from methods reported in in our previous work (Gamble & Song, 2017; Jeff Moher & Song, 2013, 2014).

Using custom MATLAB (MathWorks) software, we conducted off-line data analysis on the pointing movement data. Movement velocity was calculated from the

3D position traces after filtering with a low-pass filter (cutoff frequency of 10 Hz). An algorithm using velocity criteria of 10 cm/s (10.4º/s) detected the beginning and end of pointing movements. The algorithm's identification of these movements was visually inspected to verify its accuracy for every trial (Gamble & Song, 2017; Jeff Moher et al., 2015; Jeff Moher & Song, 2013, 2014). Pointing movements were classified as correct responses if they landed within a standardized target boundary used for all targets (6 × 6 cm or 6.2º × 6.2º of visual angle). Movements landing within the nontarget object's boundaries were marked as incorrect.

Initiation latency (IL) was defined as the time elapsed between stimulus onset and pointing movement onset. *Movement time* (MT) was defined as the time elapsed between movement onset and movement offset/target landing. Maximum curvature was calculated by tracing the path of the hand, and calculating an ideal direct path between the movement's starting and end points. The perpendicular deviation of the hand position from the ideal path was calculated at every time point. The maximum deviation length divided by the length of the ideal path results in the unitless ratio, referred to as maximum curvature. Larger ratios thus represent a greater maximum deviation from the ideal path, and greater overall curvature in the movement's trajectory.

For each task and each measure we performed paired t-tests comparing congruent and incongruent trials within subjects. In order to compare the two tasks directly, we additionally performed 2x2 repeated measures ANOVAs with factors of congruency (congruent vs. incongruent) and task (image size vs. familiar size judgments) for each measure. We also report partial eta squared, with values of .2

indicating a small effect size, .5 indicating a medium effect size, and .8 indicating a large effect size (Cohen, 1973).

We additionally examined the temporal dynamics of the movement trajectories. In order to average and compare across trials, which naturally vary in length, we normalized all hand movements to 100 evenly spaced data points based on the distance of the hand from its starting point to the screen (the z-dimension). We then calculated the distance in cm of the participant's hand from its starting point in the x-dimension, at each normalized data point. Movements to the left and right sides of the screen were collapsed such that larger positive values indicate greater proximity to the correct target. We then calculated difference scores by subtracting these values for the incongruent from the congruent trials. Comparing this difference score to zero reveals at which points there was a significant difference in position between congruent and incongruent trials, indicating interference from the task-irrelevant feature (e.g. in the familiar size task difference scores significantly above zero indicate significant interference from image size). It is important to note that both the distance from the movement starting point and the difference score based on these distances are different measures than the aforementioned *maximum curvature* ratio used as an overall curvature measure for a given trial. More detail on this normalization and the subsequent analysis can be found in the appendix.

Results

We excluded 5.34% (± 1.09%) of trials from data analysis for the image size task and 5.19% (± 1.48%) for the familiar size task due to technical issues (e.g. sampling drop). Accuracy was 97.47% (± 2.79%) for the image size task and 97.17% (± 2.83%) for the familiar size task. All subsequent analyses were restricted to correct trials.

Image size task

As seen in Figure 2A, in the image size task (leftmost bars) participants performed more accurately on congruent trials (black bars) compared to incongruent trials (cyan bars). This result indicates that interference from familiar size was strong enough to lead to incorrect choices when familiar size was in conflict with image size, $t(13) = 2.83$, $p = .014$, $d = .697$.

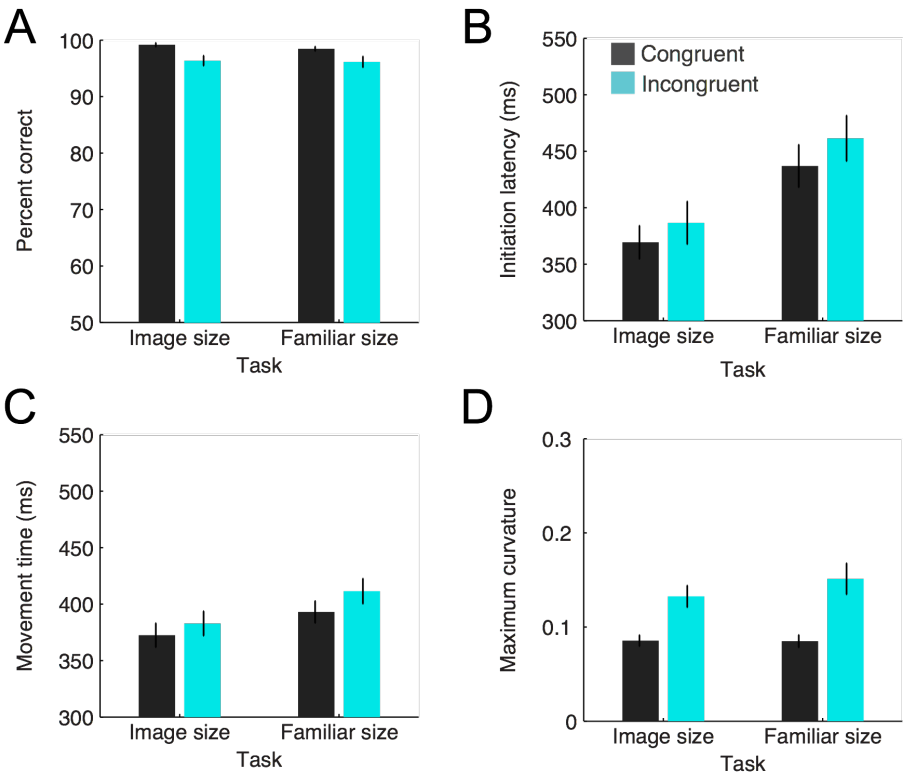

Figure 2. Experiment 1 results for congruent versus incongruent trials in the image size and familiar size tasks. All error bars represent between-subjects standard error. **A.** Accuracy. Accuracy was lower for the incongruent conditions than the congruent conditions in both tasks. **B.** Initiation latency. IL was faster for congruent compared to incongruent trials in both tasks, and was faster overall for the image size task. **C.** Movement time. MT was faster for the congruent conditions in both tasks, and faster overall for the image size task. **D.** Maximum curvature. Movements were more curved in the incongruent trials for both tasks. Note, curvature values represent a unitless ratio.

A congruency effect was seen in initiation latency (Figure 2B) such that participants were faster overall to initiate movements when image size and familiar size were congruent compared when they were incongruent, $t(13) = -2.84$, $p = .014$, $d = -.199$. Similarly, congruency also affected online movement time such that movements were executed more quickly when image size and familiar size were congruent compared to incongruent, $t(13) = -3.62$, $p < .001$, $d = -.259$ (Figure 2C).

Finally, we examined maximum curvature over the course of the movement as

a measure of how much movements were pulled toward the incorrect object before ultimately landing on the correct object. Figure 2d shows that the average maximum curvature of pointing movements was greater when image size and familiar size were incongruent compared when they were congruent, showing that familiar size interfered with the image size task, e.g., when the task was to choose the larger object based on its image size, participants' hand movements were drawn toward the object with the larger *familiar* size, $t(13) = -5.24$, $p < .001$, $d = -1.18$.

Overall the results from the image size task indicate that the higher-level feature familiar size significantly interferes with the lower-level image size when the two are incongruent, even when familiar size is task-irrelevant. This is consistent with prior findings on the "familiar size Stroop task" (Konkle & Oliva, 2012b).

Familiar size task

Figure 2A shows that, as in the image size task, participants were more accurate on average for congruent compared to incongruent trials for the familiar size task (rightmost bars). Similarly, this suggests that image size interferes with familiar size even when it was task-irrelevant. However, unlike in the image size task this effect was only marginally significant, $t(13) = 2.43$, $p = .030$, $d = .802$. Similarly, there was also an effect of congruency in IL, $t(13) = -3.58$, $p = .003$, $d = -.328$. (Figure 2B) and MT, $t(13) = -2.95$, $p = .011$, $d = -0.461$ (Figure 2C) such that participants were slower when image size and familiar size were incongruent. Finally maximum movement curvature was significantly greater when image size and familiar size were incongruent, $t(13) = -3.91$, $p = .002$, $d = -0.876$ as it was in the

image size task as well (Figure 2D).

Overall these results suggest that there is significant interference from image size in the familiar size task such when the two are incongruent performance is impaired, despite the fact that image size here is task-irrelevant.

Comparing image and familiar size

We additionally compared performance on the image and familiar size tasks in all the aforementioned measures. We observed no difference between the tasks for accuracy, $F(1,13) = .068$, $p = .799$, $\eta_p^2 = .005$, or maximum curvature, $F(1,13) = .636$, $p = .439$, $\eta_p^2 = .047$. For initiation latency we observed that participants were faster to initiate movements in the image size judgment task compared to the familiar size judgment task, $F(1,13) = 69.22$, $p < .001$, $\eta_p^2 = .842$. Similarly online movement execution was faster, with faster MTs observed for the image size task, $F(1,13) = 11.96$, $p = .004$, $\eta_p^2 = .479$. There were no interactions between congruency and task for any of the measures.

Overall then, participants took longer to plan and execute their movements in the familiar size task compared to the image size task, perhaps suggesting that evaluating this aspect of image size is more difficult overall/requires more cognitive processing than evaluating image size. This effect though was not seen in accuracy or maximum curvature, suggesting that timing is the key difference between the two tasks.

Timecourse of movement modulation in the image and familiar size tasks

Our analyses of the trajectory of hand movements revealed key differences in the maximum curvature over the course of movements when image size and familiar size were incongruent, in both the image and familiar size tasks (Figure 2D). In addition to this spatial measure which refers to a discrete point in the movement, we can additionally examine the dynamics of interference over the course of our continuous movement data. Comparing hand positions over the course of the movement for congruent and incongruent trials in the image and familiar size tasks provides insight into *when* image and familiar size interact in addition to previous measures of *how much* they interact. It is important to note that the movements were normalized to 100 datapoints based on distance from the screen, removing any confound of timing differences between movements. Thus, we discuss the percentage into the course of the movement at which differences occur as opposed to the confounded variable of time in a traditional sense.

In the familiar size task (blue line), where image size is the competing feature, difference scores are significantly greater than zero between 15% - 91%, indicating that the average paths of the congruent and incongruent trials were significantly different in the interim (Figure 3). In contrast, in the image size task (red line), where familiar size is the competing feature, the congruent and incongruent trajectories size task deviated later than in the familiar size task, approximately 36% - 90% into the movement. Thus, congruency becomes a factor in the familiar size task after a smaller portion of the movement; or said another way, image size influences movements at an earlier proportion than familiar size does. There is no significant difference in the

points at which the difference scores return to zero, indicating that congruent and incongruent trials converge at similar points the movement for the image and familiar size tasks. Individual analyses for congruent versus incongruent trials in both tasks can be found in the appendix.

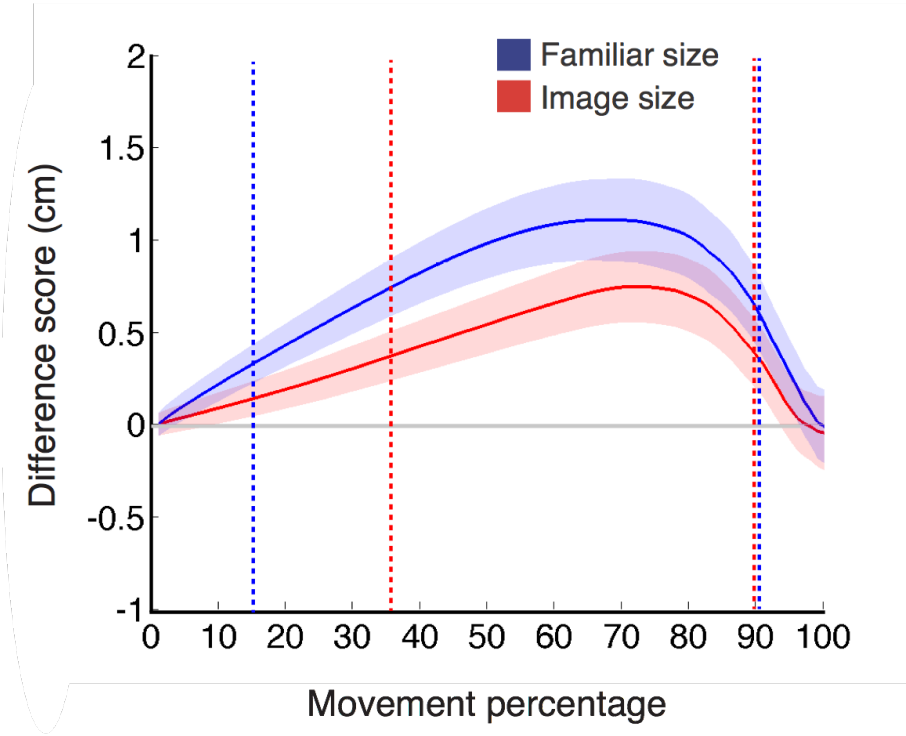

Figure 3. Difference scores between congruent and incongruent trials representing the magnitude of interference by incongruency, in the image and familiar size tasks. Scores in the familiar size task where image size is the interfering task-irrelevant factor rise significantly above zero earlier and peak earlier than the scores for the image size task where familiar size is the interfering feature.

Taken together, these results suggest that the image sizes of objects impact movement to a greater degree than familiar size, as demonstrated by a greater effect of congruency in the familiar size compared to the image size task. Not only is the magnitude greater, but the impact of image size is observed earlier in the course of the decision-making process than familiar size. This suggests that image size may be

processed more robustly overall than familiar size, though once again both are automatic and robust enough to interfere with the other.

Summary

Overall, Experiment 1 demonstrated that both the *image* and *familiar sizes* of real world objects play a role in how they are perceived and interacted with. Specifically, when we manipulated the congruency of targets' image and familiar sizes, each of these two aspects of object perception interfered with the other. This suggests that both image size and familiar real-world size are aspects of object perception and identification that occur automatically, even when task-irrelevant, and furthermore are not independent from action. Despite the bidirectional interference, however, image size may be the more robustly processed and represented of the two, and interfere with familiar size judgments more than familiar size interferes with image size judgments. This observation was investigated in more detail in Experiment 2, along with questions regarding absolute and relative familiar size differences and their relationship with action.

Experiment 2: Effects of familiar size difference magnitude on action

Following Experiment 1, we examined whether familiar size is simply conceptualized as "large" or "small," as it has largely been treated in the existing literature, or rather along a gradient of real world sizes (Chao & Martin, 2000; Downing et al., 2006; N Kanwisher, 2001; Macuga & Papailiou, 2012; Wang & MacKenzie, 1999). We expanded our set of real world objects to include a wider

range of familiar sizes, and systematically manipulated the magnitude of the difference in familiar sizes between paired targets. We hypothesize that if familiar size is treated as a spectrum, varying the magnitudes of familiar size differences may lead to corresponding graded effects on action and on the interference between image and familiar size.

Methods

Participants

Thirteen right-handed participants (11 female, mean age 21.6) with normal color vision, and normal or corrected-to-normal visual acuity completed both visually guided pointing tasks: familiar size judgment and image size judgment. Of these, 12 (10 female, mean age 21.7) additionally performed a familiar size rating task to validate our relative familiar size category manipulation.

Apparatus

The same apparatus was used as in Exp. 1.

Stimuli

Experiment 2 stimuli were similar to those used in Experiment 1. We created image pairs from individual objects in the Konkle et al. "Object Size Range" database (Konkle & Oliva, 2011). Images in this database are divided into eight groups based on their familiar real-world sizes. These groups were independently defined and validated by participants (Konkle & Oliva, 2011). Using these eight familiar size

groups, we defined four categories of paired images ranging from small to large familiar size differences. Objects in Category 1 were selected from within the same size group (e.g. a peanut and a paperclip [both group 1], or a space shuttle and an airplane [both group 8]), Category 2 were two groups apart (e.g. a wineglass [group 3] and a teabag [group 1]), Category 3 were four groups apart (e.g. a cooler [group 5] and a die [group 1]), and Category 4 were six groups apart (e.g. a car [group 7] and a key [group 1]). All eight groups were represented in all four categories. Thus, in this 4 category by 8 group manipulation there were a total of 32 image pairs. Examples of pairs from each category, in their congruent and incongruent configurations, are shown in Figure 4.

Figure 4. Representative examples of each of the four relative familiar size categories for object pairs, in both congruent and incongruent conformations. Categories 1-4 have progressively greater differences in familiar size magnitude.

Procedure

The Exp. 2 procedure was the same as in Exp. 1.

Our four relative familiar size category manipulation based on the established image dataset was validated by participants' ratings of how different the familiar sizes of the objects in each pair were on a 1-10 scale. All image pairs from the pointing

tasks were presented with a rating bar at the bottom of the screen representing a continuum from 0 to 10. Participants were instructed to use the mouse to click anywhere within the bar rating how large the relative familiar size difference was for the object pair shown (e.g. “How different are the sizes of a rubber duck and a boat in the real world?”). As in Experiment 1, object pairs were presented with relative image size and familiar size either congruent or incongruent. This task took place after both the image and familiar size judgment tasks in order not to bias performance.

Data analysis

All data analysis was identical to Experiment 1, with the following exceptions.

The measure *rating* was defined as the average value given to each object pair when participants were instructed to rate the pairs based on their relative *familiar size* differences.

To analyze all metrics we performed 2x4 repeated measures ANOVAs with factors of congruency (congruent or incongruent) and category (1-4). Additionally, we also compared between the two tasks as in Exp. 1, by performed 2x4x2 ANOVAs with factors of congruency, category, and task (image size vs. familiar size judgment).

Results

In total, 10.75% (± 1.02%) of trials were excluded from data analysis from the image size task and 10.93% (± 1.27%) from the familiar size task due to technical

issues (e.g. sampling drop). Accuracy for the image size task was 89.25 % (± 1.02%) and 88.09 (± 1.27%) for the familiar size task. All data analyses were restricted to non-rejected trials.

Ratings

To validate the four categories we designed based on relative familiar size difference magnitude, we asked participants to rate this difference for object each pair. Additionally, we presented each pair in both its congruent and incongruent conditions, in order to evaluate the effect of congruency on subjective ratings of familiar size difference.

Figure 5 shows the average ratings assigned by participants to the image pairs in each of the four relative familiar size difference categories (1-4), when the relative familiar and image sizes were congruent (black) and incongruent (cyan). Participant ratings validate our manipulation of creating image pairs that fit these four categories—Figure 5 shows a clear trend of average rating increasing in a stepwise manner across categories 1-4 (small to large familiar size difference). This was supported by a 2x4 repeated measures ANOVA with factors of congruency (congruent vs. incongruent) and category (1-4), which revealed a main effect of category, $F(3,30) = 55.80$, $p < .001$, $\eta_p^2 = .848$.

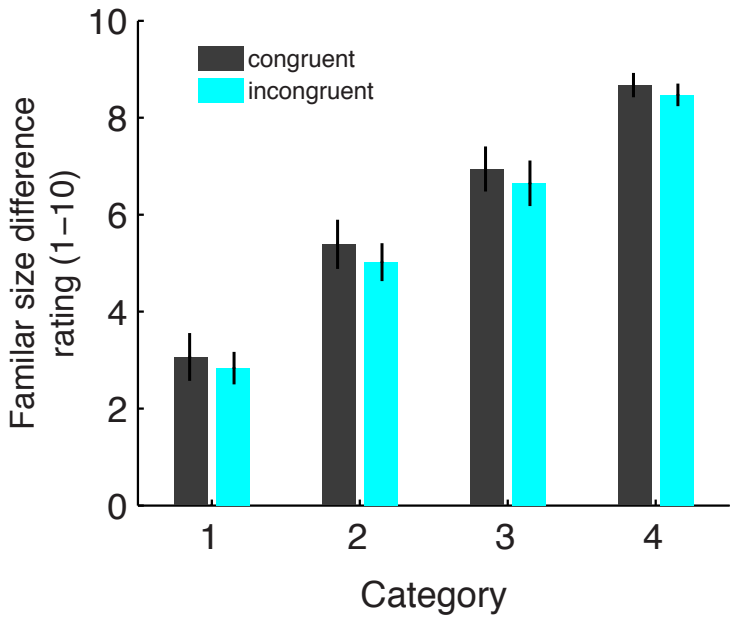

Figure 5. Average ratings of relative familiar size differences for image pairs in each relative image size category, when paired objects' image and familiar sizes are congruent and incongruent. Ratings supported our category definitions, with higher ratings given to categories designed to show larger familiar size differences. There was no difference in rating based on condition.

Figure 5 appears to show a trend such that ratings of the familiar size differences were higher on average in the congruent compared to incongruent condition. Such an effect would suggest that participants attended to the objects' image sizes despite task-irrelevance, and that congruent *image size* differences magnified the perceived difference in familiar size. However, there was no significant effect of congruency, $F(1,10) = .874$, $p = .372$, $\eta_p^2 = .080$, and no interaction between congruency and category, $F(3,30) = .705$, $p = .557$, $\eta_p^2 = .066$. This could be due to the absence of a meaningful effect, or insufficient power. This latter possibility may reflect the relative weakness of a perceptual button-press task compared to the more robust action measures employed in the main task, which show consistent effects of congruency on the action-based metrics employed.

Image size task

Accuracy. As shown in Figures 6a, there were no clear trends in accuracy was across conditions in the image size task. There was no main effect of congruency (*congruent* vs. *incongruent*), $F(1,12) = .223$, $p = .648$, $\eta_p^2 = .024$, or category (1-4), $F(3,33) = 1.42$, $p = .259$, $\eta_p^2 = .136$. There was however a significant interaction between the two such that the strength of the congruency effect was different in different categories, $F(3,33) = 6.62$, $p = .002$, $\eta_p^2 = .424$. This difference does not appear to follow a systematic trend across categories as familiar size difference magnitude varies, and thus it is impossible to make any claims about a meaningful effect of category on congruency or vice versa.

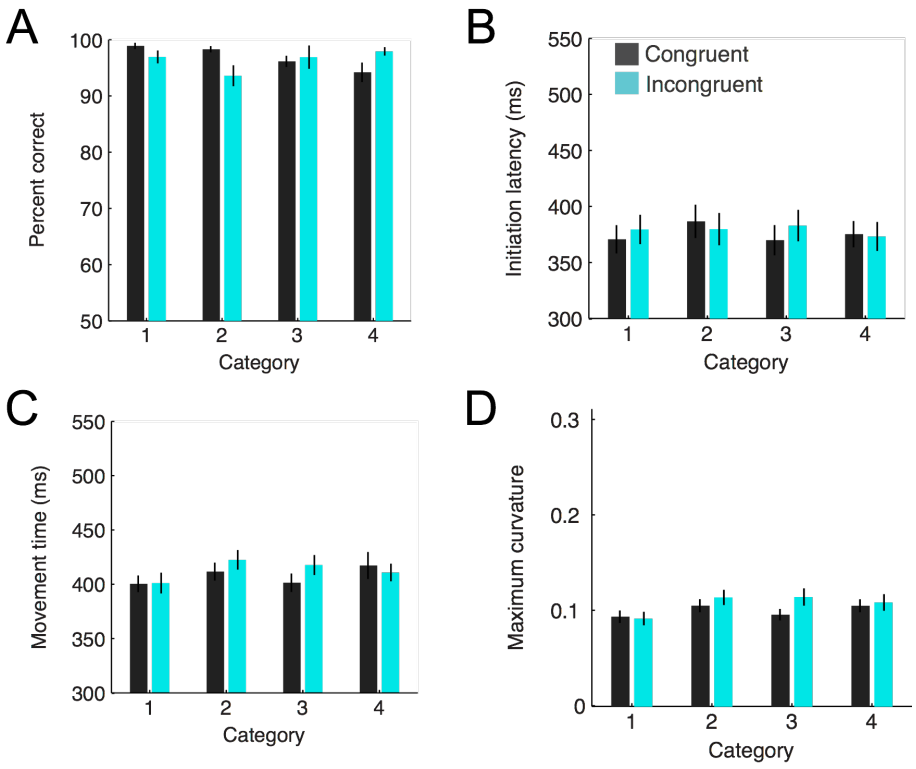

Figure 6. Experiment 2 results for congruent versus incongruent trials across relative familiar size conditions in the image size task. All error bars represent between-subjects standard error. **A.** Accuracy. Accuracy was consistent across all conditions. **B.** Initiation latency. IL was consistent across all conditions. **C.** Movement time. MT was faster for congruent trials, and for larger relative familiar size difference categories. **D.** Curvature. Movements were more curved in the incongruent trials overall, and for categories with lower relative familiar size differences.

Initiation latency. In order to examine how congruency and the relative differences between real world objects' familiar sizes affected movement preparation we again analyzed initiation latency (IL). Figure 6b shows that for the image size task, unlike in Exp. 1, IL was consistent across conditions. There was no significant difference based on congruency, $F(1,12) = 1.27$, $p = .282$, $\eta_p^2 = .096$, category, $F(3,36) = 2.37$, $p = .087$, $\eta_p^2 = .165$, and no interaction, $F(3,36) = 2.34$, $p < .085$, $\eta_p^2 = .166$.

Movement time. Again, to examine how congruency and familiar size difference category affected the online control of pointing we analyzed movement time (MT). Figure 6C shows that in the image size task there was a marginal effect of congruency on MT such that movements were faster overall when image and familiar size were congruent, $F(1,12) = 4.02$, $p = .068$, $\eta_p^2 = .251$. Additionally we observed that with larger familiar size differences, MTs were slower overall, $F(3,36) = 10.10$, $p < .001$, $\eta_p^2 = .457$. As in accuracy there was an interaction between congruency and category, $F(3,36) = 5.36$, $p = .004$, $\eta_p^2 = .309$. Again though, this effect does not appear to vary systematically with category; Figure 6C shows that categories 2 and 3 display greater differences between congruent and incongruent trials than 1 and 4, so we can draw no conclusions about the interaction in terms of MT.

Maximum Curvature. In the image size task, maximum curvature results are consistent with those seen in movement time, and replicate the congruency effect seen in maximum curvature in Exp. 1 (Figure 2D, left). Maximum curvature was greater overall in the incongruent conditions, $F(1,12) = 6.72$, $p = .024$, $\eta_p^2 = .359$, suggesting interference from familiar size when the two were incongruent (Figure 6D). Maximum curvature was also larger when familiar size differences were larger, $F(3,36) = 7.68$, $p < .001$, $\eta_p^2 = .390$. There was additionally an interaction between these effects such that differences based on congruency increased as familiar size difference increased, $F(3,36) = 2.99$, $p = .044$, $\eta_p^2 = .199$. As seen in Figure 6D, the increase in maximum curvature across categories appears to be driven largely by the incongruent conditions while curvature in the congruent conditions remained constant, consistent with the interaction between category and congruency. Overall,

this points to increasing familiar size differences systematically increasing familiar size's interference in the image size task.

Familiar size task

Accuracy. In the familiar size task, we see several effects in accuracy not seen in the image size task. As seen in Figure 7A, there was a significant effect of congruency such that accuracy was lower when image and familiar size were incongruent, $F(1,12) = 11.37$, $p = .008$, $\eta_p^2 = .558$. There was additionally an effect of category such that accuracy was lower for the conditions with smaller familiar size differences, $F(3,33) = 32.48$, $p < .001$, $\eta_p^2 = .783$. This suggests that judgments of relative familiar size were more difficult when paired objects were closer in their familiar size. Here familiar size was the task-relevant feature while it was task-irrelevant in the image size task. Thus, it is not surprising to see an effect of category here but not in the image size task (Figure 6A). In Figure 7A there appears to be a trend such that the congruency had a smaller effect in larger categories, suggesting that larger familiar size differences were processed more robustly and more successfully resisted interference from image size, however this interaction was only marginally significant, $F(3,33) = 2.61$, $p = .072$, $\eta_p^2 = .225$.

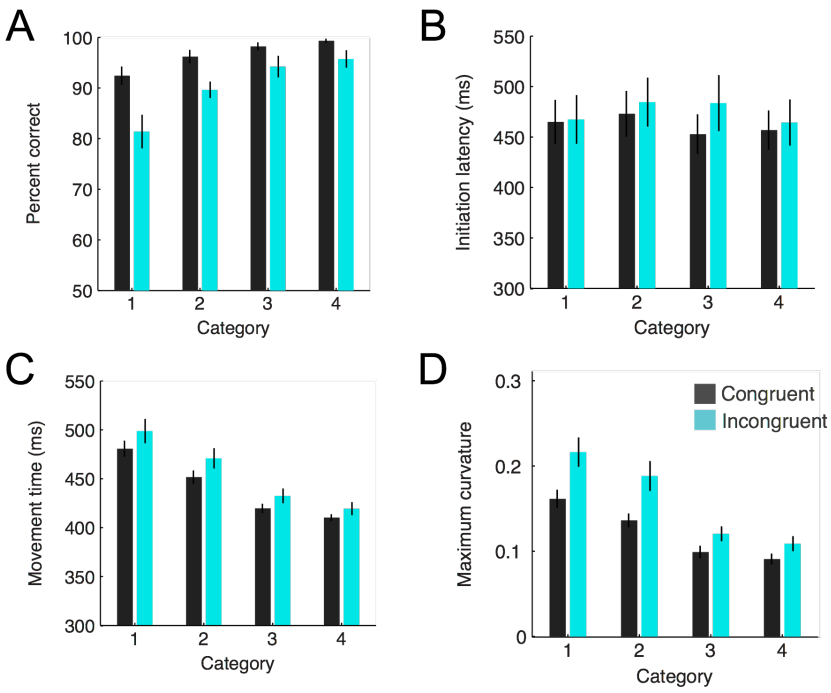

Figure 7. Experiment 2 results for congruent versus incongruent trials across relative familiar size conditions in the familiar size task. All error bars represent between-subjects standard error. **A.** Accuracy. Accuracy was higher for congruent compared to incongruent conditions, and for larger relative familiar size category. **B.** Initiation latency. IL was faster for congruent trials. **C.** Movement time. MT was faster for congruent trials, and for larger relative familiar size difference categories. **D.** Curvature. Movements were more curved in the incongruent trials overall, and for categories with lower relative familiar size differences.

Initiation latency. Figure 7B shows that, unlike in the image task, ILs were marginally slower for incongruent compared to congruent trials, $F(1,12) = 4.53$, $p = .055$, $\eta_p^2 = .274$. Additionally, there was a significant effect of category, $F(3,36) = 5.35$, $p = .004$, $\eta_p^2 = .308$, and interaction between congruency and category, $F(3,36) = 3.48$, $p = .026$, $\eta_p^2 = .225$.

In the image size task, familiar size was the task-irrelevant interfering factor, whereas here in the familiar size task, image is the interfering factor. Overall, familiar size failed to exert any influence on IL in the image size task (Figure 6B), but image size significantly interfered with the speed of movement initiation for the familiar size

task. Additionally, unlike the image size task, differences in familiar size impacted IL, as might be expected given that image size here was the task-relevant feature. However, these differences between category do not appear to follow any systematic trend, but rather be driven primarily by Category 3. Thus, no strong claims can be made based on this effect.

It is worth noting that when the image and familiar size tasks were combined there was a significant main effect overall of congruency, $F(1,12) = 6.15$, $p = .029$, $\eta_p^2 = .339$, which did not appear in either task independently. This perhaps suggests that there was a trend overall as in Exp. 1 (Figure 2B) but the power in Exp. 2 was not sufficient to reveal the effect in both tasks.

Movement time. Figure 7C shows that in the familiar size task movements were faster overall when image and familiar size were congruent, $F(1,12) = 12.74$, $p = .004$, $\eta_p^2 = .515$. Additionally, MTs were significantly faster when familiar size differences were larger (category 1-4), $F(3,36) = 78.06$, $p < .001$, $\eta_p^2 = .867$. There was no interaction between these effects, $F(3,36) = .216$, $p = .885$, $\eta_p^2 = .018$. As with IL, it is not surprising that category, which is based on relative familiar size difference, would modulate the familiar size task more than the image size task. That said, a clear asymmetry exists between image size's influence on familiar size, and familiar size's influence on image size, as seen in the difference between congruency effects in Figure 6C and 7C.

Maximum Curvature. As in the image size task, maximum curvature was again greater overall in the incongruent compared to congruent conditions, $F(1,12) = 18.47$, $p < .001$, $\eta_p^2 = .606$, (Figure 7d). Here though, there was less maximum

curvature overall when familiar size differences were smaller compared to larger (categories 1-4), $F(3,36) = 68.95$, $p < .001$, $\eta_p^2 = .852$. Again, familiar size here is the task-relevant factor while it is the interfering factor in the image size task, leading to opposite effects of increasing familiar size difference in the two tasks. What is consistent across both is that with larger familiar size differences, there is a larger effect of familiar size.

Similarly, there was an interaction between these two effects such that the incongruency effect decreased as category increased, $F(3,36) = 40.96$, $p < .001$, $\eta_p^2 = .773$. Again, this reflects a decreasing interference from image size as familiar size differences increase, and is expectedly the reverse of the effect seen in image size.

Comparisons between image and familiar size tasks

In addition to the above within task measures, we again compared the image and familiar size tasks directly. We found effects of task in all measures; there was greater accuracy in the image size task, $F(1,12) = 6.48$, $p = .031$, $\eta_p^2 = .419$. Participants were faster overall to initiate movements, $F(1,12) = 40.06$, $p < .001$, $\eta_p^2 = .770$, and to execute movements, $F(1,12) = 46.41$, $p < .001$, $\eta_p^2 = .795$, in the image size task. Taken together with the accuracy results, this suggests that the familiar size task may have been more difficult than the image size task, consistent with participants' subjective reports. Finally, maximum curvature was greater overall for the familiar size task, $F(1,12) = 107.25$, $p < .001$, $\eta_p^2 = .899$.

There were additionally task by congruency interactions in accuracy, $F(3,36) = 7.20$, $p = .025$, $\eta_p^2 = .444$, movement time, $F(1,12) = 84.62$, $p < .001$, $\eta_p^2 = .876$,

maximum curvature, $F(1,12) = 10.81$, $p = .006$, $\eta_p^2 = .474$, and a marginally significant effect in initiation latency, $F(1,12) = 4.37$, $p = .059$, $\eta_p^2 = .267$. Together, these all point to image size interfering in the familiar size task more than familiar size did in the image size task.

For movement time, $F(1,12) = 84.79$, $p < .001$, $\eta_p^2 = .876$, and maximum curvature, $F(1,12) = 10.81$, $p = .006$, $\eta_p^2 = .474$, there were also interactions between category (i.e. the degree of familiar size difference between paired objects) and task such that category had more of an effect in the familiar size compared to the image size task. This effect is not surprising given that familiar size was task-relevant in the familiar size task, and task-irrelevant in the image size task.

Finally, for maximum curvature, there was a three-way interaction between task, congruency, and category. In understanding how category differently impacts the congruency between image and familiar size in each respective task it is useful to compare the figures for each task independently. In the image size task (Figure 6D), larger familiar size differences (category) led to more curved trajectories. However this effect seems to be driven entirely by the incongruent conditions—maximum curvature increases across the incongruent conditions based on category, while the congruent trials are consistent across category. This suggests that increasing the familiar size difference increases the interference of familiar size in performing the image size task. However, when familiar size and image size are congruent familiar size difference plays no role, or a negligible role compared to the perception of image size.

In the familiar size task, there was an overall decrease in maximum curvature as the familiar size difference (category) increased (Figure 7D). This is the reverse of the effect seen in the image size task because here participants' decisions were made based on familiar size as opposed to image size. Thus, the lower maximum curvature for the greater familiar size differences may reflect lower task difficulty. Similarly, the interaction effect suggests that the effect of congruency is different across categories. Specifically, the congruency effect is greater in the smaller familiar size difference categories, showing that image size interferes with participants' ability to judge familiar size more when the familiar size difference is smaller.

Taken together with the converging evidence that image size is processed more robustly than familiar size, this suggests that image size is the greater influence on trajectory overall, but that familiar size exerts greater influence with greater familiar size differences. This increased modulation of movement by familiar size leads both to greater interference from familiar size in the image size task, and greater resistance against interference from image size in the familiar size task.

Timecourse of movement modulation in the image and familiar size tasks

As in Experiment 1, we again calculated the normalized timecourse between tasks and conditions to examine the influence of image and familiar size over time. Specifically, we were interested in the effect of varying the magnitude of familiar size differences between paired images on the timecourse of both image and familiar size influence on movements.

We first performed the same timecourse analysis as in Exp. 1 comparing image size and familiar size difference scores between congruent and incongruent trials overall. Figure 8 shows difference scores significantly above zero 53% - 71% into the movement for the image size task and 14% - 97% into the movement for the familiar size task. This replicates our Exp. 1 findings that image size came online and influenced movements earlier in the course of movements than familiar size did.

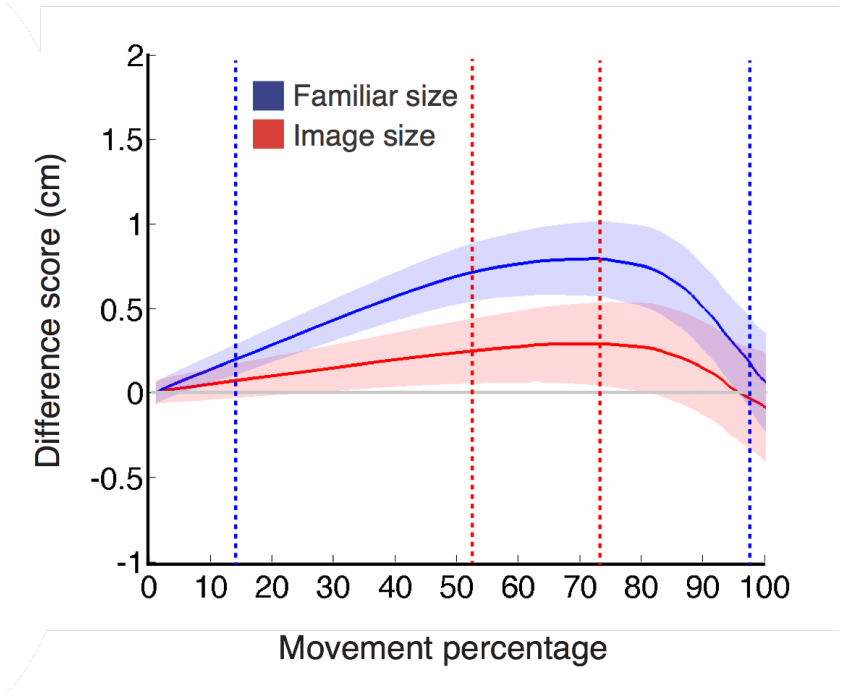

Figure 8. Difference scores between congruent and incongruent trials representing the magnitude of interference by incongruency, in the image and familiar size tasks. Scores in the familiar size task where image size is the interferer rise significantly above zero earlier than the scores for the image size task where familiar size is the interferer.

It is worth noting that the precise timing and the magnitude of interference in Exp. 2 did not completely replicate the results in Exp. 1. In the image size task specifically, familiar size interfered later and less robustly in Exp. 2 than in Exp. 1. This could reflect the fact that the range of familiar sizes was much larger in Exp. 2

compared to Exp. 1, and thus there was a wider range of interference effects and more noise overall.

We additionally compared the influences of image and familiar size on the movements between categories. Figure 8 shows the timecourse of difference scores for each category, with the image size task presented in red and the familiar size task in blue: Figure 9A represents Category 1 trials and the smallest familiar size difference magnitudes, Fig. 9B shows Category 2, Fig. 9C shows Category 3, and Fig. 9D shows Category 4, which has the greatest familiar size difference magnitudes.

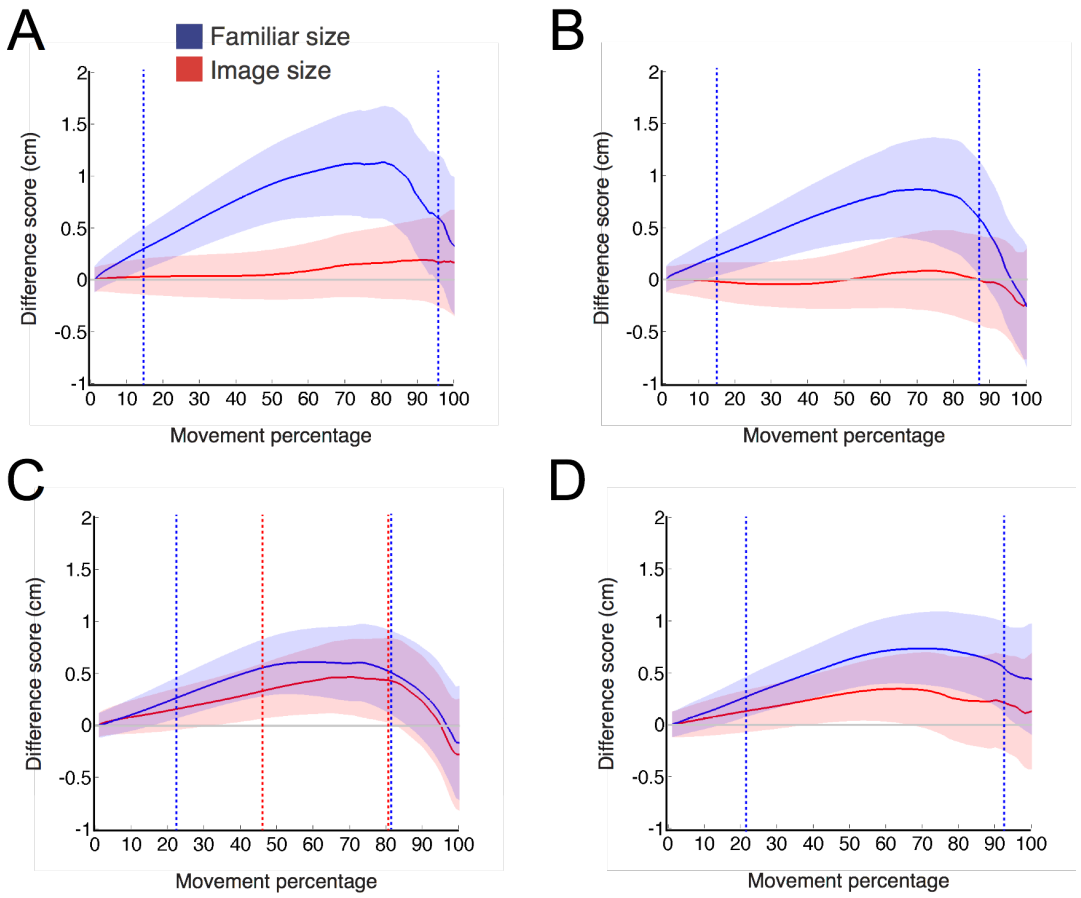

Figure 9. Experiment 2 trajectory time courses. All error bars represent 95% confidence intervals. **A.** Category 1 trials in the image and familiar size tasks. Only the familiar size task where image size was the interfering factor showed difference scores significantly above zero. **B.** Category 2 trials in the image and familiar size tasks. Only the familiar size task showed difference scores significantly above zero. **C.** Category 3 trials in the image and familiar size tasks. Both the familiar size and image size tasks showed difference scores significantly above zero, with scores rising above zero later in the image size task. **D.** Category 4 trials in the image and familiar size tasks. Only the familiar size task showed difference scores significantly above zero.

For the image size task, where familiar size was the interfering factor, there was an overall main effect of congruency. However, only Category 3 independently displays a difference scores significantly above zero, 46% - 82% into the movements. Thus, familiar size interference in the known size task cannot be compared between all familiar size categories.

In the familiar size task where image size was the interfering factor, difference scores were significantly greater than zero for all categories, 15% - 96% into the movement for category 1, 16% - 88% for category 2, 23% - 81% for category 3, and 22% - 93% for category 4. Thus, there was no overall effect of category in terms of the where in the movement interference from image size came online, indicating that the magnitude of the familiar size difference did not significantly impact how congruence effects unfolded.

Overall then, we replicate the timecourse effect seen in Exp. 1 (Figure 3), with image size influencing trajectory earlier in the course of the movement than familiar size. However, when we separate out the categories defined by familiar size difference, we see no differences in the timing of a congruency effect in the familiar size task, and no reliable congruency effect in the image size task. Thus, category modulated movements in both the image and familiar size tasks in terms of *trajectory* (i.e. maximum curvature), but not in terms of *timing*. This suggests that differences in the familiar sizes of objects leads to corresponding differences in the degree of interference between image and familiar size, but not when the interference occurrs.

Summary

In Experiment 2, we again demonstrated bidirectional interference between the perception of image size and familiar size when the two are presented in an incongruent manner, though here we also found evidence of image size exerting greater influence on familiar size than vice versa. Furthermore, we observed several trends associated with greater magnitudes of familiar size differences between paired

objects. Namely, in the familiar size judgment task, the larger the familiar size difference the lower the maximum curvature overall. This is consistent with greater differences in familiar size making familiar size judgments easier.

Additionally, the incongruence effect in the familiar size task diminished with increasing familiar size difference. This indicates that image size did interfere with familiar size judgment across categories, but did less so when the familiar size difference was greater. Similarly, in the image size judgment task, the interference from familiar size increased with increasing familiar size difference across the four categories. Overall this is consistent with image size perception being the more automatic of the two, and exerting greater influence on the decision making process and on hand movements. However, the greater the difference between the familiar real-world sizes of the objects, the greater the effect that familiar size has, and the more it mitigates/interferes with image size's influence.

Discussion

In the current study we presented participants with pairs of real world objects, and manipulated their relative *image* and *familiar* sizes. By using a visually-guided pointing paradigm and decision-making task based on either image size or familiar size, we were able to assess the relationship between these two aspects of object perception and their impacts on visually-guided action.

Mechanisms of image and familiar size perception

As mentioned earlier, object perception relies on a hierarchy of perceptual processes representing increasingly complex object features (Riesenhuber & Poggio, 1999). Image size is a low-level feature, and is represented essentially by the size of the stimulus on the retina—far earlier in the visual processing pathway than anything related to object identity.

However, the assumption that image size is a more intrinsic feature with stronger, more fundamental neural correlates than familiar size is inaccurate. As early as V1 representations have been shown to reflect the subjective perception of objects' sizes as opposed to their veridical image size. Sperandio, Chouinard, and Goodale (2012) found that, despite constant retinal image size, V1 activity reflected perceived object size in a size constancy task that manipulated target viewing distance, suggesting that image size perception is influenced by other aspects of perception even at this early stage in processing.

Furthermore, the familiar sizes of real world objects have been shown to have neural representations independent of image size. Konkle and Oliva (2012b) showed that familiar object size is represented in the occipitotemporal cortex (OT) much like object categories, with larger objects represented in medial OT and smaller objects in lateral OT. Thus, our observation that both image size and familiar size are processed automatically is consistent with known mechanisms underlying object perception.

Here, we report evidence for interference that suggests interactions between image and familiar size mechanisms. Image size was consistently the more dominant of the two—it was processed earlier and more robustly, and participants anecdotally

reported finding it more salient than familiar size. That said, we demonstrated in Experiment 2 that the robustness of familiar size effects increased with increasing familiar size magnitude, and this robustness mitigated image sizes' effects when the two were in conflict. Essentially the more robust process, image size judgment, became *less* robust and more susceptible to influence from the task-irrelevant feature of familiar size when the familiar size difference was greater in magnitude.

Similarly we observed that, in the familiar size task, task-irrelevant image size processing interfered *less* the greater the magnitude of the familiar size difference. Thus in both tasks greater familiar size differences more strongly counteracted the influence of image size. This is possibly due to increased salience of familiar size as a feature when the familiar sizes of the two paired real world objects was more discrepant. Furthermore, the parametric nature of our manipulation in Experiment 2 and the resulting graded effects of familiar size suggest that familiar size may be represented in a continuous manner as opposed to the binary "large object" and "small object" areas found by Konkle & Oliva (2012b).

Overall, we present converging evidence that image size is processed earlier and more robustly than familiar size, but that increasing familiar size differences somewhat mitigate this effect, indicating dynamic interactions between image and familiar size perception, and action.

Processing conflict in the familiar size Stroop task

The "familiar size Stroop" task used here was inspired by the classic Stroop task in which identifying the color a word is printed in is impaired when the word is

the name of an incongruent color (Konkle & Oliva, 2012a; Stroop, 1935). In order to accurately perform the Stroop task participants must suppress the automatic response produced by a *direct processing pathway* in order to respond to the relevant feature for their current goal, processed by an *indirect processing pathway* (Botvinick et al., 2001; Ridderinkhof, van der Molen, & Bashore, 1995; Shenhav, Botvinick, & Cohen, 2013; Van der Stigchel, van Koningsbruggen, Nijboer, List, & Rafal, 2012).

The prioritization of task-relevant over task-irrelevant features is a key aspect of cognitive control, and the Stroop task has been investigated extensively within the cognitive control literature (Memelink & Hommel, 2013). Resolving conflict in the Stroop task is thought to comprise three processes: monitoring conflict between the direct pathway and indirect pathway, adjusting the response threshold by inhibiting motor output, and recruiting top-down processes in order to resolve conflict between the two pathways (Botvinick et al., 2001; Erb et al., 2016; Shenhav et al., 2013). Erb et al. (2016) investigated these individual processes in a classic Stroop task using a visually-guided pointing paradigm, and showed that they manifested in different aspects of visually-guided action. Specifically, movement initiation latency was shown to reflect the response threshold adjustment process while maximum curvature reflected the final conflict resolution between the direct and indirect pathways.

By using a similar visually-guided pointing paradigm and the familiar size Stroop task we are able to speculate about the processing of image size and familiar size, and the conflict between the two. When objects' image and familiar sizes were in conflict participants were slower to initiate movements, and their movements were more curved toward the incorrect response. We propose that the former effect results

from motor output being suppressed to allow for more processing time, an early conflict resolution process. The latter effect suggests that representations of both alternatives persist even after movements are initiated (Erb et al., 2016). Thus, conflict resolution processes begin early, but conflict is not resolved until later. This also demonstrates that both image size and familiar size, as well as their conflict, influence both movement preparation and movement execution, with a larger effect magnitude from image size.

Again though, despite the fact that image size influenced familiar size more than familiar size did image size, we observed bidirectional interference. While the classical Stroop effect is largely reported in terms of the unidirectional influence of reading a word on reporting a color, a "reverse Stroop effect" has also been observed in which participants' ability to read a color name is impaired by incongruent text color (MacLeod, 1991). However, the effect of the written word on printed color identification is more pronounced than the impact of ink color on reading the written word. Thus, interference in the classical Stoop effect is bidirectional but asymmetrical, like our reported effects in the familiar size Stroop.

Based on these results, processing image size in the familiar size Stroop task parallels reading the word in the classical Stroop task, and familiar size processing parallels reporting the text color. From this we speculate that the perception of object *image size* is a direct pathway process and the perception of *familiar size,* an indirect pathway process, again consistent with participants' subjective reports of their relative ease.

This observation has important implications for target selection, action control, and perception and action integration more broadly. There are a number of reasons image size processing could be a direct pathway process in this action-based Stroop paradigm. First, image size is arguably more relevant for the guidance of action than familiar size is—we can process the size of an object in front of us and interact with it even if it is not an object we are familiar with, and when familiar objects' image and familiar sizes are incongruent their current image size is far more important for action than their typical familiar size.

In the classic Stroop task the direct pathway process is reading a word while the indirect process is naming the color of the ink, again somewhat counterintuitive given that reading is a higher order process than color perception. However, reading proceeds more automatically due to the relative frequency of performing this learned behavior. Similarly, attending to image size in isolation may be performed more frequently in daily life than processing familiar size in isolation. These two explanations are not mutually exclusive. It is likely that the automaticity of image size processing and its influence on action is the result of its frequency and utility in daily life.

That said, our results show that familiar size is processed automatically as well. This learned behavior is more relevant to visual perception than visually guided action in a classical perception/action dissociation framework. However, as we have shown, perception and action are not truly distinct and perception does influence action. Thus, if image size influences action more readily and familiar size influences perception more readily, this doesn't mean that familiar size doesn't influence action,

just that the influence emerges later as in other perception/action integration processes.

Conclusion

By examining the modulation of goal-directed hand movements by the image sizes and familiar sizes of real world objects, the present study can contribute to a more complete picture of how objects are perceived and identified, how hand movements are guided, and how these processes interact. Comparing the impact of image size and familiar size, image size appears to exert more impact, and be processed faster than familiar size. That said, the more complex and difficult perceptual process of judging the familiar sizes of objects, requiring higher level perceptual identification and the recruitment of prior experiences and memory, also occurs automatically and robustly enough to interfere with judgments of image size. Critically, both image and familiar size are processed even when task-irrelevant.

The strength of this bidirectional influence of image size on familiar size judgment, and familiar size on image size judgment is not absolute, however. Experiment 2 demonstrated that when the familiar size difference between paired objects was larger, the effects of familiar size on action became more robust. This had two effects. First, choosing the larger or smaller object based on its familiar size in the real world became easier the larger the difference between the two, despite the fact that a difference was always readily apparent. Secondly, and more importantly, familiar size interfered with the effects of image size—image size judgments in the image size task, and image size *interference* in the incongruent trials of the familiar

size task—more strongly with increasing familiar size difference, suggesting greater salience and representation robustness.

Overall, the present study provides evidence that even high-level aspects of visual perception—the identification of real world objects and integration of prior knowledge regarding their sizes in the real world—interact with visually-guided action automatically and systematically. This points to a far more integrated view of perception and action than classically hypothesized. However, the current study alone is insufficient to explain these interactions on a mechanistic level. Further investigations are needed to identify the mechanisms responsible for the perception of object size (image size, familiar size, and other aspects), decision-making, visually-guided action, and their relationships.

Appendix

In both Experiments 1 and 2, after pointing movements were normalized over the distance from the screen (z-dimension position), these normalized positions were analyzed using a cluster-based permutation test. All 100 datapoints, representing the average position in the x-dimension for hand movements at that percentage into the movement, were compared to a baseline of zero representing no significant difference between congruent and incongruent conditions. In order to correct for the multiple comparison problem arising from conducting 100 t-tests, we used the Monte Carlo method to sample the datapoints in 500 iterations and find those points that were consistently more significant than the calculated test statistic. This analysis was performed using the Fieldtrip toolbox for Matlab (Oostenveld, Fries, Maris, & Schoffelen, 2011). The key datapoint in this subset is the first datapoint that is significantly greater than zero, indicating the point at which the trajectories of congruent and incongruent trials begin to deviate on average.

Figure A1 shows average Experiment 1 trajectories for congruent and incongruent trials independently in both the image and familiar size tasks. The red lines indicate the average trajectories in the image size task, and the blue lines, the familiar size task. The solid lines are congruent conditions and the dotted lines are the incongruent conditions. Here the key timepoint indicating significant deviations in hand movements is the point of deviation between the congruent and incongruent trials in each task individually. Consistent with the difference score analysis presented in the main text, congruent and incongruent trials deviate earlier in the familiar size

task than the known size task, indicating earlier interference from image size than familiar size.

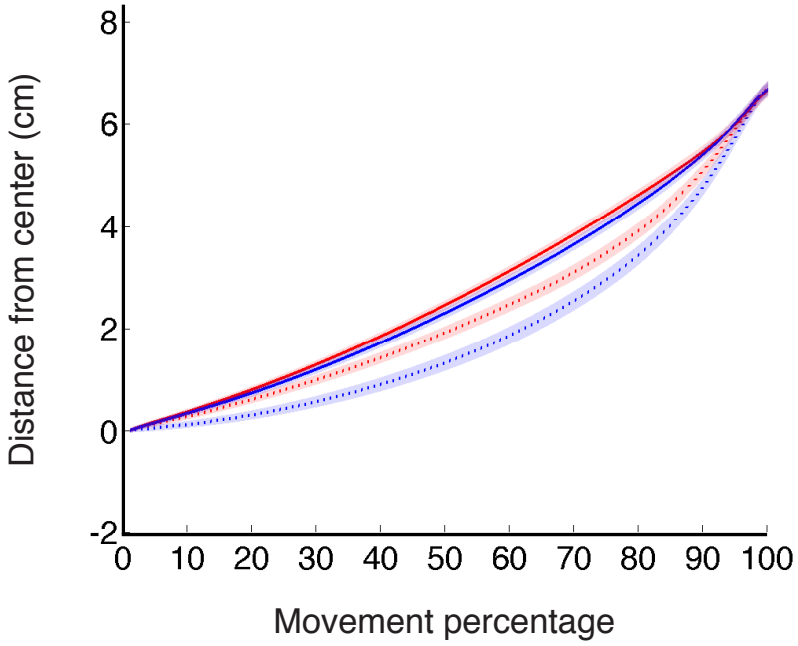

Figure A1. Experiment 1 trajectories for congruent trials (solid lines) and incongruent trials (dotted lines), in the image size task (red lines) and familiar size task (blue lines). All error bars represent 95% confidence intervals. Consistent with Figure 3, congruent and incongruent trials deviate in the familiar size task earlier than in the image size task.

General discussion

The studies presented here represent differing visual perceptual processing requirements, and differing visually-guided action tasks. We examine not just simple paired perception and action measures, but rather a range of interpretations of both "perception" and "action."

Specifically, we address forms of action which have been relatively ignored in the perception and action literature despite being common in daily life. In the real world we might quickly reach to press a button on an elevator door to prevent it from closing. This is an example of a rapid goal-directed pointing movement, and thus it would be modulated by the size of the button (Fitts, 1954b; Murata & Iwase, 2001) and by other alternate button options (Hick, 1952; Teichner & Krebs, 1974). In a normal day we also make countless saccadic eye movements, both goal-directed saccades like moving your eyes to a teacup in front of you in preparation for picking it up, and exploratory saccades like moving your eyes back and forth between two teacups before selecting which one you prefer (Epelboim et al., 1997; Gielen et al., 1984; Walker, Walker, Husain, & Kennard, 2000).

Similarly, we examined a range of perceptual processes, including higher-level forms of target perception than those commonly investigated alongside action. For example, our perception of real-world objects involves conceptualization of how large or small they are in the real world—we expect a rubber duck to be physically smaller than a boat (though artists have taught us that this isn't always the case)

(Konkle & Oliva, 2011, 2012a, 2012c). Thus, we are able contribute novel insights into how different forms of perception and different forms of action interact with themselves and with each other.

Chapter 1 implications

In Chapter 1 we found evidence that the Ponzo illusion influences aspects of both visually-guided hand movements and saccadic eye movements. Specifically, movement preparation for both actions was faster when targets were perceived as larger based on the illusion, just as they were when the targets were actually larger in their image size. Thus, this aspect of action appears not to differentiate between the illusory and veridical physical nature of targets. In contrast, the online execution phase of movements of both types was faster when targets were physically larger, but not when the illusion caused them to appear larger. Thus, movement *execution* responded only to image size while movement preparation responded to both image size and illusory size. The relationship between the image size and illusory size of the stimuli can additionally be seen as a conflict to be resolved by the visual system. This conflict resolution process may additionally contribute to the effects seen on visually guided action, as further discussed later.

Further, though hand and eye movements serve very different purposes in the real world, and are controlled by largely different mechanisms (Johansson, Westling, Backstrom, & Flanagan, 2001; Land, Mennie, & Rusted, 1999; Land & McLeod, 2000; Land & Hayhoe, 2001), here they responded to the illusion in a highly consistent manner. Specifically, the degree to which pointing movements and

saccades were influenced by the illusion was correlated within subjects, which we interpret as evidence of a shared, effector-general mechanism for the perception of illusion and its influence on action. While the studies presented here are not sufficient to speak to this actual neural mechanism, past research has shown that the superior colliculus (SC) modulates target selection for both hand and eye movements in an effector-general manner (J.-H. Song, Rafal, & McPeek, 2011). Thus, the SC may be responsible, or part of a network responsible for integrating illusion perception and target selection across movement effectors.

Finally, this study additionally compared hand and eye movements when they were independent, versus coordinated in a more naturalistic manner. Independent movements are often studied in the lab, however in the real world they are typically coupled, both in space and time (Bekkering, Abrams, & Pratt, 1995; Carey, Coleman, & Della Sala, 1997; Fisk & Goodale, 1985; Gielen, van den Heuvel, & van Gisbergen, 1984; Jackson, Newport, Mort, & Husain, 2005; Johansson, Westling, Bäckström, & Flanagan, 2001; Neggers & Bekkering, 2000, 2001; Sailer, Eggert, Ditterich, & Straube, 2000; Song & McPeek, 2009; Vercher & Gauthier, 1988). By manipulating whether hand and eye movements were independent or coordinated, we found evidence that illusion influences both forms of action equally when performed independently, but shifts to only affect eye movements when the two are performed simultaneously. Thus, the aforementioned mechanism may allocate its resources preferentially to the eyes. Behaviorally, this suggests that the interactions between illusory size and action are not static, and vary based on task demands.

Chapter 2 implications

The study described in Chapter 2 showed further evidence of influences from even higher-level perception processes on visually-guided action. By manipulating the *image* and *familiar sizes* of real-world objects, we showed that visually guided action is modulated by both the lower-level feature *image size* and the higher-level feature *familiar size*. Crucially, both were processed automatically, even when task-irrelevant. This automatic processing of a task-irrelevant feature led to impairment in performing the task at hand—when image size and familiar size were incongruent, movements took more time to be initiated and executed, and were more curved toward the incorrect target option.

While this conflict was bidirectional—image size interfered in the familiar size judgment task and familiar size interfered in the image size judgment task—the influence of image size was more robust overall and appeared earlier in the movements than familiar size. Thus, to use the terminology of cognitive control interpretations of the classic Stroop task, we propose that image size is processed by the *direct pathway,* which requires top-down suppression to overcome in favor of the *indirect pathway* process, familiar size perception.

However, by varying the magnitude of the familiar size differences, we found that larger differences produce a more robust influence on action. When the relative familiar size differences between paired objects was larger, familiar size interfered more in the image size task, and mitigated the interference from image size in the familiar size task. Thus, the relative strength of image size and familiar size

representations are not fixed, and the two display reciprocal interactions despite having large differences in processing complexity and underlying neural mechanisms.

Interactions between levels of perceptual processing

In Chapter 1 we saw illusion effects primarily in initiation latency, particularly when examining pointing movements. This could simply reflect illusion's influence on the action preparation phase, or a more cognitive decision-making conflict as well. Previous research into reach-tracking as a methodology for investigating underlying cognitive processes has characterized distinct aspects of pointing movements as reflecting specific components of cognitive control (Erb et al., 2016). Here, initiation latency was shown to reflect the inhibition of a motor response in order to allow adjustments of the response threshold for selecting a target. This is an early stage conflict resolution mechanism, in contrast to later stage choice conflict persisting after movement initiation, which we did not find evidence for. Thus, the effect of illusion on initiation latency but not movement time is consistent with early conflict resolution—decisions regarding image size and illusory size can be made relatively soon after stimulus presentation, with online calibration during the movement being unnecessary.

In Chapter 2 image size and, more importantly, familiar size impacted both the initiation latency *and* movement time/curvature of pointing movements, suggesting that conflict was more difficult or took longer to resolve than in Chapter 1. Again, the effect in initiation latency suggests earlier attempts at conflict resolution, here between image size and familiar size. However, the effect seen in curvature

suggests that the conflict is not totally resolved and the correct target completely selected until later, after the movement has begun. The robust curvature effect points to consistent co-activation of familiar size and image size representations, again, even though only one feature was relevant at a time, and in each task trials were blocked to minimize any effect of task-switching. Thus, there are early and late components to the disambiguation of image size and familiar size, perhaps reflecting the earlier processing of image size and the later processing of familiar size.

In both Chapter 1 and Chapter 2, we see perception not just interacting with action, but interactions between different levels of perceptual processing as well. In Chapter 1, both image size and illusory size contributed to the effects seen in the behavioral measures investigated. In Chapter 2, image size and familiar size were in direct conflict. These effects on action would not be possible if perception and action were separate, but also would not be possible if perception were a feedforward process such that it lacked reciprocal interactions between high and low levels of processing.

The present studies can't directly compare illusory and familiar size perception and the influence of each on action. However based on the present evidence we hypothesize that the relatively lower level process of the two, illusory size perception, would exert earlier and more robust influence on action. Future studies could attempt to address this question by systematically varying illusory size and familiar size in a unified paradigm as we did with image size and familiar size in Chapter 2.

Furthermore, the role of *environmental size* could be similarly disambiguated from other aspects of object size, and examined. Environmental size refers to the size of an object within its environment, and this integration has been shown to occur at an early processing phase, ahead of even mental scaling (Bennett & Warren, 2002). In Chapter 1, targets are presented on the screen alongside a rich 3D texture. Consequently, our measure of *illusory size* relies on the environmental size of the stimulus as integrated into the 3D scene, while *image size* is essentially the retinal image size. In Chapter 2 no scene information is provided on the screen, but the stimuli are viewed binocularly providing depth information about the position of the screen itself. Thus retinal image size and environmental size might be confounded in our measure of *image size*.

Again, based on previous evidence that environmental size is processed earlier than more complex functions like mental scaling and presumably object identification, we would expect it to come online earlier and more robustly than familiar size, but later than the low-level feature of retinal image size. The relationship between environmental size and action is more complex though. Environmental size is arguably more important for guiding action than either familiar size or retinal image size, and thus it might take more time to process, but influence action execution more strongly than retinal image size. Again, directly manipulating retinal image size, environmental size, and familiar size in one paradigm would be valuable in addressing these questions.

Size constancy in the Ponzo illusion and real-world size perception

In both Chapters 1 and 2 the methods employed exploit discrepancies between the size of a stimulus presented on the screen, and the manner in which participants experience the stimuli. In Chapter 1 this involves the Ponzo illusion causing circles to appear to be different sizes based on the context in which they appear. This illusion largely draws on size constancy mechanisms. By imitating a 3D scene in which lines understood to be parallel converge and texture gradients understood to be uniform shrink on one side, an object presented on this side is understood to be farther away. In the real world, when a stimulus occupies the same amount of space on the retina but is understood to be farther away, it must necessarily be physically larger.

Thus, it can be argued that in our task there is conflict between the implied distance of the stimuli (based on 3D depth cues) and binocular information about the distance of the screen in front of the participant. Similarly, in Chapter 2 we create conflict between the environmental size of the image as presented on the screen, and familiar sizes of real-world objects as they exist within their typical environments.

Thus, both chapters may rely on size constancy mechanisms to disambiguate the nature of the stimulus as presented on the screen, and as understood to exist within its environment. The present evidence suggests that the conflict introduced in Chapter 1 is easier to overcome. Conflict between image size and illusory/environmental size is resolved early, in the movement preparation phase, and fails to impact the movement execution phase for isolated hand and eye movements (Exp. 1). When eye movements precede the initiation of the hand movements, the conflict resolution is reflected in the preparation and execution of the eye movements,

but not the hand movements (Exp. 2). Thus, the effector-general mechanism which prioritizes the eyes over the hands may be a size constancy mechanism, as opposed to or in addition to a target selection mechanism. In Chapter 2, the conflict is resolved over the course of the movement and results in curved trajectories, suggesting a later conflict resolution mechanism. This is again consistent with familiar size being processed later than both image size and environmental size (Bennett, 2007).

Insights into perception/action dissociation and integration

Both Chapters 1 and 2 address holes in the existing dual-stream hypothesis and perception/action dissociation literature. Here we provide evidence for novel forms of perception-action interaction, contradicting the notion of a substantial functional dissociation between perception and action.

Again, the classical dual-stream hypothesis for vision states that two individual visual processing streams exist: the "what pathway" for the perception and identification of objects in the ventral stream, and the "where/how" in the dorsal stream for guiding action. The most oft-cited behavioral study endorsing this hypothesis demonstrated a dissociation between perception and action in healthy normal subjects using the Ebbinghaus illusion and a grasping paradigm (Aglioti et al., 1995). While participants consistently reported their percepts of the targets within the illusion being different sizes, they were able to reach out and grasp the objects in a way that was unaffected by the illusion. Thus the authors claim that the dorsal stream processed the stimuli accurately independently of the ventral stream's perception of the illusion.

Such strong early claims of a complete functional separation between perception and action have since been softened (M. A. Goodale, 2014; Milner & Goodale, 2008). However, the fact remains that clinical neurological evidence and behavioral evidence together point to some degree of disparity between the two streams. The question then becomes in what circumstances, and to what degree do the two streams interact?

Prior studies primarily looked at movement execution, and largely saw no impact of illusory size (N. Bruno & Franz, 2009; Ganel et al., 2008; Van Donkelaar, 1999). However, we showed that even when movement execution is immune to illusory size, movement preparation is not. Similarly, prior studies largely studied hand movements, and those that did study eye movements studied them in isolation (de Brouwer et al., 2014; Knox, 2010; McCarley et al., 2003). We showed that illusion impacts eye movements more than it does hand movements. Furthermore, when the two are performed at the same time as they typically were in prior studies and are in daily life, the effects of illusion shift entirely to eye movement execution.

Finally, prior studies have largely viewed the "perception" in "perception/action dissociation" to mean lower level perceptual processing. However, both behavioral and neurological evidence point to higher level perceptual features as being intrinsic aspects of object perception, and as being processed automatically along with lower level features (Caramazza & Shelton, 1998; Chao & Martin, 2000; Konkle & Oliva, 2011, 2012c). Thus, our evidence of interactions between familiar size and action could inspire future perception and action work to similarly expand into higher level perceptual features and processes.

Conclusion

Overall, the studies presented here contribute to a greater understanding of the interactions between levels of visual perceptual processing, and interactions between visual perception and action. It is not controversial that the brain's functions are well integrated, but advancements in research continue to show interactions between unexpected processes. Here, we demonstrate that more complex forms of perception fundamentally influence less complex forms (Chapter 2), and that functionally distinct forms of action can dramatically alter each others' responses to the same stimuli (Chapter 1). We additionally provide evidence that visually-guided action is modulated by varying levels of target size perception as opposed to lower level features like image size only. While this relationship between perception and action is not uniform across levels of processing, vision for perception and vision for action overall are highly interconnected.

In daily life, assuming everything is working correctly, we never notice the seams in our perceptual experience. We don't think of the teacup in front of us as being 15 cm across first and a vessel for holding tea second, and we don't perform the calculations necessary to reach out and grasp it. We also don't notice the dynamic shifts that occur in perception when task demands change, with the exception perhaps of noticing that making one decision is harder than another. Again though, we do not keep a running tab of the accumulating evidence for one option over another—the brain performs such tasks automatically and subconsciously.

It is commonly said that this is the brain "tricking us" into thinking that our experience of the world is more complete than it is, and that our actions and behaviors

are effortless. However, a more accurate view might be that it is instead showing us several important truths: how complete our environment is, how well-adapted we are to it (Gibson, 1986), and how well integrated the brain's myriad functions are with the environment and with each other.

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