

Dynamic modulation of illusory and physical target size on separate and coordinated eye and hand movements

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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 perceived and physical 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 both physically and perceptually larger targets produced faster preparation for both effectors. Furthermore, participants who showed a greater influence of the 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 illusions. However, only physical but not perceptual target sizes influenced saccade and pointing execution. When pointing was coordinated with saccades, we observed different dynamics: pointing no longer showed modulation from illusory size, while saccades showed illusion modulation for both preparation and execution. Interestingly, in independent and coordinated movements, the illusion modulated saccade preparation more than pointing preparation, with this effect more pronounced during coordination. These results suggest a shared mechanism, dominated by the eyes, may underlie visually guided action preparation across effectors. Furthermore, the influence of illusions 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 nonessential loci (Hayhoe, Shrivastava, Mruczek, & Pelz, 2003; Land & Hayhoe, 2001; Land & Lee, 1994; 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; Neggers & Bekkering, 2000, 2001; Sailer, Eggert, Ditterich, & Straube, 2000; Song & McPeck, 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 nonhuman 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

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close coupling between eye and hand movements as well as 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 physical sizes of objects, and the perceptual sizes induced by the illusions (Bruno, 2001; Bruno & Bernardis, 2002; Franz, 2001; Glover & Dixon, 2002; Milner & Goodale, 2008). For example, an early paper by Aglioti, DeSouza, and Goodale (1995) demonstrated that while the perceived sizes of disks presented within the Ebbinghaus illusion were modulated by the illusion, the grasp aperture of hand movements relied more on their physical sizes, in accord with the dual-streams hypothesis proposing separate vision for perception and vision for action (Goodale & Milner, 1992; Milner & Goodale, 1995, 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 illusions 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 modulation based on the illusion when coordinated with hand movements as opposed to being performed independently.

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

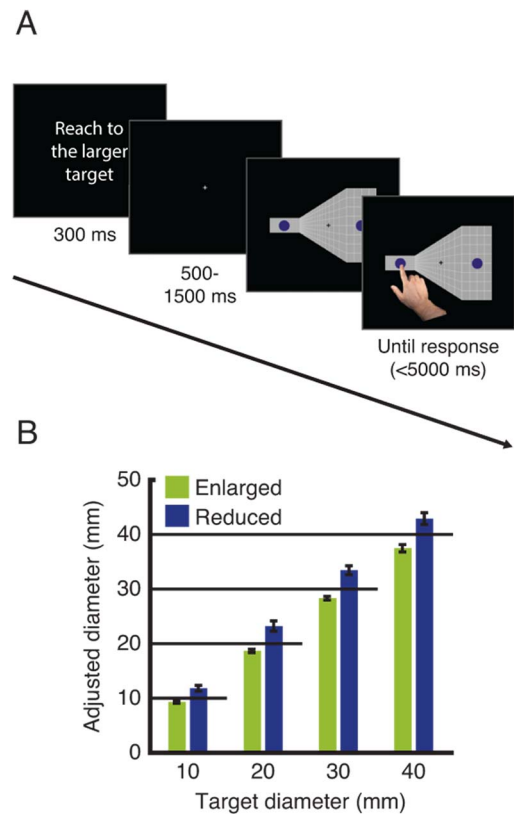


Figure 1. Experimental paradigm and illusion performance. (A) Illusion and pointing trial diagram. Within the illusion configuration shown, the circle on the left (enlarged condition) is perceived as being farther away from the viewer, and therefore larger than the circle on the right (reduced condition). 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 physical sizes in the enlarged conditions, and significantly smaller in the reduced conditions, across all physical target sizes. Error bars represent between-subjects standard error.

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 veridical physical sizes of targets. By presenting identical illusions for both saccade and pointing tasks we were able to directly compare the modulation of illusory and physical target sizes for each effector, both during movement preparation and execution (Experiment 1). We also 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 (Experiment 2). Furthermore, we compared the results in the movement preparation and execution phases between isolated (Experiment 1) and

coordinated movements (Experiment 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.

Experiment 1: Effects of illusory and physical target size on independent pointing and eye movements

The execution of goal-directed pointing movements has long been known to be modulated by the physical size and distance of targets. Fitts' law states that the higher the index of difficulty (ID; the smaller or farther away a target is), the slower the movement time to hit a 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 physical 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 physical target size decreases (Wu, Kwon, & Kowler, 2010). The effect of illusory rather than physical 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 illusions (for review, see Bruno, Knox, & de Grave, 2010). For example, McCarley, Kramer, and DiGirolamo (2003), and DiGirolamo, McCarley, Kramer, and Griffin (2008) showed that the amplitudes of both voluntary and reflexive saccades were scaled with the illusory lengths of lines that were physically the same size. Thus, in Experiment 1, we addressed how pointing and saccades are individually modulated by illusory target size in contrast to physical target 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 the 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 (Moher & Song, 2013, 2014). All experimental protocols were approved by the Institutional Review Board at Brown University.

Participants were compensated monetarily (\$8 per hour) or with course credit.

Participants

Seventeen right-handed participants (11 women, six men; mean age 24 years) 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 44.1×33.0 cm onto the Plexiglas. 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 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, Kanata, ON, Canada) and recorded at a rate of approximately 250 Hz.

Stimuli

All stimuli were presented on a black background. A white fixation cross, measuring 7×7 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 size (10 mm, 1.09° ; 20 mm, 2.17° ; 30 mm, 3.26° ; or 40 mm, 4.34°) in diameter were presented at a distance of 12.5 cm (12.37°) 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 (Adobe Systems, San Jose, CA) and comprised a white and gray grid simulating a wall receding into the distance, similar to stimuli used in prior studies (Ganel, Tanzer, & Goodale, 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 physical sizes. 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 physical sizes, 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 (eight women, six men; mean age 21) was presented with the illusion (Figure 1A) with one circle in either the enlarged or reduced condition, and another circle 10.5 cm (9.22°) 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 2×4 repeated measures ANOVA with factors of illusion condition (enlarged vs. reduced) and physical target diameter (10 mm, 20 mm, 30 mm, and 40 mm), revealed main effects of illusion condition, $F(1, 13) = 4.789$, $p = 0.048$, $\eta_p^2 = 0.269$, and physical size, $F(3, 39) = 912.3$, $p < 0.001$, $\eta_p^2 = 0.986$, and no interaction, $F(3, 39) = 2.25$, $p = 0.098$, $\eta_p^2 = 0.148$. Together, this indicates that the illusion was effective and participants perceived the enlarged condition as significantly larger than the reduced condition, consistent across physical target 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 per block) with each block containing targets of only one of the four physical sizes (two blocks per size). All participants completed all blocks and were presented with all physical and illusory size conditions. Each block was broken into two sub-blocks (24 trials per sub-block) in which the targets were consistently either the perceptually enlarged or perceptually reduced condition only. Thus, each illusion condition of each

physical 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 physical 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 physical target sizes. Within sub-blocks, trials were counterbalanced for target presentation on the left or the right side of the screen, and for the background illusion to be 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 54×54 mm ($4.97^\circ \times 4.97^\circ$) 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) software, 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 nontarget 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 nontarget 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 unsigned *constant error* of the pointing movements was calculated from the average absolute 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 $100^\circ/\text{sec}$ 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 100° visual angle/sec was performed successfully hitting the target, this was defined as a *corrective saccade*. Saccadic IL was defined as the time elapsed between stimulus onset and initial saccade onset. As in Wu et al. (2010), 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 the unsigned constant error was calculated as the absolute distance from the target center to the final landing position of the saccade, 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% ($\pm 0.80\%$) and 93.14% ($\pm 2.13\%$), respectively. These accuracy rates were consistent across conditions for both tasks. Approximately 10% of 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% ($\pm 2.4\%$) for the pointing

task and 87.17 ($\pm 3.2\%$) for the saccade task. All subsequent data analyses were restricted to nonrejected correct (i.e., illusion-consistent) pointing and saccadic eye movements. Only illusion-consistent responses were included to ensure that all analyzed trials involved the dissociation between physical and illusory size necessary to reveal any dissociation between perception and action.

Effect of illusory and physical 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 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 physical target diameters. 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 size increased from 10 mm to 40 mm. These observations were supported by a 2×4 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, $F(1, 13) = 5.99$, $p = 0.029$, $\eta_p^2 = 0.316$, a main effect of stimulus size, $F(3, 39) = 8.81$, $p < 0.001$, $\eta_p^2 = 0.404$, and no interaction $F(3, 39) = 1.82$, $p = 0.159$, $\eta_p^2 = 0.123$. Thus, both the illusory and physical sizes of targets modulated the initiation latency for pointing movements.

Pointing execution: To examine the impact of the size-contrast illusion on the execution of pointing movements across the four physical target 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 physical target size such that movements were faster to the physically larger targets and slower to the physically smaller targets across subjects, consistent with Fitts' law (Fitts, 1954).

A 2×4 repeated measures ANOVA with factors of illusion condition and target diameter here revealed no effect of the illusion, $F(1, 13) = 0.493$, $p = 0.495$, $\eta_p^2 = 0.037$, a significant main effect of target diameter, $F(3, 39) = 6.34$, $p = 0.001$, $\eta_p^2 = 0.328$, and no interaction $F(3, 39) = 0.644$, $p = 0.591$, $\eta_p^2 = 0.047$. Thus, in contrast to pointing preparation, this result suggests that manipulating physical 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

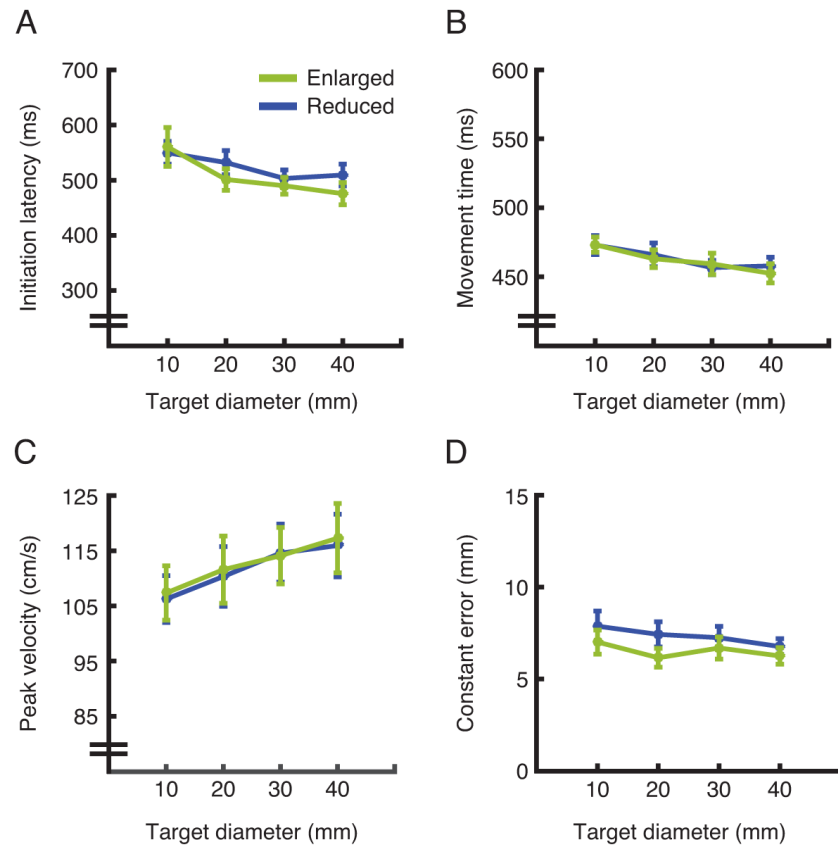


Figure 2. Independently performed pointing measures (Experiment 1). All error bars represent between-subjects standard error. (A) Pointing initiation latency. IL was faster when targets were either perceived as larger due to the illusion, or were physically larger. (B) Pointing movement time. MT was faster when targets were physically 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 targets were physically 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 was larger for the perceptually smaller targets than for the perceptually larger targets, but no difference was seen based on physical target size.

fact that movements were faster to physically larger objects 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 physical 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 2×4 repeated measures ANOVA which revealed no significant effect of the illusion, $F(1, 13) = 1.13$, $p = 0.307$, $\eta_p^2 = 0.080$, a significant effect of target size, $F(3, 39) = 10.51$, $p < 0.001$, $\eta_p^2 = 0.447$, and no interaction $F(3, 39) = 0.468$, $p = 0.706$, $\eta_p^2 = 0.035$. This is consistent with our other measure of movement execution, MT, which also showed impact based on physical target diameter but not illusion condition.

Thus, both movement execution measures were modulated by the physical 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 physical target sizes, we confirmed that participants overall performed the pointing task accurately across all conditions. As shown in Figure 2D, constant error was modulated by physical and illusory size during pointing. Pointing movements more precisely landed on the centers of their targets as both the physical target 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 condition, $F(1, 13) = 9.31$, $p = 0.009$, $\eta_p^2 = 0.417$ and stimulus size, $F(3, 39) = 4.92$, $p = 0.005$, $\eta_p^2 = 0.274$, and no interaction $F(3, 39) = 2.03$, $p = 0.125$, $\eta_p^2 = 0.135$.

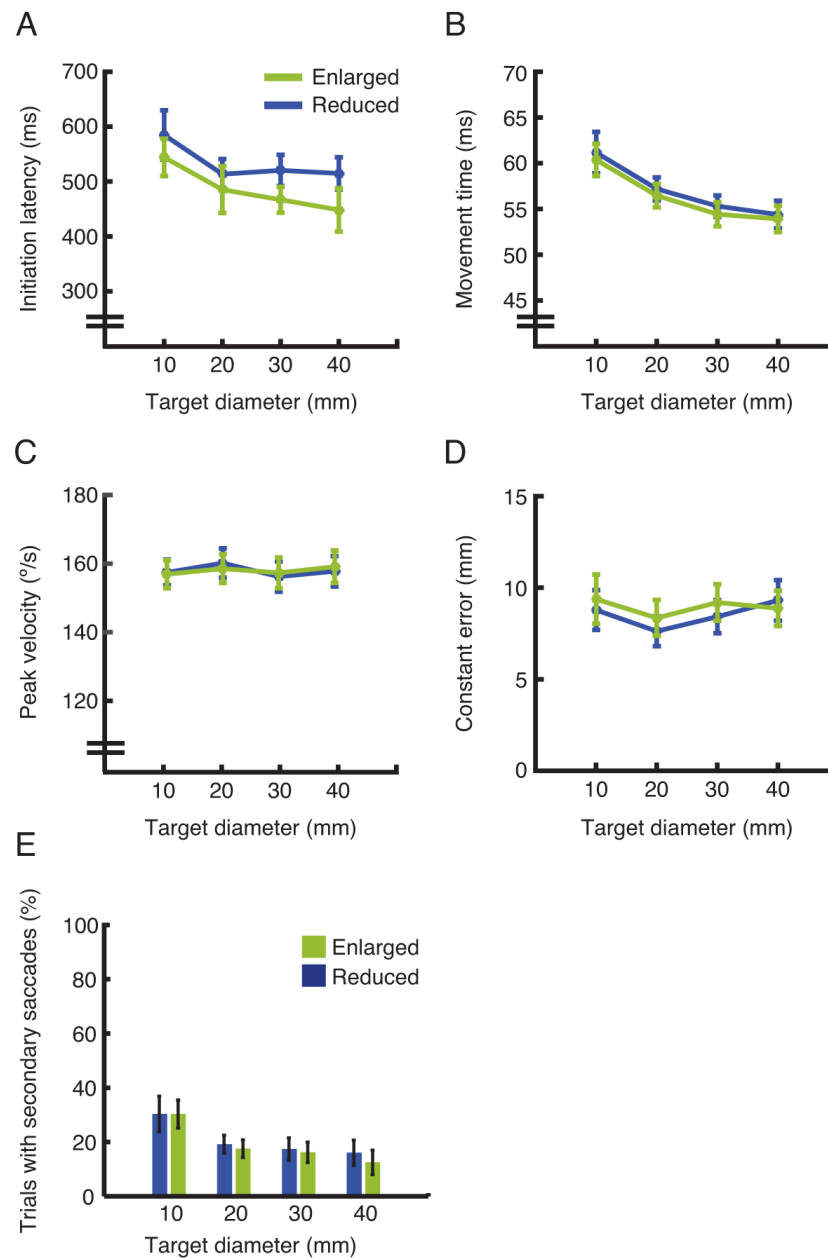


Figure 3. Independently performed saccade measures (Experiment 1). All error bars represent between-subjects standard error. (A) Saccade initiation latency. IL was faster when targets were either perceived as larger due to the illusion, or were physically larger. (B) Saccade total MT. MT was faster when targets were physically larger, but not when targets were perceived as larger due to the illusion. (C) Saccade peak velocity. There was no difference in saccades' peak velocities based on either physical 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 physical or perceptual illusory size.

Effect of illusory and physical sizes on saccade task

Saccade preparation: To determine the role of illusory target size in saccadic eye movement preparation, we compared the initiation latencies (IL) of saccades between perceptually enlarged and reduced targets across the four physical target 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 physical target size. A 2×4 ANOVA with factors of illusion condition and stimulus size supported these observations, with a significant main effect for illusion condition $F(1, 13) = 5.83, p = 0.031, \eta_p^2 = 0.310$, and a significant main effect for physical targets size $F(3, 11) = 4.391, p = 0.032, \eta_p^2 =$

0.568. No interaction was observed $F(3, 39) = 1.28, p = 0.296, \eta_p^2 = 0.089$. This modulation of saccadic eye movement preparation based on both illusory and physical target size (Figure 3A) is consistent with the results seen in pointing movement preparation (Figure 2A).

Saccade execution: We also examined the modulation of saccadic eye movement execution by physical and illusory target size by analyzing saccadic movement time (MT). Figure 3B shows that MT decreased as physical target size increased, indicating that the total time required between saccade initiation and landing within the intended target was modulated by physical target 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 illusory size on saccadic eye movement execution.

Here we found no main effect of illusion condition, $F(1, 13) = 2.51, p = 0.137, \eta_p^2 = 0.162$, a main effect of target diameter, $F(3, 39) = 15.38, p < 0.001, \eta_p^2 = 0.542$, and no interaction, $F(3, 39) = 0.098, p = 0.961, \eta_p^2 = 0.007$ 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 physical target 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 physical or illusory size (Figure 3C); unlike with hand movements (Figure 2C), saccades in all conditions showed approximately the same velocity profile. Thus there was no effect of the illusion, $F(1, 13) = 0.004, p = 0.95, \eta_p^2 < 0.001$, no effect of stimulus size, $F(3, 39) = 0.996, p = 0.405, \eta_p^2 = 0.071$, and no interaction $F(3, 39) = 1.30, p = 0.289, \eta_p^2 = 0.091$. 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 physical size; there was no main effect of illusion condition, $F(1, 13) = 1.12, p = 0.309, \eta_p^2 = 0.079$, no effect of stimulus size, $F(3, 39) = 1.74, p = 0.175, \eta_p^2 = 0.118$, and no interaction $F(3, 39) = 0.688, p = 0.565, \eta_p^2 = 0.050$.

Interestingly, we also noticed a higher prevalence of corrective saccades in trials with smaller physical target sizes than trials with larger targets (Figure 3E), supported by a 2×4 ANOVA with no main effect of illusion condition $F(1, 13) = 2.25, p = 0.157, \eta_p^2 = 0.148$, a main effect of physical size $F(3, 39) = 9.35, p < 0.001, \eta_p^2 = 0.418$, and no interaction, $F(3, 39) = 0.419, p = 0.740, \eta_p^2 = 0.031$. 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 physical 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 the 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 the 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 physical 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 illusory and physical target sizes for IL, and modulation based on physical target 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:

$$\text{Illusion Index}_{\text{IL}} = \frac{\text{Mean IL}_{\text{reduced}} - \text{Mean IL}_{\text{enlarged}}}{\text{Mean IL}_{\text{reduced}} + \text{Mean IL}_{\text{enlarged}}} \quad (1)$$

where $\text{Mean IL}_{\text{reduced}}$ and $\text{Mean IL}_{\text{enlarged}}$ indicate the mean initiation latency of all reduced and enlarged conditions, respectively, by collapsing across physical target diameter.

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 IL differences between 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, $r = 0.66, p = 0.01$. The least-squares regression line (solid) demonstrates this trend. The unity line (dotted) indicates equal modulation based on the 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, $t(13) = 2.18, p = 0.048, d = 0.58$. Thus, the illusion affected the preparation of eye movements more than hand movements overall.

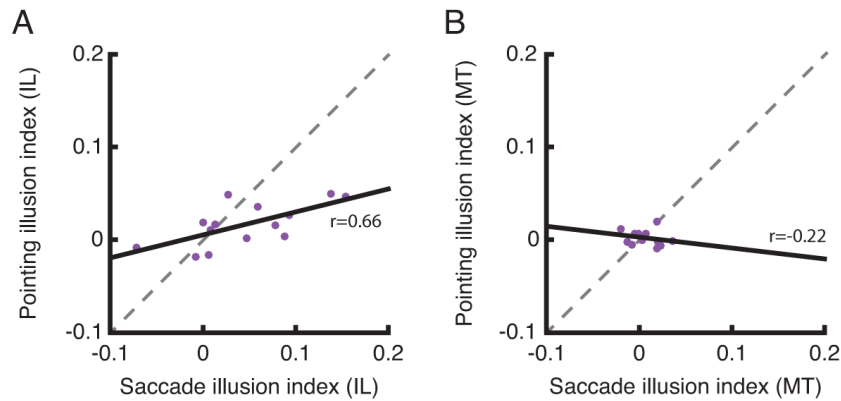


Figure 4. Correlations between illusion impact on independent pointing and saccades (Experiment 1). (A) Correlation in illusion’s impact on initiation latency. The effect of the illusion on IL for both pointing and saccades was positively correlated such that subjects with more of an influence of the illusion on pointing IL also had a larger influence for saccadic IL. Additionally, a significant number of subjects showed a higher illusion index for saccades than for pointing. (B) Correlation in the illusion’s impact on movement time. There was no relation between the influence of the illusion on pointing and saccadic initiation latency.

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

$$\text{Illusion Index}_{\text{MT}} = \frac{\text{Mean MT}_{\text{reduced}} - \text{Mean MT}_{\text{enlarged}}}{\text{Mean MT}_{\text{reduced}} + \text{Mean MT}_{\text{enlarged}}} \quad (2)$$

As expected, given that we saw no effect of the illusion on movement time in pointing (Figure 2B) or saccades (Figure 3B), we saw no relation between the impact of the 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 $r = -0.22$, $p = 0.44$, again shown by the least-squares regression line (solid). Comparing the data points to the unity line (dotted) here reveals no systematic bias, $t(13) = 0.76$, $p = 0.46$, $d = 0.20$, suggesting that both pointing and saccade movement time are impacted by the illusion to a similar degree, consistent with neither showing a significant effect of illusion condition. 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 the illusion than pointing preparation.

Summary

Overall, Experiment 1 demonstrated that when goal-directed pointing and saccadic eye movements are performed independently, both respond to the perceptual size illusion in similar ways. Namely, the perceived illusory sizes of targets affected the preparation portion of pointing and saccadic eye move-

ments, 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 illusions can and do influence some aspects of action, provide new insight for the perception/action dissociation literature. Interestingly, we also demonstrated that while the influence of the illusion on pointing and saccade preparation was positively correlated, saccades were more susceptible to the 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 physical size on eye-hand coordination

Experiment 2 had two primary goals: to examine how size-contrast illusions modulate 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 Experiment 1. In order to answer these questions, we asked participants to perform the same pointing task as in Experiment 1, but without constraining eye movements. The resulting coordinated eye-hand movements within an otherwise identical paradigm to Experiment 1 enabled us to directly compare whether illusory size modulates independent and coordinated eye and hand movements differently.

Methods

Participants

Seventeen right-handed participants (13 women, four men; mean age 23 years) 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 Experiment 1.

Procedure

The task performed in Experiment 2 was the same as the pointing task in Experiment 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 Experiment 1.

Saccadic eye movements: The same algorithm as in Experiment 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 plus 1.8° 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 Experiment 1.

Results

Overall illusion-consistent target selection accuracy for the pointing task was 98.96% ($\pm 1.34\%$), which was consistent across conditions. As in Experiment 1, we confined our pointing analyses to correct (i.e., illusion-

consistent) trials. Furthermore, approximately 10% of the trials were excluded from data analysis from each task due to technical issues (e.g., sampling drop), such as erratic movements. Thus, the total percent of trials included in data analysis across subjects was 92.3% ($\pm 1.5\%$). We first report the results from the pointing component of the experiment, then the results from the free saccadic eye movements.

Effects of illusory and physical size on pointing with unconstrained saccades

Pointing preparation: Figure 5A compares the initiation latency of pointing performed alongside free saccades as a function of physical target 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, $F(1, 13) = 1.91$, $p = 0.190$, $\eta_p^2 = 0.128$. This differs from what we observed in the pointing movements performed alongside eye fixation in Experiment 1, where pointing IL was faster in the enlarged than the reduced conditions (Figure 2A). However, as in Experiment 1, IL was also faster for physically larger compared to smaller targets $F(3, 39) = 9.82$, $p < 0.001$, $\eta_p^2 = 0.430$. There was no significant interaction between effects of illusory and physical sizes on IL, $F(3, 39) = 0.767$, $p = 0.519$, $\eta_p^2 = 0.056$. Thus, this result shows that only the physical and not the illusory target size influences the preparation of pointing movements paired with natural eye movements.

Pointing execution: Figure 5B depicts the impact of the illusion on the execution of pointing movements. We found no significant difference in movement time (MT) based on illusory size, $F(1, 13) = 1.90$, $p = 0.191$, $\eta_p^2 = 0.127$, while physically larger targets facilitated MT marginally, $F(3, 39) = 2.60$, $p = 0.066$, $\eta_p^2 = 0.167$. There was no significant interaction effect of illusory and physical conditions on MT, $F(3, 39) = 0.066$, $p = 0.978$, $\eta_p^2 = 0.005$. This is consistent with the pointing movements performed with eye fixation in Experiment 1 (Figure 2B), in which physical size but not illusory size modulated pointing movement execution.

We also examined the peak velocity of pointing movements, as in Experiment 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 $F(1, 13) = 0.871$, $p = 0.368$, $\eta_p^2 = 0.063$, but peak velocity was higher for physically larger targets, $F(3, 39) = 7.70$, $p < 0.001$, $\eta_p^2 = 0.372$. There was no interaction effect, $F(3, 39) = 0.698$, $p = 0.559$, $\eta_p^2 = 0.059$. This is also consistent with the pattern observed with eye fixation in Experiment 1, in which physical size but not perceived illusory size modulated the peak velocity reached over the course of pointing movement execution. As shown

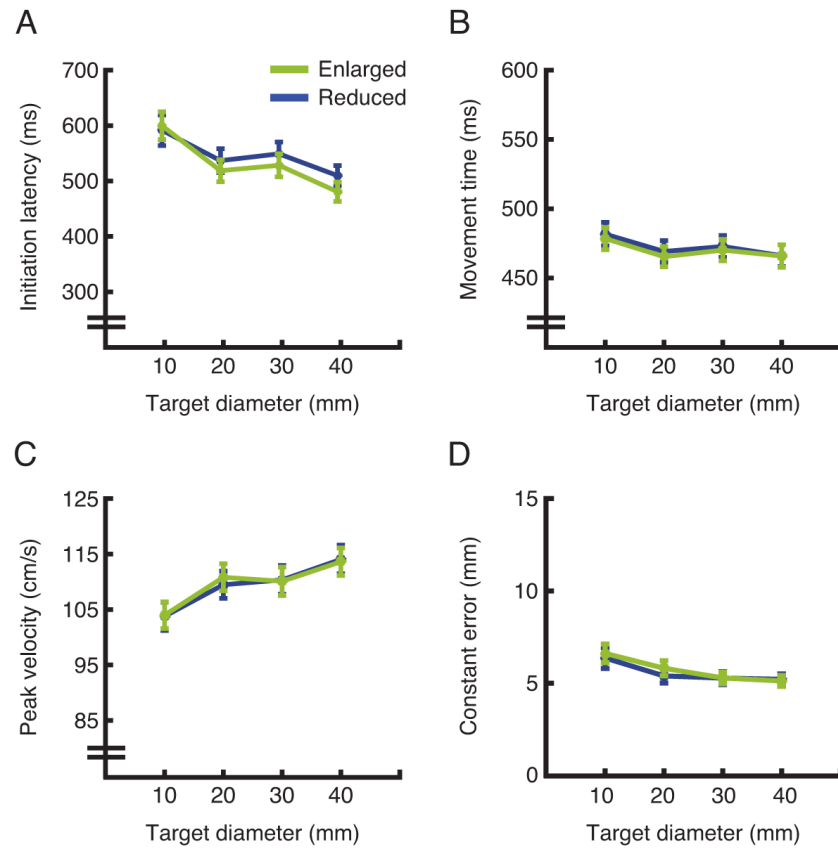


Figure 5. Pointing measures when performed in coordination with saccades (Experiment 2). All error bars represent between-subjects standard error. (A) Pointing initiation latency. IL was faster when targets were physically larger, but not when targets were perceived as larger due to the illusion. (B) Pointing movement time. MT was faster when targets were physically 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 targets were physically 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 pointing landing position and target center based on either physical or perceptual illusory size.

in Figure 5D, there was no effect of illusory target size on constant error, $F(1, 13) = 0.299$, $p = 0.594$, $\eta_p^2 = 0.022$, a marginally significant effect of physical size, $F(3, 39) = 2.58$, $p = 0.067$, $\eta_p^2 = 0.166$, and no interaction, $F(3, 39) = 1.23$, $p = 0.311$, $\eta_p^2 = 0.087$. Thus, constant error was consistent, suggesting that pointing movements were performed consistently across illusion conditions. Overall then, physical 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 Experiment 1, here eye movements were unconstrained and were not a task requirement. Trials with unreadable eye movements due to excessive head movement, blinking, or erratic saccades were excluded from saccade analysis ($27.20 \pm 4.00\%$ total excluded). Although unconstrained eye movements were allowed, we observed that participants made only

a very small number of targeted saccades (1.70 ± 0.55 per trial) and acquired the target within 1.38 saccades on average (± 0.24 ; Figure 6A). Thus, in a typical trial, participants looked directly at the target, though some trials involved looking at both the target and nontarget 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 & McPeck, 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, $F(1, 13) = 1.49$, $p = 0.243$, $\eta_p^2 = 0.103$, though significantly fewer saccades were made as the physical target size increased from 10mm to 40mm, $F(3, 39) = 13.52$, $p < 0.001$, $\eta_p^2 = 0.510$. There was no interaction effect, $F(3, 39) = 0.255$, $p = 0.857$, $\eta_p^2 = 0.019$. In Figure

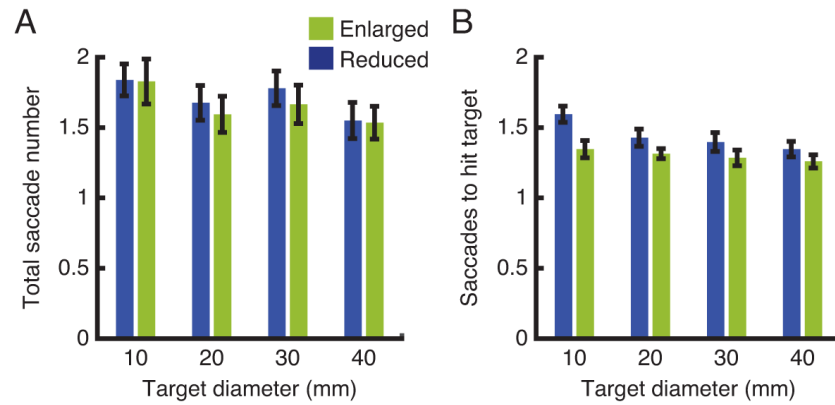


Figure 6. Patterns of free saccadic eye movements performed in coordination with pointing (Experiment 2). All error bars represent between-subjects standard error. (A) Total saccade number. Overall, more free saccadic eye movements were made per trial when targets were physically smaller, but not when 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 the target was physically smaller, and perceptually smaller based on the illusion.

6B, similarly, we compared the number of saccades made until the target was acquired. We demonstrated that the larger the illusory size, $F(1, 13) = 16.50$, $p < 0.001$, $\eta_p^2 = 0.559$, or physical size, $F(3, 39) = 5.08$, $p = 0.005$, $\eta_p^2 = 0.281$, the fewer saccades were needed to hit the target. There was no interaction between illusory and physical sizes, $F(3, 39) = 2.01$, $p = 0.129$, $\eta_p^2 = 0.134$. This suggests that as illusory or physical target size increases, participants more efficiently land their eyes on the target with fewer saccades.

Preparation of target saccade: We examined how the perceptual illusion affected freely coordinated eye movements toward 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, TIL was faster for larger physical target diameters. These observations were supported by a 2×4 repeated measures ANOVA which showed a significant main effect for illusion condition, $F(1, 13) = 34.29$, $p < 0.001$, $\eta_p^2 = 0.725$, and physical target size, $F(3, 39) = 3.57$, $p = 0.022$, $\eta_p^2 = 0.216$, and no interaction, $F(3, 39) = 0.754$, $p = 0.527$, $\eta_p^2 = 0.055$. Thus, the movement preparation of unconstrained saccades that were coordinated with pointing movements was modulated both by the illusory and physical sizes of targets. This is consistent with the pattern of the illusion's influence on the initiation latency of separate goal-directed saccades seen in Experiment 1 (Figure 3A), though these two measures are not identical.

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 physically larger compared to smaller targets. This was supported by an ANOVA showing a main effect of illusory size, $F(1, 13) = 27.39$, $p < 0.001$,

$\eta_p^2 = 0.678$, a main effect of physical size, $F(3, 39) = 3.83$, $p = 0.017$, $\eta_p^2 = 0.227$, and no interaction, $F(3, 39) = 1.53$, $p = 0.221$, $\eta_p^2 = 0.106$. Thus, the execution of unconstrained target saccades was modulated by both illusory and physical target size. Overall, the execution of unconstrained saccades (Experiment 2) differed from that of constrained goal-directed saccades (Experiment 1), in that here saccade execution was influenced by the physical and illusory sizes of targets, as opposed to physical size alone.

As seen in Figure 7C, we found no difference in peak velocity based on illusory size, $F(1, 13) = 1.34$, $p = 0.268$, $\eta_p^2 = 0.093$, a marginally significant effect of physical target size, $F(3, 39) = 2.81$, $p = 0.052$, $\eta_p^2 = 0.178$, and no interaction, $F(3, 39) = 1.40$, $p = 0.259$, $\eta_p^2 = 0.097$, suggesting that saccadic eye movements, like hand movements, were faster for physically but not perceptually larger targets.

Finally, as seen in figure 7D, physically larger targets resulted in larger constant errors, with no difference based on illusory size. An ANOVA revealed no main effect of illusion condition, $F(1, 13) = 0.392$, $p = 0.542$, $\eta_p^2 = 0.029$, a main effect of physical target size, $F(3, 39) = 5.80$, $p = 0.002$, $\eta_p^2 = 0.309$, and no interaction, $F(3, 39) = 0.456$, $p = 0.715$, $\eta_p^2 = 0.034$. However, overall there was no clear systematic pattern of illusory or physical size modulating landing position across experiments and effectors.

It is worth noting that the target saccade initiation latencies here (Figure 7A) were shorter overall than the initiation latencies of the independent saccades in Experiment 1 (Figure 3A). Thus, these fast unconstrained saccades which land on the targets ahead of the pointing movements may provide better visual feedback for the hand, and account for the reduced effect of the illusion on pointing.

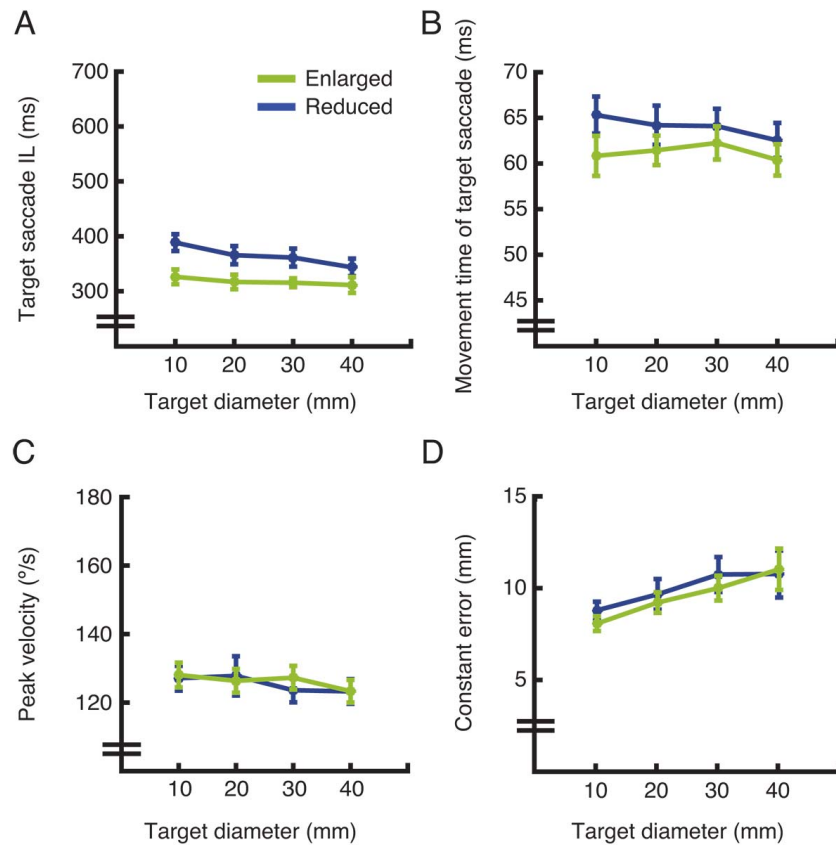


Figure 7. Free saccadic eye movement measures when performed in coordination with pointing (Experiment 2). All error bars represent between-subjects standard error. (A) Target saccade initiation latency. The latency to the onset of the target saccade was faster when targets were either perceived as larger due to the illusion, or were physically larger. (B) Saccade total movement time. Total MT was faster when targets were either perceived as larger due to the illusion, or were physically larger. (C) Saccade peak velocity. The peak velocity reached over the course of the movements was faster when targets were physically larger, but not when targets were perceived as larger due to the illusion. (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 physical target size.

Uncorrelated illusion modulation for coordinated pointing and saccades

Unlike in Experiment 1 where both pointing and saccade movement preparation (initiation latency) were modulated by the illusion, in Experiment 2 illusory size modulated the initiation latency measure for saccades but not for pointing. Nevertheless, as in Experiment 1 (Figure 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 Experiment 2, in Equation 3, we replaced Illusion Index_{IL} with Illusion Index_{TIL} using target saccade initiation latency (TIL; see Methods) to estimate the effect of the illusion on saccadic preparation.

$$\text{Illusion Index}_{\text{TIL}} = \frac{\text{Mean TIL}_{\text{reduced}} - \text{Mean TIL}_{\text{enlarged}}}{\text{Mean TIL}_{\text{reduced}} + \text{Mean TIL}_{\text{enlarged}}} \quad (3)$$

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

As anticipated given that there was only a measurable effect of the illusion on saccade preparation and not on pointing preparation, there was no significant correlation between the Illusion Index_{TIL} (Equation 3) for saccades and Illusion Index_{IL} (Equation 1) for pointing ($r = 0.29$, $p = 0.31$), 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 Experiment 1, we found that the illusion influenced the saccade task far more than pointing, resulting in higher illusion indices across subjects, and the data points falling below unity on average. This was supported by a paired t test which showed significantly higher illusion index values for

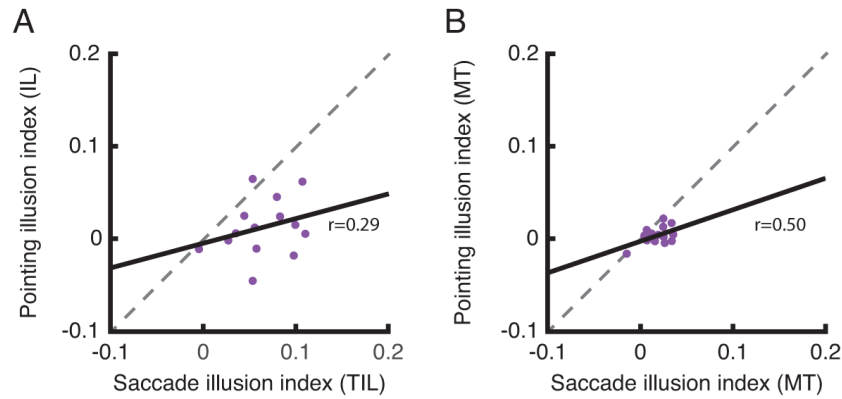


Figure 8. Correlations between the illusion impact on coordinated pointing and saccades (Experiment 1). (A) Correlation in the illusion's impact on initiation latency. There was no relation between the influence of the illusion on coordinated pointing and saccadic initiation latency. However as in Experiment 1, the illusion index was larger overall for saccades than for pointing. (B) Correlation in the illusion's impact on movement time. There was no relation between the influence of the illusion on coordinated pointing and saccadic movement time. Additionally, movement time illusion indices were also larger for saccades than for pointing.

saccades than for pointing across subjects, $t(13) = 4.98$, $p < 0.001$, $d = 1.33$.

As shown in Figure 8B, there was no correlation between $\text{Illusion Index}_{\text{MT}}$ for pointing and saccades ($r = 0.50$, $p = 0.07$), 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 Experiment 1, here there was a shift below unity, indicating that saccadic MT was significantly more impacted by the illusion than pointing MT, $t(13) = 4.79$, $p < 0.001$, $d = 1.28$.

Thus, when eye and hand movements are naturally coordinated as in Experiment 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 modulation based on the illusion compared to constrained eye movements, and compared 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 the illusion on saccade compared to pointing movement preparation, and the different patterns of the illusion's influence seen in Experiment 1 and Experiment 2, we compared the illusion indices for movement preparation between hand and eye movements in both Experiments 1 and 2. Figure 9 shows the mean $\text{Illusion Index}_{\text{IL}}$ and $\text{Illusion Index}_{\text{TIL}}$ (i.e., the degree to which the illusion modulated movement preparation) for both effectors and experiments. Again, the pointing task was identical

in Experiments 1 and 2. The saccades performed in Experiment 1 were goal-directed like the pointing movements in both experiments, and independent like the pointing movements in Experiment 1. In contrast, the saccades performed in Experiment 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 illusion's influence on the preparation of each respective saccade type.

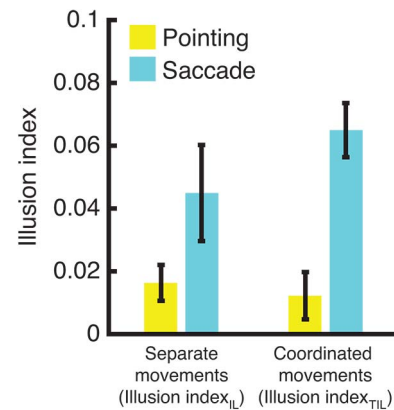


Figure 9. Relative illusion impacts on movement preparation between task conditions and effectors. All error bars represent between-subjects standard error. Saccadic initiation latencies were overall more influenced by the illusion than pointing initiation latencies. Overall, coordinated movement IL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

In both experiments, saccadic preparation showed larger illusion indices than pointing movements, with Experiment 2 showing this effect more strongly than Experiment 1. A 2×2 ANOVA with a within-subject factor of movement effector (saccade vs. pointing), and a between-subjects factor of experiment (Experiment 1 vs. Experiment 2) revealed a significant main effect of effector, $F(1, 26) = 10.60$, $p < 0.001$, $\eta_p^2 = 0.290$, and a significant main effect of experiment $F(1, 26) = 4.70$, $p = 0.040$, $\eta_p^2 = 0.153$. This suggests that eye movements are overall more susceptible to the illusion than pointing movements, and that modulation by the illusion was higher overall in Experiment 2 than in Experiment 1. This effect of experiment is driven by the increase in the saccade illusion index across the two experiments; there is no difference in the pointing illusion index between Experiment 1 and Experiment 2. Thus, the difference between pointing and saccades in terms of susceptibility to illusions appears to be more robust with coordinated, naturalistic movements (Experiment 2) compared to independent (Experiment 1) eye and hand movements. This observation is supported by a marginally significant interaction effect between effector and experiment, $F(1, 26) = 3.90$, $p = 0.059$, $\eta_p^2 = 0.130$.

Summary

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

General discussion

In the present study, we dissociated the illusory and physical 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, physical target 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 the 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 physical target size continued to modulate 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 toward 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 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 (Experiment 1), we observed that those participants who showed more influence of the illusion on pointing preparation also showed more influence of the illusion on saccade preparation (Figure 4A). Thus, the impact of the illusion on movement preparation was correlated between pointing and saccadic eye movements, though the impact of physical 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 (Figure 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 nonhuman primates has demonstrated common target selection characteristics for saccades and pointing movements (Song & McPeck, 2015; Song, Rafal, & McPeck, 2011). For instance, in visual search, as the number of distractors increases, target selection is facilitated for saccades (Arai & Keller, 2005; Arai, McPeck, & Keller, 2004; McPeck & Keller, 2001; McPeck, 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 (Bichot & Schall, 1999, 2002; McPeck & Keller, 2002; McPeck et al., 1999) and pointing (Moher & Song, 2013; Song & Nakayama, 2006). Song and McPeck (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 for both 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 nonhuman primates support the existence of a shared neural mechanism for target selection in eye and arm movements (McPeck & Keller, 2014; Song & McPeck, 2015; Song et al., 2011). Song et al. (2011) 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 & McPeck (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 target size for saccade and pointing movements.

Dominant illusion modulation for saccade over pointing preparation

While we found in Experiment 1 that the impact of illusory size on initiation latency for independent saccades and pointing movements was correlated, the 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 when they are coordinated, but not when they are independent, 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 nonhuman primates (e.g., Bekkering & Neggers, 2002; Frens & Erkelens, 1991; Horstmann & Hoffmann, 2005; Johansson et al., 2001; Land & Hayhoe, 2001; Land & McLeod, 2000; Neggers & Bekkering, 2000, 2001; Scherberger, Goodale, Andersen, & 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 McPeck (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 surmise 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.

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 Patient DF, an aperceptive agnosia patient (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 normal healthy participants have also evaluated whether vision for perception and vision for action are dissociated using size contrast illusions, and found evidence that action is either immune to illusion, or less susceptible to it than perception (Ganel et al., 2008; Haffenden & Goodale, 1998; Haffenden, Schiff, & Goodale, 2001; McCarley et al., 2003; Shmuelof & Zohary, 2005). In a number of these studies, hand movements (typically grasping) have typically been performed in the presence of natural eye movements 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 the 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 the 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 saccade or pointing movement execution. 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 Experiment 2. This suggests 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 et al., 1995; Ganel et al., 2008). For example, Carnahan, Goodale, and 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 visual feedback between the two tasks. A difference in visual coding between pointing and grasping has also been 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, and 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, see 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. Multiple studies have shown that grasp aperture *can* be adjusted to the illusory sizes of objects rather than their veridical physical sizes, potentially with the same degree of illusion modulation as for perception, in contrast with a strict interpretation of perception–action dissociation (Franz, Fahle, Bühlhoff, & Gegenfurtner, 2001; Franz, Gegenfurtner, Bühlhoff, & Fahle, 2000; Pavani, Boscagli, Benvenuti, Rabeffetti, & Farne, 1999). Furthermore, others have shown that measures other than grasp aperture are susceptible to visual illusions, such as movement amplitude (de Grave, Brenner, & 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, see Bruno et al., 2010). Thus, it is argued that illusory perception does have an effect on aspects of action.

Glover and colleagues (Glover, 2004; Glover & Dixon, 2001, 2002) propose 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 the illusion on initiation latency but not movement time seem to support this. However, multiple studies have found contradictory results. Although they did not measure movement preparation, van Donkelaar and colleagues (Lee & van Donkelaar, 2002; van Donkelaar, 1999), did find that movement time was affected by the illusory sizes of targets in the Ebbinghaus illusion. Furthermore, Handlovsky, Hansen, Lee, and 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 et al. (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, as well as contradictions within the aforemen-

tioned dual stream hypothesis literature, 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 illusions as shown in the present study, illusory modulation of goal-directed action would correspondingly increase. For instance in open-loop paradigms, in which participants must necessarily rely on planning mechanisms in the absence of visual feedback during control, an influence of illusion could manifest in control–execution measures as well (e.g., Bartelt & Darling, 2002; Bruno & Morrone, 2007; Haffenden & Goodale, 1998; Pavani et al., 1999). Similarly, in rapid pointing and saccade tasks in which 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 online, particularly in pointing movements when subjects are deprived of visual feedback of the hand. This, we surmise, could explain the influence of illusion on action seen in a number of studies (e.g., Binsted & Elliott, 1999; Franz et al., 2001; Meegan et al., 2004).

Conclusions

By examining the modulation of a size-contrast illusion on 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 goal-directed action phases (planning vs. execution), effectors (eye vs. hand), and independence (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 illusions modulate visually guided action. Though we surmise 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 from the illusion while hand movements show decreased modulation. This suggests that the mechanism impacted by illusions 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 illusions—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 the 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 illusions on action, or its on underlying mechanisms. Further investigations are needed to identify the mechanism or mechanisms responsible for the influence of perceptual illusions on movement preparation, and how they may modulate other forms of visually guided action.

Keywords: eye–hand coordination, pointing, saccades, size contrast illusion, visually guided action

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References

- Aglioti, S., DeSouza, J. F. X., & Goodale, M. A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology*, *5*, 679–685.
- Andersen, R., Snyder, L., Bradley, D., & Xing, J. (1997). Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annual Review of Neuroscience*, *20*, 303–330.
- Arai, K., & Keller, E. L. (2005). A model of the saccade-generating system that accounts for trajectory variations produced by competing visual stimuli. *Biological Cybernetics*, *92*, 21–37.
- Arai, K., McPeck, R. M., & Keller, E. L. (2004). Properties of saccadic responses in monkey when multiple competing visual stimuli are present. *Journal of Neurophysiology*, *91*, 890–900.
- Bartelt, R., & Darling, W. G. (2002). Opposite effects on perception and action induced by the Ponzo illusion. *Experimental Brain Research*, *146*, 433–440.
- Bekkering, H., Abrams, R. A., & Pratt, J. (1995). Transfer of saccadic adaptation to the manual motor system. *Human Movement Science*, *14*, 155–164.
- Bekkering, H., & Neggers, S. F. W. (2002). Visual search is modulated by action intentions. *Psychological Science*, *13*, 370–374.
- Bernardis, P., Knox, P., & Bruno, N. (2005). How does action resist visual illusion? Uncorrected oculomotor information does not account for accurate pointing in peripersonal space. *Experimental Brain Research*, *162*, 133–144.
- Bichot, N. P., & Schall, J. D. (1999). Effects of similarity and history on neural mechanisms of visual selection. *Nature Neuroscience*, *2*, 549–554.
- Bichot, N. P., & Schall, J. D. (2002). Priming in macaque frontal cortex during popout visual search: Feature-based facilitation and location-based inhibition of return. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *22*, 4675–4685.
- Binsted, G., & Elliott, D. (1999). Ocular perturbations and retinal/extraretinal information: The coordination of saccadic and manual movements. *Experimental Brain Research*, *127*, 193–206.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436.
- Brenner, E., & Smeets, J. B. (1996). Size illusion influences how we lift but not how we grasp an object. *Experimental Brain Research*, *111*, 473–476.
- Bruno, A., & Morrone, M. C. (2007). Influence of saccadic adaptation on spatial localization: Comparison of verbal and pointing reports. *Journal of Vision*, *7*(5):16, 1–13, doi:10.1167/7.5.16. [PubMed] [Article]
- Bruno, N. (2001). When does action resist visual illusions? *Trends in Cognitive Sciences*, *5*, 379–382.
- Bruno, N., & Bernardis, P. (2002). Dissociating perception and action in Kanizsa’s compression illusion. *Psychonomic Bulletin & Review*, *9*, 723–730.
- Bruno, N., Knox, P. C., & de Grave, D. D. J. (2010). A meta-analysis of the effect of the Müller-Lyer illusion on saccadic eye movements: No general support for

- a dissociation of perception and oculomotor action. *Vision Research*, 50, 2671–2682.
- Carey, D. P., Coleman, R. J., & Della Sala, S. (1997). Magnetic misreaching. *Cortex*, 33, 639–652.
- Carnahan, H., Goodale, M. A., & Marteniuk, R. G. (1993). Grasping versus pointing and the differential use of visual feedback. *Human Movement Science*, 12, 219–234.
- Culham, J. C., Danckert, S. L., DeSouza, J. F. X., Gati, J. S., Menon, R. S., & Goodale, M. A. (2003). Visually guided grasping produces fMRI activation in dorsal but not ventral stream brain areas. *Experimental Brain Research*, 153, 180–189.
- de Grave, D. D., Brenner, E., & Smeets, J. B. (2004). Illusions as a tool to study the coding of pointing movements. *Experimental Brain Research*, 155, 56–62.
- de Grave, D. D., Franz, V. H., & Gegenfurtner, K. R. (2006). The influence of the Brentano illusion on eye and hand movements. *Journal of Vision*, 6(7):5, 727–738, doi:10.1167/6.7.5. [PubMed] [Article]
- DiGirolamo, G. J., McCarley, J. S., Kramer, A. F., & Griffin, H. J. (2008). Voluntary and reflexive eye movements to illusory lengths. *Visual Cognition*, 16, 68–89.
- Edwards, M. G., & Humphreys, G. W. (1999). Pointing and grasping in unilateral visual neglect: Effect of on-line visual feedback in grasping. *Neuropsychologia*, 37, 959–973.
- Epelboim, J., Steinman, R. M., Kowler, E., Pizlo, Z., Erkelens, C. J., & Collewijn, H. (1997). Gaze-shift dynamics in two kinds of sequential looking tasks. *Vision Research*, 37, 2597–2607.
- Filimon, F. (2010). Human cortical control of hand movements: Parietofrontal networks for reaching, grasping, and pointing. *The Neuroscientist*, 16(4), 388–407.
- Fisk, J. D., & Goodale, M. A. (1985). The organization of eye and limb movements during unrestricted reaching to targets in contralateral and ipsilateral visual space. *Experimental Brain Research*, 60, 159–178.
- Fitts, P. M. (1954). The information capacity of the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology*, 47, 381–391.
- Foerster, R. M., Carbone, E., Koesling, H., & Schneider, W. X. (2012). Saccadic eye movements in the dark while performing an automatized sequential high-speed sensorimotor task. *Journal of Vision*, 12(2):8, 1–15, doi:10.1167/12.2.8. [PubMed] [Article]
- Franz, V. H. (2001). Action does not resist visual illusions. *Trends in Cognitive Sciences*, 5, 457–459.
- Franz, V. H., Fahle, M., Bühlhoff, H. H., & Gegenfurtner, K. R. (2001). Effects of visual illusions on grasping. *Journal of Experimental Psychology: Human Perception and Performance*, 27, 1124–1144.
- Franz, V. H., Gegenfurtner, K. R., Bühlhoff, H. H., & Fahle, M. (2000). Grasping visual illusions: No evidence for a dissociation between perception and action. *Psychological Science*, 11, 20–25.
- Frens, M. A., & Erkelens, C. J. (1991). Coordination of hand movements and saccades: Evidence for a common and a separate pathway. *Experimental Brain Research*, 85, 682–690.
- Fukui, T., Takemura, N., & Inui, T. (2006). Visuo-motor transformation process in goal-directed prehension: Utilization of online vision during preshaping phase of grasping. *Japanese Psychological Research*, 48, 188–203.
- Ganel, T., Tanzer, M., & Goodale, M. A. (2008). A double dissociation between action and perception in the context of visual illusions. *Psychological Science*, 19, 221–225.
- Gielen, C. C. A. M., van den Heuvel, P. J. M., & van Gisbergen, J. A. M. (1984). Coordination of fast eye and arm movements in a tracking task. *Experimental Brain Research*, 56, 154–161.
- Glover, S. (2004). Separate visual representations in the planning and control of action. *Behavioral and Brain Sciences*, 27, 1–76.
- Glover, S., & Dixon, P. (2002). Dynamic effects of the Ebbinghaus illusion in grasping: Support for a planning/control model of action. *Perception & Psychophysics*, 64, 266–278.
- Glover, S., & Dixon, P. (2004). A step and a hop on the Müller-Lyer: Illusion effects on lower-limb movements. *Experimental Brain Research*, 154, 504–512.
- Glover, S. R., & Dixon, P. (2001). Dynamic illusion effects in a reaching task: Evidence for separate visual representations in the planning and control of reaching. *Journal of Experimental Psychology: Human Perception and Performance*, 27, 560–572.
- Gonzalez, C. L., Ganel, T., & Goodale, M. A. (2006). Hemispheric specialization for the visual control of action is independent of handedness. *Journal of Neurophysiology*, 95, 3496–3501.
- Goodale, M. A. (2014). How (and why) the visual control of action differs from visual perception. *Proceedings of the Royal Society B: Biological Sciences*, 281(1785), 20140337.
- Goodale, M. A., & Milner, A. D. (1992). Separate

- visual pathways for perception and action. *Trends in Neurosciences*, *15*, 20–25.
- Grafton, S., Arbib, M., Fadiga, L., & Rizzolatti, G. (1996). Localization of grasp representations in humans by positron emission tomography. *Experimental Brain Research*, *112*, 103–111.
- Haffenden, A. M., & Goodale, M. A. (1998). The effect of pictorial illusion on prehension and perception. *Journal of Cognitive Neuroscience*, *10*, 122–136.
- Haffenden, A. M., Schiff, K. C., & Goodale, M. A. (2001). The dissociation between perception and action in the Ebbinghaus illusion: Nonillusory effects of pictorial cues on grasp. *Current Biology*, *11*, 177–181.
- Handlovsky, I., Hansen, S., Lee, T. D., & Elliott, D. (2004). The Ebbinghaus illusion affects on-line movement control. *Neuroscience Letters*, *366*, 308–311.
- Hayhoe, M. M., Shrivastava, A., Mruczek, R., & Pelz, J. B. (2003). Visual memory and motor planning in a natural task. *Journal of Vision*, *3*(1):6, 49–63, doi:10.1167/3.1.6. [PubMed] [Article]
- Horstmann, A., & Hoffmann, K. P. (2005). Target selection in eye–hand coordination: Do we reach to where we look or do we look to where we reach? *Experimental Brain Research*, *167*, 187–195.
- Jackson, S. R., Newport, R., Mort, D., & Husain, M. (2005). Where the eye looks, the hand follows: Limb-dependent magnetic misreaching in optic ataxia. *Current Biology*, *15*, 42–46.
- Jackson, S. R., & Shaw, A. (2000). The Ponzo illusion affects grip-force but not grip-aperture scaling during prehension movements. *Journal of Experimental Psychology: Human Perception and Performance*, *26*, 418–423.
- James, T. W., Culham, J., Humphrey, G. K., Milner, A. D., & Goodale, M. A. (2003). Ventral occipital lesions impair object recognition but not object-directed grasping: An fMRI study. *Brain*, *126*, 2463–2475.
- Johansson, R. S., Westling, G., Bäckström, A., & Flanagan, J. R. (2001). Eye–hand coordination in object manipulation. *The Journal of Neuroscience*, *21*, 6917–6932.
- Khan, A. Z., Song, J.-H., & McPeck, R. M. (2011). The eye dominates in guiding attention during simultaneous eye and hand movements. *Journal of Vision*, *11*(1):9, 1–14, doi:10.1167/11.1.9. [PubMed] [Article]
- Land, M. F., & Hayhoe, M. (2001). In what ways do eye movements contribute to everyday activities? *Vision Research*, *41*, 3559–3565.
- Land, M. F., & Lee, D. N. (1994). Where we look when we steer. *Nature*, *369*(6483), 742–744.
- Land, M. F., & McLeod, P. (2000). From eye movements to actions: How batsmen hit the ball. *Nature Neuroscience*, *3*, 1340–1345.
- Lee, J. H., & van Donkelaar, P. (2002). Dorsal and ventral visual stream contributions to perception–action interactions during pointing. *Experimental Brain Research*, *143*, 440–446.
- McCarley, J. S., Kramer, A. F., & DiGirolamo, G. J. (2003). Differential effects of the Müller-Lyer illusion on reflexive and voluntary saccades. *Journal of Vision*, *3*(11):9, 751–760, doi:10.1167/3.11.9. [PubMed] [Article]
- McPeck, R. M., & Keller, E. L. (2001). Short-term priming, concurrent processing, and saccade curvature during a target selection task in the monkey. *Vision Research*, *41*, 785–800.
- McPeck, R. M., & Keller, E. L. (2002). Saccade target selection in the superior colliculus during a visual search task. *Journal of Neurophysiology*, *88*(4), 2019–2034.
- McPeck, R. M., & Keller, E. L. (2014). Saccade target selection in the superior colliculus during a visual search task. *Journal of Neurophysiology*, *88*, 2019–2034.
- McPeck, R. M., Maljkovic, V., & Nakayama, K. (1999). Saccades require focal attention and are facilitated by a short-term memory system. *Vision Research*, *39*, 1555–1566.
- McSorley, E., & Findlay, J. M. (2003). Saccade target selection in visual search: Accuracy improves when more distractors are present. *Journal of Vision*, *3*(11):20, 877–892, doi:10.1167/3.11.20. [PubMed] [Article]
- Meegan, D. V., Glazebrook, C. M., Dhillon, V. P., Tremblay, L., Welsh, T. N., & Elliott, D. (2004). The Müller-Lyer illusion affects the planning and control of manual aiming movements. *Experimental Brain Research*, *155*, 37–47.
- Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford Psychology Series, No. 27. Oxford, UK: Oxford University Press.
- Milner, A. D., & Goodale, M. A. (2008). Two visual systems re-viewed. *Neuropsychologia*, *46*, 774–785.
- Mishkin, M., Ungerleider, L. G., & Macko, K. A. (1983). Object vision and spatial vision: Two cortical pathways. *Trends in Neurosciences*, *6*, 414–417.
- Moher, J., & Song, J.-H. (2013). Context-dependent sequential effects of target selection for action.

- Journal of Vision*, 13(8):10, 1–13, doi:10.1167/13.8.10. [PubMed] [Article]
- Moher, J., & Song, J.-H. (2014). Target selection bias transfers across different response actions. *Journal of Experimental Psychology: Human Perception and Performance*, 40, 1117–1130.
- Moher, J., & Song, J.-H. (2015). Target selection biases from recent experience transfer across effectors. *Attention, Perception, & Psychophysics*, 78, 415–426.
- Moher, J., & Song, J. H. (2016). Target selection biases from recent experience transfer across effectors. *Attention, Perception, & Psychophysics*, 78(2), 415–426.
- Neggers, S. F., & Bekkering, H. (2000). Ocular gaze is anchored to the target of an ongoing pointing movement. *Journal of Neurophysiology*, 83, 639–651.
- Neggers, S. F. W., & Bekkering, H. (2001). Gaze anchoring to a pointing target is present During the entire pointing movement and is driven by a non-visual signal. *Journal of Neurophysiology*, 86, 961–970.
- Neggers, S. F. W., & Bekkering, H. (2002). Coordinated control of eye and hand movements in dynamic reaching. *Human Movement Science*, 21, 349–376.
- Nummela, S. U., & Krauzlis, R. J. (2010). Inactivation of primate superior colliculus biases target choice for smooth pursuit, saccades, and button press responses. *Journal of Neurophysiology*, 104, 1538–1548.
- Patla, A. E., & Vickers, J. N. (2003). How far ahead do we look when required to step on specific locations in the travel path during locomotion? *Experimental Brain Research*, 148, 133–138.
- Pavani, F., Boscagli, I., Benvenuti, F., Rabuffetti, M., & Farnè, A. (1999). Are perception and action affected differently by the Titchener circles illusion? *Experimental Brain Research*, 127, 95–101.
- Rice, N. J., Tunik, E., & Grafton, S. T. (2006). The anterior intraparietal sulcus mediates grasp execution, independent of requirement to update: New insights from transcranial magnetic stimulation. *The Journal of Neuroscience*, 26, 8176–8182.
- Robertson, I. H., Nico, D., & Hood, B. M. (1995). The intention to act improves unilateral left neglect: Two demonstrations. *Neuroreport*, 7, 246–248.
- Rothkopf, C. A., Ballard, D. H., & Hayhoe, M. M. (2007). Task and context determine where you look. *Journal of Vision*, 7(14):16, 1–20, doi:10.1167/7.14.16. [PubMed] [Article]
- Sailer, U., Eggert, T., Ditterich, J., & Straube, A. (2000). Spatial and temporal aspects of eye–hand coordination across different tasks. *Experimental Brain Research*, 134, 163–173.
- Sailer, U., Eggert, T., Ditterich, J., & Straube, A. (2002). Global effect of a nearby distractor on targeting eye and hand movements. *Journal of Experimental Psychology: Human Perception and Performance*, 28, 1432–1446.
- Schall, J. D. (1995). Neural basis of saccade target selection. *Reviews in the Neurosciences*, 6, 63–85.
- Scherberger, H., Goodale, M. A., & Andersen, R. A. (2003). Target selection for reaching and saccades share a similar behavioral reference frame in the macaque. *Journal of Neurophysiology*, 89, 1456–1466.
- Shmuelof, L., & Zohary, E. (2005). Dissociation between ventral and dorsal fMRI activation during object and action recognition. *Neuron*, 47, 457–470.
- Sidaway, B., Christina, R. W., & Shea, J. B. (1988). A movement constraint interpretation of the response complexity effect on programming time. *Advances in Psychology*, 55(C), 87–102.
- Smeets, J. B., & Brenner, E. (1999). A new view on grasping. *Motor Control*, 3, 237–271.
- Snyder, L. H., Calton, J. L., Dickinson, A. R., & Lawrence, B. M. (2002). Eye–hand coordination: Saccades are faster when accompanied by a coordinated arm movement. *Journal of Neurophysiology*, 87, 2279–2286.
- Soechting, J. F., Engel, K. C., & Flanders, M. (2001). The Duncker illusion and eye–hand coordination. *Journal of Neurophysiology*, 85, 843–854.
- Song, J., & McPeck, R. (2015). Neural substrates of target selection for reaching movements in superior colliculus. *Journal of Neurophysiology*, 113, 1414–1422.
- Song, J. H., & McPeck, R. M. (2009). Eye–hand coordination during target selection in a pop-out visual search. *Journal of Neurophysiology*, 102, 2681–2692.
- Song, J.-H., & Nakayama, K. (2006). Role of focal attention on latencies and trajectories of visually guided manual pointing. *Journal of Vision*, 6(9):11, 982–995, doi:10.1167/6.9.11. [PubMed] [Article]
- Song, J. H., & Nakayama, K. (2008). Target selection in visual search as revealed by movement trajectories. *Vision Research*, 48, 853–861.
- Song, J. H., Rafal, R. D., & McPeck, R. M. (2011). Deficits in reach target selection during inactivation of the midbrain superior colliculus. *Proceedings of*

- the National Academy of Sciences, USA, 108*, E1433–E1440.
- Stoerig, P., & Cowey, A. (1997). Blindsight in man and monkey. *Brain, 120*, 535–559.
- Tang, R., Whitwell, R. L., & Goodale, M. A. (2015). The influence of visual feedback from the recent past on the programming of grip aperture is grasp-specific, shared between hands, and mediated by sensorimotor memory not task set. *Cognition, 138*, 49–63.
- Tipper, S. P. (2005). Reaching affects saccade trajectories. In *Neurobiology of Attention* (Vol. 136, pp. 175–180). New York: Springer-Verlag.
- van Donkelaar, P. (1999). Pointing movements are affected by size-contrast illusions. *Experimental Brain Research, 125*, 517–520.
- Vercher, J. L., & Gauthier, G. M. (1988). Cerebellar involvement in the coordination control of the oculo-manual tracking system: Effects of cerebellar dentate nucleus lesion. *Experimental Brain Research, 73*, 155–166.
- Wu, C. C., Kwon, O. S., & Kowler, E. (2010). Fitts's law and speed/accuracy trade-offs during sequences of saccades: Implications for strategies of saccadic planning. *Vision Research, 50*, 2142–2157.
- Zelinsky, G. J., Rao, R. P. N., Hayhoe, M. M., & Ballard, D. H. (1997). Eye movements reveal the spatiotemporal dynamics of visual search. *Psychological Science, 8*(6), 448–453.