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Different spatial representations guide eye and hand movements

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Our visual system allows us to localize objects in the world and plan motor actions toward them. We have recently shown that the localization of moving objects differs between perception and saccadic eye movements (Lisi & Cavanagh, 2015), suggesting different localization mechanisms for perception and action. This finding, however, could reflect a unique feature of the saccade system rather than a general dissociation between perception and action. To disentangle these hypotheses, we compared object localization between saccades and hand movements. We flashed brief targets on top of double-drift stimuli (moving Gabors with the internal pattern drifting orthogonally to their displacement, inducing large distortions in perceived location and direction) and asked participants to point or make saccades to them. We found a surprising difference between the two types of movements: Although saccades targeted the physical location of the flashes, pointing movements were strongly biased toward the perceived location (about 63% of the perceptual illusion). The same bias was found when pointing movements were made in open-loop conditions (without vision of the hand). These results indicate that dissociations are present between different types of actions (not only between action and perception) and that visual processing for saccadic eye movements differs from that for other actions. Because the position bias in the double-drift stimulus depends on a persisting influence of past sensory signals, we suggest that spatial maps for saccades might reflect only recent, short-lived signals, and the spatial representations supporting conscious perception and hand movements integrate visual input over longer temporal intervals.

Introduction

Visually guided behaviors, such as picking up a cup of coffee from the table or shifting our gaze toward an approaching car, require many computational steps, ranging from the sensory acquisition of the target to the generation of the appropriate motor command. It seems natural that the planning of motor actions toward visible objects would use the same visual information that allows us to perceive those objects. However, many experimental findings have challenged this idea, suggesting instead that visual information undergoes largely independent processing when used for action as opposed to perception (Bridgeman, Kirch, & Sperling, 1981; Burr, Morrone, & Ross, 2001; Goodale, Milner, Jakobson, & Carey, 1991). For example, in healthy subjects, the evidence for different processing mechanisms is based on a reduction of the influence of visual illusion when tested with actions rather than perception (e.g., Aglioti, DeSouza, & Goodale, 1995). These findings are typically interpreted according to the influential two visual system theory (Goodale & Milner, 1992; Milner & Goodale, 2008), which maintains that the ventral and dorsal visual pathways in the cerebral cortex can be distinguished in terms of the function they serve: The ventral stream would mediate the perceptual identification of objects and the dorsal stream the sensorimotor transformation required to generate motor actions toward those objects. However, the interpretation of these findings is controversial (Bruno, 2001; Dassonville, Bridgeman,

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Kaur Bala, Thiem, & Sampanes, 2004; Franz, 2001; Kopiske, Bruno, Hesse, Schenk, & Franz, 2016, in press; Schenk & McIntosh, 2010; Whitwell & Goodale, in press). For example, Cardoso-Leite and Gorea (2010) argue that the existing evidence is still consistent with a unique visual processing mechanism that supports both perception and action.

In support of the hypothesis of different processing mechanisms for perception and action, we have recently reported a large and robust dissociation between the perceptual localization and the saccadic targeting of moving double-drift targets (Lisi & Cavanagh, 2015). In this study, we presented Gabor patterns moving back and forth along a straight trajectory that, due to the drift of the internal sinusoidal pattern, appeared tilted up to 50° relative to its physical trajectory. In spite of this striking perceptual effect, we found that saccadic eye movements targeted the actual trajectory and were indistinguishable from a control condition in which there was no illusory shift in the orientation of the trajectory.

Although these results would point to a strong dissociation in visual processing between perception and action, it is unclear whether all actions share a common representation of visual space. A recent study by Gomi, Abekawa, and Shimojo (2013) compared manual and ocular following responses to visual motion and found evidence for a dissociation, suggesting that visual motion processing may be carried out independently for different motor functions. However, this result is based only on reflexive, involuntary movements that are known to have different functional goals: The ocular following response serves to stabilize the image on the retina (Gellman, Carl, & Miles, 1990) whereas reflexive hand movements are used to adjust hand reaching with respect to concurrent body movements (Gomi, 2008). Therefore, it is not clear whether these results point to independent visual processing for different motor functions (hand vs. eye movements) or instead reflect the specific requirements of different motor goals (compensate for body movements vs. stabilize retinal image).

In the present study, we adapted our double-drift stimulus to compare spatial localization between voluntary, goal-directed eye and hand movements. We presented brief targets—green Gaussian blobs flashed on top of the Gabor at one or the other end of its motion path—and asked participants to either saccade to them or point to their location on the screen with their index finger. We compared the spatial distributions of saccade landing and pointing locations and found a large difference across the two types of actions: Although saccadic eye movements were mostly veridical and seemed not affected by the visual illusion, pointing movements (either with or without vision of the hand during the movement) showed a large bias in the direction expected for the visual illusion. Overall, these results provide clear evidence that different motor functions aiming for the same goal can show a different processing of motion and position information.

Materials and methods

Participants

Six observers (one author, five females; mean age 30.83, $SD = 2.64$) participated in Experiment 1 (both perceptual and saccade tasks), and seven observers (one author, six females; mean age 30.86, $SD = 3.80$) participated in Experiment 2. Including the author, four of the observers who participated in Experiment 1 also participated in Experiment 2. All observers were right-handed and had normal or corrected-to-normal vision. Informed consent was obtained in writing prior to participation, and the protocols for the study were approved by the Université Paris Descartes ethics review board, CERES, in accordance with French regulations and the Declaration of Helsinki. All participants were experienced psychological observers, and all except the author were naïve to the specific purpose of the experiments.

Setup

In all experiments, participants sat in a dark and quiet room. Gaze position was recorded by means of an SR Research Eyelink 1000 desktop mounted eye tracker at a sampling rate of 1 kHz. The participant's head was positioned on a chin rest with adjustable forehead rest at 60 cm in front of the experimental display. An Apple computer running MATLAB (Mathworks) with the Psychophysics and Eyelink toolboxes controlled the stimulus presentation and response collection.

Experiment 1: Saccade

The screen used to display the stimuli was a gamma linearized Compaq P1220 CRT screen (vertical refresh rate 120 Hz). In this experiment, we recorded the right eye gaze position.

Experiment 2: Pointing

The display was a gamma linearized, 27-in. screen with touch functionality—the Wacom Cintiq 27QHD touch (vertical refresh rate 60 Hz)—that was used to present stimuli and to record the final position of pointing movements. For these experiments, the eye tracker was not centered but positioned on the left side

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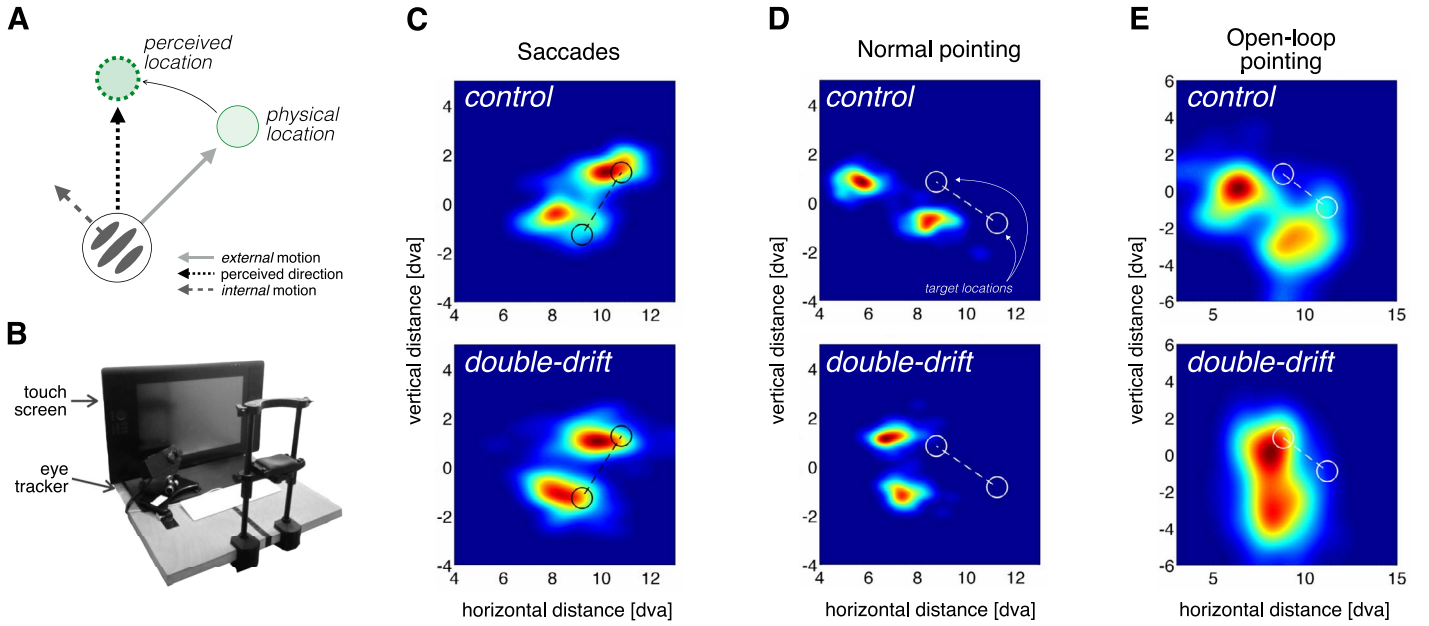

Figure 1. Stimuli, setup, and examples of distributions of pointing locations and saccade end points. (A) The double-drift stimulus: The internal motion (the drifting of the Gabor sinusoidal pattern) can make a tilted path appear vertical and shift the location of a brief flash presented at the end point (see main text for detail). Depending on the direction of the internal motion relative to the external one, both a right-tilted path (shown in figure) and a left-tilted path can be made to appear vertical by inducing a counterclockwise and a clockwise illusory rotation of the motion trajectory, respectively. (B) The experimental setup used in the pointing experiment, allowing the concurrent registration of hand-pointing responses and gaze positions (see main text for more details). (C–E) Kernel density estimates of distributions of landing/pointing locations (each panel shows data from one participant and one tilt). The empty circles connected by the dashed lines represent the target locations for that specific participant and condition. Top panels show the control condition and bottom panels the double-drift conditions—that is, the condition in which the internal motion made the target flashed at the two end points appear vertically aligned. It can be seen that the distribution of saccade end points is not influenced by the presence or absence of the internal drifting motion. In contrast, the distribution of pointing locations targeting the top or bottom targets are more vertically aligned in the double-drift condition (with internal motion present) than in the control condition (panels D and E, see main text for more details).

of the setup with its camera pointed toward the left eye (which was the recorded eye) in order to leave enough space for the participants to comfortably execute a pointing movement to the touch screen (Figure 1B). For the experiment with open-loop pointing, this setup was extended with shutter goggles, Plato Visual Occlusion Spectacles (Translucent Technologies Inc., Toronto, ON, Canada). The opening and closing of the shutters was controlled by the same computer controlling stimulus presentation through an Arduino UNO board (Arduino LLC, Somerville, MA). In the "shutter open" state, Plato goggles are able to transmit approximately 80% of incident light (Translucent Technologies, Inc., 2012), allowing the monitoring of gaze position with video-based eye trackers.

Stimuli

In all experiments, the stimulus was a Gabor pattern (a sinusoidal luminance modulation within a Gaussian contrast envelope) with a spatial frequency of 2 c/° and 100% contrast. The standard deviation of the contrast envelope was 0.1°. The Gabor was moving back and forth along a linear path of length 3° with a speed of 2°/s (*external* motion; see Figure 1A). The sinusoidal grating had the same orientation of the motion path and drifted in an orthogonal direction with a temporal frequency of 3 Hz (*internal* motion; corresponding to 1.5°/s), reversing its direction in synchrony with path reversals at the two end points every 1.5 s (*double-drift* condition). The combination of internal and external motion can make a tilted path appear vertical (see Figure 1A): A right-tilted path can appear vertical if the internal motion is to the left while the Gabor moves upward (and to the right when it moves downward) and vice versa for a left-tilted path. We included also a condition in which the internal sinusoidal pattern was static for the whole trial (*control* condition). The stimulus was presented on a uniform gray background (5.3 cd/m^2), and the midpoint of the trajectory was placed at 10° from fixation to the right on the horizontal midline.

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The saccadic/pointing target was a green Gaussian blob with $SD = 0.18°$ and peak luminance 128 cd/m^2. The green target was presented only for one monitor frame, superimposed on the moving Gabor and always in correspondence to the end point of the linear trajectory.

Procedure

Experiment 1: Saccades

Perceptual task

In the first part, we presented Gabor patterns moving along paths with different orientations with the green flashed target presented at each reversal. Participants were asked to judge the left/right position of the target flashed at the top location relative to the green target flashed at the bottom location. The stimulus was displayed until participants responded with the left or right arrow key. Gaze position was recorded and monitored online with the eye tracker, and trials in which the participant shifted gaze away from the fixation point or blinked before giving the response were immediately aborted and repeated. The physical orientation of the path, and therefore the position of the two flashed green targets, was adjusted by means of multiple interleaved QUEST staircases that converged to a 50% proportion of responses "right." Trials with left and right path orientations were randomly interleaved. Each participant performed two sessions of 200 trials each, divided into five blocks.

Saccade task

In the second part, participants were presented only the orientations of the motion path that had produced a perceived vertical alignment of the two green targets in the perceptual task. Each trial started when the participant fixated a black dot (a circle of 0.2° diameter) in the center of the screen. After a random interval, of duration uniformly distributed within the interval of 400 to 600 ms, the Gabor appeared at one of the two end points and started moving. In this condition, the green target was flashed only once, and the appearance of the green target was the cue for the participant to make a saccade directed toward the green target location. The green target could appear at either the first or the second reversal. As soon as the gaze position was detected outside a circular area with 2° of radius around fixation, the Gabor was removed so that participants received no postsaccadic visual feedback about their saccades. Based on offline analysis of the gaze position traces, we estimated that the Gabor, on average, disappeared 22 ms ($SD = 15$ ms) before saccade landing time. Participants ran a minimum of two sessions of the task, each comprising eight blocks of 32 trials (512 trials in total). Gaze position was recorded and monitored online; trials in which participants shifted gaze or blinked before the disappearance of the fixation point were aborted and repeated within the same block.

Experiment 2: Pointing

Perceptual task

The procedure was identical to that used in Experiment 1 except that it was run on the setup used for pointing experiments (Figure 1B). Each participant performed one session of 160 trials each, divided into four blocks.

Pointing task: Normal pointing

In the second part, participants were presented only the orientations of the motion path that had produced a perceived vertical alignment of the two green targets in the perceptual task. The sequence for each trial was the same as the sequence in the saccade experiment with the following differences. Each trial started only when two conditions were verified: Fixation was checked at the fixation point, and the participant pressed the space bar of a standard computer keyboard. Participants were instructed to hold down the space bar using their right index finger until they saw the green target, then release it and perform a fast pointing movement aiming toward and touching the screen at the location of the green target.

As soon as the space bar was released, the stimulus was removed from the screen and a brief, full-field mask was presented. The mask consisted of three frames (about 50 ms) of a checkered pattern of 3,072 (64×48) squares, each $0.5° \times 0.5°$, colored different shades of gray, and drawn (independently for each frame) from a Gaussian distribution with a mean 20.4 cd/m^2.

Participants ran a minimum of two sessions of the task, each comprising eight blocks of 32 trials (512 trials in total). Gaze position was recorded at 1 kHz and monitored online; trials in which participants shifted gaze or blinked before the onset of the pointing movement were aborted and repeated within the same block.

Pointing task: Open-loop pointing

The open-loop pointing condition was the same as the normal pointing condition except that the participants wore shutter goggles, and at the onset of the movement (the release of the spacebar) the goggles

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changed from the "shutter open" state (transparent) to the "shutter closed" state (light scattering), blocking the vision of the subject. Because there was no visual feedback from the hand during the movement, we called this condition *open loop* in contrast to the normal (or *closed loop*) control of hand movements with which visual feedback from the hand can be used to make adjustments while the hand is in motion. Importantly, while in the shutter-closed state, the lens of the goggles scatter the light (resulting in a translucent gray texture and impeding vision) but do not block it completely so that the eyes remain illuminated and do not have to readapt to light when the shutter opens. In our experiment, the shutter was reopened at the end of the pointing movement as soon as a response was recorded (the finger of the participant detected on the screen). Participants ran a minimum of two session of the task, each comprising eight blocks of 32 trials (512 trials in total). Gaze position was recorded and monitored online; trials in which participants shifted gaze or blinked before the onset of the pointing movement were aborted and repeated within the same block.

Analysis

To analyze the results of the perceptual task, we computed for each participant and condition the orientation of the motion path that yielded perceived vertical alignment of the two flashes presented at the two end points. This was computed as the orientation corresponding to 0.5 probability of "right" responses according to a cumulative Gaussian psychometric function fit on the data using maximum likelihood estimation. These were the path orientations used in the saccade conditions so that the perceived path appeared vertical in the double-drift trials for each participant.

For the experiments involving saccades, we first detected saccade onsets and offsets using an algorithm based on two-dimensional eye velocity (Engbert & Mergenthaler, 2006). The landing and pointing positions were then analyzed using the same procedure described in Lisi and Cavanagh (2015). In brief, for each participant, we fitted a multivariate linear model in order to recover the positions on the screen targeted by the saccadic or pointing movements. The model included as linear predictors the horizontal and vertical coordinates of the target together with the condition (*control* vs. *double-drift*) and the interaction between condition and target coordinates. A visual inspection of the residuals of these models did not reveal any obvious deviation from normality or homoscedasticity. The predicted values of the multivariate model were then used to compute the orientation angle of the path as "seen" by each motor effector. The difference in the recovered orientation angle between the control and double-drift conditions was taken as a measure of the effect of the internal motion of the Gabor on each type of movement.

In the experiment involving saccades, we excluded trials with latency less than 100 ms or longer than 600 ms (0.36% of total trials); the average latency of the remaining trials was 279.89 ms ($SD = 45.88$ ms). In the experiment involving pointing, we excluded trials in which the total response time (i.e., the interval between the presentation of the target and the recording of a touch response on the tactile screen) was longer than 3 s (normal pointing: 0.45% of total trials; open-loop pointing: 0.26% of total trials). The average response time in the remaining trials was 1213.53 ms ($SD =$ 351.61 ms) for the experiment with normal pointing and 1004.70 ms ($SD = 209.83$ ms) for the experiment with open-loop pointing.

Results

Experiment 1: Saccades

In the perceptual task, the path orientation that yielded the perceived vertical alignment of the two targets flashed at the end points deviated strongly from "physical" vertical: −46.82° ($SD = 7.54$) for the left-tilted path and 41.10° ($SD = 18.37$) for the right-tilted path orientations. We didn't find any difference between the size of the perceptual effect between left and right path orientations, $t(6) = 1.16$, $p = 0.30$; therefore, in Figure 3A, we represented the effects averaged over the two orientations. Next, we recovered the positions of the targets as seen by the saccadic system from the vertical and horizontal saccade amplitudes (Figure 2). The multivariate linear model was fitted on average with 549 saccades per observer; the average value of r^2 for the fits was 0.47 for the horizontal components ($SD = 0.08$) and 0.73 for the vertical components ($SD = 0.15$). The effect of internal motion was quantified as the difference in the angles recovered in the double-drift condition minus the angle recovered in the control condition (control minus double-drift for the left tilt and double-drift minus control for the right tilt so that a positive difference value would indicate a shift in the direction of the illusion). This difference was small—on average, 17.25% of the perceptual effect—and did not differ significantly from zero for either the left, $t(5) = 1.72$, $p = 0.14$, or the right, $t(5) = 1.49$, $p = 0.19$, path orientations (paired t tests).

In order to evaluate whether the effect of the internal motion depended on the latency of the saccade, we divided trials according to individual latency quartiles and computed the differences in the tilts recovered in

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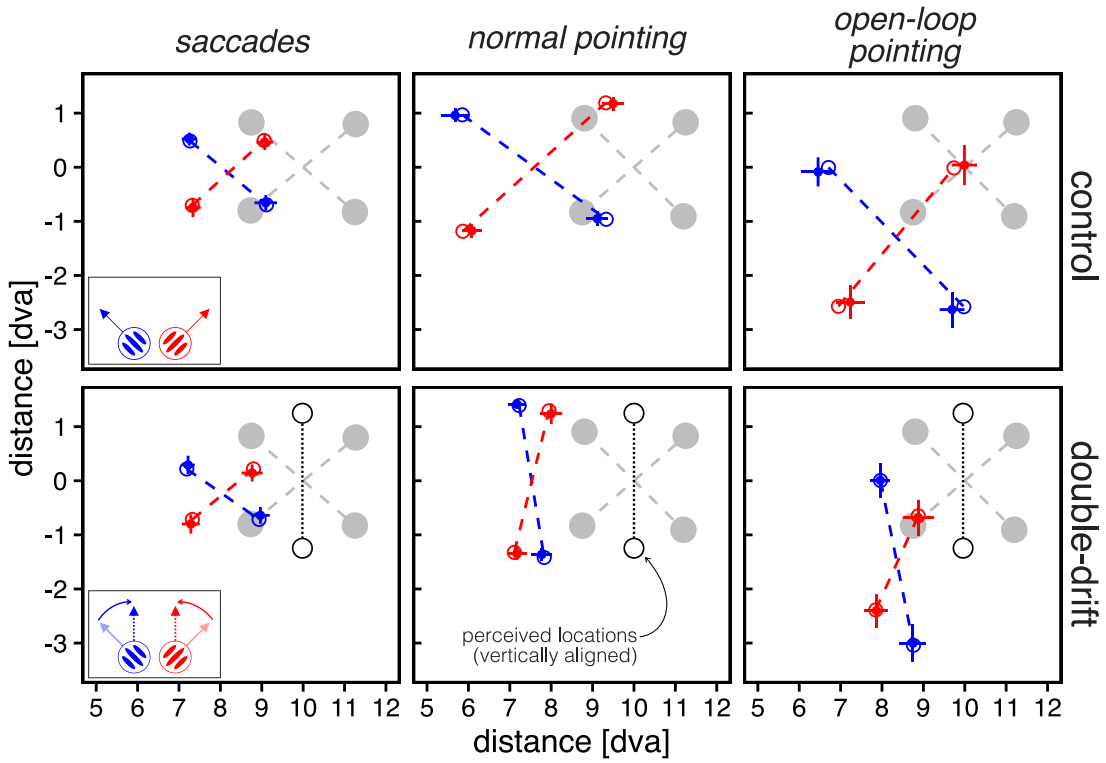

Figure 2. Example of data analysis for one participant. Filled dots represent the average saccade/pointing location (error bars represents 95% CI); blue dots represent left tilt and red dots right tilt. Empty blue/red circles represent the fitted values of the multivariate linear model used in the analysis (see text for details). Gray filled dots represent the physical locations of the targets, and the empty black circles in the double-drift panels represent the expected alignment of the target locations according to perceptual judgments. For saccades, the orientation of the lines connecting the two locations shows little or no change across the two conditions (control vs. double-drift, upper and lower panels, respectively). However, in the case of hand-pointing movements, the angle is much closer to the perceived vertical path in the double-drift condition than in the control condition. All the data are from the same observer (one of the four observers who ran both saccade and pointing experiments).

the two conditions for each quartile (see Figure 4). We analyzed these differences with a repeated-measures ANOVA with latency quartile and physical path orientation (left/right) as predictors. The effect of latency quartile was not significant, $F(3, 15) = 1.33$, $p = 0.30$, nor was the effect of path orientation, $F(1, 5) = 4.76$, $p = 0.08$, nor the interaction between latency quartile and orientation, $F(3, 15) = 2.01$, $p = 0.16$. The effect of latency did not reach statistical significance even when tested on the tilt difference averaged across the two orientations (as displayed in Figure 4), $F(3, 15) = 2.01$, $p = 0.16$.

Experiment 2: Pointing

As in Experiment 1, the path orientation that yielded the perceived vertical alignment of the two targets in the perceptual task differed strongly from the physical vertical: −47.57° ($SD = 10.25$) for the left path orientation and 45.43° ($SD = 17.38$) for the right orientation.

Normal pointing

The analysis of pointing locations followed the same procedure used for the analysis of saccade landing locations. The multivariate linear model was fitted to an average of 506 pointing responses per observer; the average value of r^2 for the fits was 0.60 for the horizontal components ($SD = 0.12$) and 0.84 for the vertical components ($SD = 0.05$). The difference in the angles recovered in the double-drift and control conditions was significantly different from zero for both the left, $t(6) = 5.08$, $p = 0.002$, and the right, $t(6) = 6.98$, $p = 0.0004$, path orientations (paired t test); this effect amounted, on average, to 64.73% of the perceptual illusion. The effect did not differ across left/right path orientations, $t(6) = 0.30$, $p = 0.78$, so in Figure 3B we represented the average effect. Next, we divided trials according to individual latency quartiles (defined as the interval between the target appearance and the onset of the movement) and repeated the analysis for each quartile (see Figure 4, middle and right panels). We analyzed the differences in the recovered angle with a repeated-measures ANOVA

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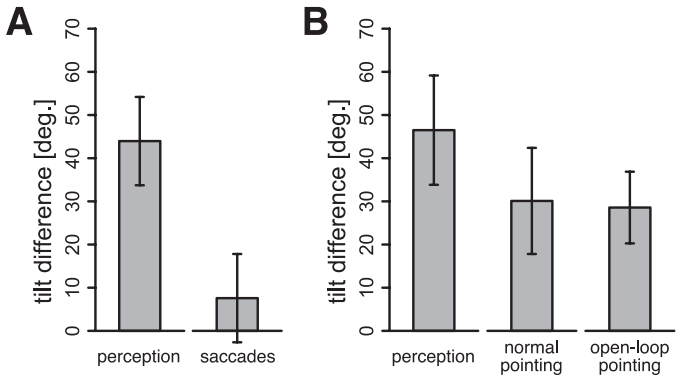

Figure 3. Effect of internal motion on perception and action. (A) The effect of the double-drift illusion as measured in perception and saccadic eye movements (Experiment 1). The left bar shows the tilt that produced a perceived vertical alignment of the targets flashed at the two end points of the motion path averaged across observers and tilts (left/right). The right bar shows the difference in tilt seen for the double-drift conditions with respect to control recovered from the analysis of saccade landings. (B) For Experiment 2, the tilt that produced a perceived vertical and the tilt differences between double-drift and control conditions for normal pointing and open-loop pointing. All error bars represent 95% CI.

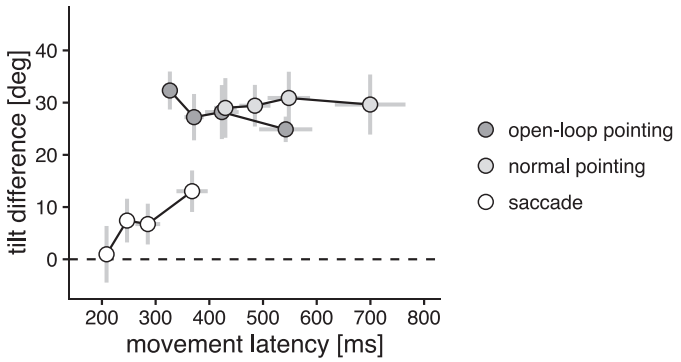

Figure 4. Effect of movement latency. The average effect of the internal motion recovered from the analysis of saccade landings or pointing locations (difference in the angle recovered in the control and double-drift conditions, coded so that positive values indicate shifts consistent with the perceptual illusion)—averaged over physical path orientations (left/tight)—is plotted as a function of the latency of the movement (either saccade or hand movement), binned according to individual latency quartiles. Note that the average latency in the first two quartiles of the open-loop pointing overlapped with the fourth saccade latency quartile. Despite the similar latencies, the effect of the internal motion resulted significantly larger in the open-loop pointing experiment, both in the first, $t(11) = 3.58$, $p = 0.002$, and the second, $t(11) = 2.34$, $p = 0.019$, quartiles (one-tailed tests), indicating that the difference between pointing and saccades cannot be explained by the different latencies of the two types of movements. Error bars represent standard errors, across observers, of the mean tilt differences (vertical bars) and of the mean movement latency (horizontal bars).

with latency quartile and physical path orientation (left/right) as predictors. The effect of path orientation was not significant, $F(1, 6) = 0.25$, $p = 0.63$, nor was the effect of latency quartile, $F(3, 18) = 0.22$, $p = 0.88$, or the interaction between orientation and latency quartile, $F(3, 18) = 0.68$, $p = 0.57$.

Open-loop pointing

The multivariate model was fitted to an average of 541 pointing responses per observer; the average value of r^2 for the fits was 0.42 for the horizontal components ($SD = 0.10$) and 0.61 for the vertical components ($SD = 0.11$). The difference between the double-drift condition and control condition was significantly different from zero for both the left, $t(6) = 11.43$, $p < 0.0001$, and the right, $t(6) = 4.90$, $p = 0.002$, path orientations (paired t test); this effect amounted, on average, to 61.43% of the perceptual illusion. We repeated the same analysis described above to investigate the effect of the latency of the movement and found that the effect of latency quartile was not significant, $F(3, 18) = 1.38$, $p = 0.28$, whereas the effect of path orientation was significant, $F(1, 6) = 7.22$, $p = 0.04$; the interaction between latency quartile and orientation was not significant, $F(3, 18) = 1.03$, $p = 0.40$. The effect of path orientation indicates that the influence of the internal motion was larger on trials with left path orientation, 33.22° ($SEM = 4.89$) than in trials with right path orientation, 23.08° ($SEM = 5.88$). For consistency of presentation, in Figure 3B, we represented the effect averaged over the two path orientations.

Discussion

In this study, we have compared the spatial localization of a brief target for two different movements: saccadic eye movements and hand-pointing movements. The target was briefly flashed on top of a double-drift stimulus (Lisi & Cavanagh, 2015; Shapiro, Lu, Huang, Knight, & Ennis, 2010; Tse & Hsieh, 2006), which consists of a moving Gabor grating whose perceived and physical direction of motion can be dissociated by making the internal pattern drift orthogonally to the physical direction. Moreover, the double-drift stimulus has been shown not only to influence perceived direction, but also to elicit large differences between perceived and physical positions (Kwon, Tadin, & Knill, 2015).

In the present experiment, the Gabor moved back and forth along an oblique linear trajectory. We asked participants to judge the locations of brief targets

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flashed on top of the Gabor at the two end points of its motion path The perceived locations showed a shift that matched the previously reported position shift of the Gabor (Lisi & Cavanagh, 2015) as if the flash were "grabbed" by the moving Gabor and displaced to the perceived location of the Gabor path (Cavanagh & Anstis, 2013). For each observer, we measured the physical orientation of the motion path that made the two flashed targets appear to be vertically aligned. Next, using that orientation, we asked the observers to make either saccadic eye movements or pointing hand movements toward the locations of the two flashes. Consistent with our previous findings, we found that saccadic eye movements are minimally affected by the internal motion (Lisi & Cavanagh, 2015) or, more specifically, that saccades made in the double-drift condition are statistically not different from the control condition in which the internal pattern was static (hence no mislocalization occurred). In contrast, hand-pointing movements were strongly biased toward the illusory locations of the two targets. This effect was reflected in the decreased difference in the horizontal coordinates of movements targeting the top and bottom target locations (Figures 1D, E and 2) and in the orientation angle of the line connecting these two points (Figure 3B). That is, although saccades were virtually immune from the illusory effect, hand-pointing movements showed a clear effect, which was robust and statistically significant in all the conditions tested and amounted to about 63% of the perceptual effect. Although perceptual judgments seemed to show a larger bias than hand pointing, this difference does not necessarily imply different spatial representations but might be related to the different task requirements. In fact, although the perceptual task required reporting the relative locations of the two targets in allocentric (i.e., observer-independent) coordinates, the hand-pointing task (and also the saccade task) required indicating the location of a single target in egocentric coordinates.

One explanation of the difference between saccades and hand movements could be that the bias in the finger landing locations resulted from online corrections of the pointing movements. Specifically, although the initial motor command might not have been influenced by the internal motion of the Gabor, the bias might have resulted from subsequent online corrections aimed at reducing the positional error between the hand position and the remembered, perceived position of the visual target—a remembered position because the target was turned off the moment the hand started to move. Indeed, it has been shown that the spatial properties of a visual target are continuously monitored to adjust hand movements toward it (Sarlegna & Mutha, 2015; Saunders & Knill, 2003, 2004). To test this hypothesis, we repeated the pointing task in a condition in which vision was blocked during the execution of the movement by means of shutter glasses (open-loop hand pointing), making it impossible to use visual feedback for online correction of the hand movement. The results of this experiment replicated those of the experiment with normal pointing; the only difference was a moderate increase in the variability of finger landing positions, which is reflected in the decreased r^2 values of the model used to analyze pointing locations in the open-loop pointing condition with respect to the "normal" pointing condition (see also Figures 1D, E and 2). Ultimately, this experiment demonstrates that the bias observed in the pointing positions does not depend on online visual feedback but must be present already in the initial motor command.

Another possible interpretation of the difference between saccades and hand-pointing movements could have been related to the difference in latency between these two types of movement. Other studies have suggested that the effect of motion-induced mislocalizations on eye movements might depend on the timing of the action (de'Sperati & Baud-Bovy, 2008) so that faster and slower actions might show different effects because they pick the visual signal at different points of its temporal evolution. However, this hypothesis seems unlikely because in the double-drift stimulus the influence of the internal motion on saccade landings does not depend on saccadic latency (Lisi & Cavanagh, 2015), a finding that has been replicated here (see Results). Moreover, even though the most rapid hand movements had latencies comparable to those of the slower eye movements, they still showed a significantly larger bias in the direction of the perceptual illusion (see Figure 4). This indicates that the different level of bias showed by hand and eye movements cannot be fully explained by the different latencies of these two types of movements.

Overall, these results point to a difference in the spatial representation of the target used to guide saccades as opposed to that used to guide hand movements. Although saccades were largely unaffected by the internal motion of the Gabor, hand-pointing movements showed a marked bias, consistent with the perceptual effect (although with a smaller amplitude). The positional bias in the double-drift stimulus seems to depend on a tracking mechanism that integrates current and past sensory signals over a surprisingly long interval, possibly in order to deal with uncertainty (Kwon et al., 2015). Specifically, the different orientation of the perceived Gabor's trajectory (with respect to the physical one) would result from an accumulation of position errors that arise when there is spatial uncertainty and the internal estimate of the target's motion direction differs from its actual trajectory. To reduce uncertainty the visual system would combine its

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current estimate of target position with an internal prediction based on the perceived direction (which, in the case of the double-drift stimulus, is very different from the physical one). This results in a position error that accumulates over the temporal integration window of motion and position signals, which seems to extend to at least 1.5 s in our stimulus. We have previously proposed that the saccade system might have access only to the most recent information (i.e., it would use a shorter integration period) and show a much reduced accumulation of position error (Lisi & Cavanagh, 2015). The current results extend our previous findings by indicating that this property does not reflect a fundamental difference between perception and action, but rather a unique characteristic of the saccade system.

Previous studies have shown that the saccadic system uses motion signals to anticipate the position that a moving target will occupy at saccade landing time (Cassanello, Nihalani, & Ferrera, 2008; Etchells, Benton, Ludwig, & Gilchrist, 2010; Gellman & Carl, 1991; Quinet & Goffart, 2015). In addition, saccades made to a static Gabor with a drifting carrier show a small shift in landing position similar to the position shift found in perception (Kosovicheva, Wolfe, & Whitney, 2014; Schafer & Moore, 2007). These results indicate that the saccadic system (a) can use motion information and (b) is not blind to motion signals coming from the drifting of a Gabor sinusoidal carrier. However, these previous articles indicate that the integration period is no more than 100 ms (the motion-induced shift in landing positions corresponds approximately to the distance traveled by the carrier in 100 ms). Our hypothesis of a reduced temporal integration in the saccadic system could reconcile these results with our earlier findings (Lisi & Cavanagh, 2015) because it would predict that the dissociation between saccades and perception should emerge only with dynamic stimuli with which the internal perceptual prediction accumulates over much longer intervals. Although for a stationary Gabor the buildup of the motion-induced displacement reaches its maximum in about 100 ms (Chung, Patel, Bedell, & Yilmaz, 2007), for a moving Gabor it seems to continue for a longer period, perhaps because there is no stable location information to anchor the position estimate. In agreement with this hypothesis, in our previous study, we found a small but systematic shift in saccade landing positions that depended only on the direction of internal motion at saccade onset but did not accumulate over time (beyond the initial 100 ms, Lisi & Cavanagh, 2015, supplemental material).

This difference between hand movements and saccades might reflect the different functional specificity of the two systems. Specifically, the priority for the saccade system might be to shift the visual axis toward the target as fast as possible with little cost for small foveating errors. If integrating past sensory signals with the current input increases processing time (Greenwald, Knill, & Saunders, 2005), the saccadic system might prefer to use current input and maximize the speed of the eye movement. For hand movements instead, a small error might make the hand miss its target with potentially large behavioral costs. In this case, then a different speed–precision trade-off might be preferable with which all available information (including past sensory signals) is used to maximize the accuracy of the movement at the expense of a small time cost. Indeed, using a different paradigm, it has already been suggested that the content of visual short-term memory has a larger influence on hand movements than on saccadic eye movements (Issen & Knill, 2012).

One interpretation of the current results is that there are two distinct spatial maps, or spatial representations, of the visual world. One map, used to guide saccadic eye movements, would represent the locations of potential saccadic targets using only recent, short-lived, sensory signals. The other, supporting conscious perception and other types of movements (such as hand movements), would integrate sensory signals over a longer temporal interval, possibly including information from multiple saccades/fixations. Although the former would be strictly retinotopic, the latter could use a range of idiosyncratic representations over multiple frames of reference (Bosco, Breveglieri, Reser, Galletti, & Fattori, 2015; Chang & Snyder, 2010). The hypothesis of different spatial maps for saccades and perception is supported also by studies of saccadic adaptation, in which intrasaccadic shifts in target position can induce saccadic adaptation even when they are not perceived (Collins, 2014; Souto, Gegenfurtner, & Schütz, 2016). Moreover, because saccadic eye movements are known to be tightly linked to visual–spatial attention (Casarotti, Lisi, Umiltà, & Zorzi, 2012; Moore, Armstrong, & Fallah, 2003), this interpretation would predict some degree of dissociation between attention (grounded in the saccade map) and conscious perception (supported by the perceptual map) in agreement with the recent view that attention and consciousness are two distinct—although partially overlapping—processes (Haladjian & Montemayor, 2015; Montemayor & Haladjian, 2015; Wyart & Tallon-Baudry, 2008).

In sum, our findings provide support to the idea that visual information can undergo different processing depending on whether it is used for action or perception (Goodale et al., 1991; Lisi & Cavanagh, 2015; Milner & Goodale, 2008) but, at the same time, refute the notion of a common spatial processing supporting all types of motor actions. Specifically, we have shown that eye and hand movements made toward identical targets can end up in different

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locations, revealing that they are based on different spatial information.

Keywords: action–perception dissociation, saccadic eye movements, hand pointing, object localization

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References

Aglioti, S., DeSouza, J. F., & Goodale, M. A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology: CB*, *5*(6), 679–685. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/7552179

Bosco, A., Breveglieri, R., Reser, D., Galletti, C., & Fattori, P. (2015). Multiple representation of reaching space in the medial posterior parietal area V6A. *Cerebral Cortex*, *25*(6), 1654–1667, doi:10.1093/cercor/bht420.

Bridgeman, B., Kirch, M., & Sperling, A. (1981). Segregation of cognitive and motor aspects of visual function using induced motion. *Perception & Psychophysics*, *29*(4), 336–342. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/7279556

Bruno, N. (2001). When does action resist visual illusions? *Trends in Cognitive Sciences*, *5*(9), 379–382, doi:10.1016/S1364-6613(00)01725-3.

Burr, D. C., Morrone, M. C., & Ross, J. (2001). Separate visual representations for perception and action revealed by saccadic eye movements. *Current Biology: CB*, *11*(10), 798–802. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11378393

Cardoso-Leite, P., & Gorea, A. (2010). On the perceptual/motor dissociation: A review of concepts, theory, experimental paradigms and data interpretations. *Seeing and Perceiving*, *23*(2), 89–151, doi:10.1163/187847510X503588.

Casarotti, M., Lisi, M., Umiltà, C., & Zorzi, M. (2012). Paying attention through eye movements: A computational investigation of the premotor theory of spatial attention. *Journal of Cognitive Neuroscience*, *24*(7), 1519–1531, doi:10.1162/jocn_a_00231.

Cassanello, C. R., Nihalani, A. T., & Ferrera, V. P. (2008). Neuronal responses to moving targets in monkey frontal eye fields. *Journal of Neurophysiology*, *100*(3), 1544–1556, doi:10.1152/jn.01401.2007.

Cavanagh, P., & Anstis, S. (2013). The flash grab effect. *Vision Research*, *91*, 8–20, doi:10.1016/j.visres.2013.07.007.

Chang, S. W. C., & Snyder, L. H. (2010). Idiosyncratic and systematic aspects of spatial representations in the macaque parietal cortex. *Proceedings of the National Academy of Sciences, USA*, *107*(17), 7951–7956, doi:10.1073/pnas.0913209107.

Chung, S. T. L., Patel, S. S., Bedell, H. E., & Yilmaz, O. (2007). Spatial and temporal properties of the illusory motion-induced position shift for drifting stimuli. *Vision Research*, *47*(2), 231–243, doi:10.1016/j.visres.2006.10.008.

Collins, T. (2014). Trade-off between spatiotopy and saccadic plasticity. *Journal of Vision*, *14*(12):28, 1–14, doi:10.1167/14.12.28. [PubMed] [Article]

Dassonville, P., Bridgeman, B., KaurBala, J., Thiem, P., & Sampanes, A. (2004). The induced Roelofs effect: Two visual systems or the shift of a single reference frame? *Vision Research*, *44*(6), 603–611, doi:10.1016/j.visres.2003.10.017.

de'Sperati, C., & Baud-Bovy, G. (2008). Blind saccades: An asynchrony between seeing and looking. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *28*(17), 4317–4321, doi:10.1523/JNEUROSCI.0352-08.2008.

Engbert, R., & Mergenthaler, K. (2006). Microsaccades are triggered by low retinal image slip. *Proceedings of the National Academy of Sciences, USA*, *103*(18), 7192–7197, doi:10.1073/pnas.0509557103.

Etchells, P. J., Benton, C. P., Ludwig, C. J. H., & Gilchrist, I. D. (2010). The target velocity integration function for saccades. *Journal of Vision*, *10*(6):7, 1–14, doi:10.1167/10.6.7. [PubMed] [Article]

Franz, V. H. (2001). Action does not resist visual illusions. *Trends in Cognitive Sciences*, *5*(11), 457–459. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11684465

Gellman, R. S., & Carl, J. R. (1991). Motion processing for saccadic eye movements in humans. *Experimental Brain Research*, *84*(3), 660–667. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/1864336

Downloaded From: http://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/936040/ on 03/02/2017

Gellman, R. S., Carl, J. R., & Miles, F. A. (1990). Short latency ocular-following responses in man. *Visual Neuroscience*, *5*(2), 107–122, doi:10.1017/S0952523800000158.

Gomi, H. (2008). Implicit online corrections of reaching movements. *Current Opinion in Neurobiology*, *18*(6), 558–564, doi:10.1016/j.conb.2008.11.002.

Gomi, H., Abekawa, N., & Shimojo, S. (2013). The hand sees visual periphery better than the eye: Motor-dependent visual motion analyses. *Journal of Neuroscience*, *33*(42), 16502–16509, doi:10.1523/JNEUROSCI.4741-12.2013.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, *15*(1), 20–25. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/1374953

Goodale, M. A., Milner, A. D., Jakobson, L. S., & Carey, D. P. (1991, Jan 10). A neurological dissociation between perceiving objects and grasping them. *Nature*, *349*(6305), 154–156, doi:10.1038/349154a0.

Greenwald, H. S., Knill, D. C., & Saunders, J. A. (2005). Integrating visual cues for motor control: A matter of time. *Vision Research*, *45*(15), 1975–1989, doi:10.1016/j.visres.2005.01.025.

Haladjian, H. H., & Montemayor, C. (2015). On the evolution of conscious attention. *Psychonomic Bulletin & Review*, *22*(3), 595–613, doi:10.3758/s13423-014-0718-y.

Issen, L. A., & Knill, D. C. (2012). Decoupling eye and hand movement control: Visual short-term memory influences reach planning more than saccade planning. *Journal of Vision*, *12*(1):3, 1–13, doi:10.1167/12.1.3. [PubMed] [Article]

Kopiske, K. K., Bruno, N., Hesse, C., Schenk, T., & Franz, V. H. (in press). Do visual illusions affect grasping? Considerable progress in a scientific debate. A reply to Whitwell & Goodale, 2016. *Cortex,* in press, doi:10.1016/j.cortex.2016.10.012.

Kopiske, K. K., Bruno, N., Hesse, C., Schenk, T., & Franz, V. H. (2016). The functional subdivision of the visual brain: Is there a real illusion effect on action? A multi-lab replication study. *Cortex*, *79*, 130–152, doi:10.1016/j.cortex.2016.03.020.

Kosovicheva, A. A., Wolfe, B. A., & Whitney, D. (2014). Visual motion shifts saccade targets. *Attention, Perception, & Psychophysics*, *76*(6), 1778–1788, doi:10.3758/s13414-014-0680-9.

Kwon, O.-S., Tadin, D., & Knill, D. C. (2015). Unifying account of visual motion and position perception. *Proceedings of the National Academy of Sciences*, *112*(26), 8142–8147, https://doi.org/10.1073/pnas.1500361112.

Lisi, M., & Cavanagh, P. (2015). Dissociation between the perceptual and saccadic localization of moving objects. *Current Biology*, *25*(19), 2535–2540, doi:10.1016/j.cub.2015.08.021.

Milner, A. D., & Goodale, M. A. (2008). Two visual systems re-viewed. *Neuropsychologia*, *46*(3), 774–785, doi:10.1016/j.neuropsychologia.2007.10.005.

Montemayor, C., & Haladjian, H. H. (2015). *Consciousness, attention, and conscious attention*. Cambridge, MA: MIT Press, doi:10.7551/mitpress/9780262028974.001.0001.

Moore, T., Armstrong, K. M., & Fallah, M. (2003). Visuomotor origins of covert spatial attention. *Neuron*, *40*(4), 671–683. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/14622573

Quinet, J., & Goffart, L. (2015). Does the brain extrapolate the position of a transient moving target? *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *35*(34), 11780–11790, doi:10.1523/JNEUROSCI.1212-15.2015.

Sarlegna, F. R., & Mutha, P. K. (2015). The influence of visual target information on the online control of movements. *Vision Research*, *110*(PB), 144–154, doi:10.1016/j.visres.2014.07.001.

Saunders, J. A., & Knill, D. C. (2003). Humans use continuous visual feedback from the hand to control fast reaching movements. *Experimental Brain Research*, *152*(3), 341–352, doi:10.1007/s00221-003-1525-2.

Saunders, J. A., & Knill, D. C. (2004). Visual feedback control of hand movements. *Journal of Neuroscience*, *24*(13), 3223–3234, doi:10.1523/Jneurosci.4319-03.2004.

Schafer, R. J., & Moore, T. (2007). Attention governs action in the primate frontal eye field. *Neuron*, *56*(3), 541–551, doi:10.1016/j.neuron.2007.09.029.

Schenk, T., & McIntosh, R. D. (2010). Do we have independent visual streams for perception and action? *Cognitive Neuroscience*, *1*(1), 52–62, doi:10.1080/17588920903388950.

Shapiro, A., Lu, Z.-L., Huang, C.-B., Knight, E., & Ennis, R. (2010). Transitions between central and peripheral vision create spatial/temporal distortions: A hypothesis concerning the perceived break of the curveball. *PloS One*, *5*(10), e13296, doi:10.1371/journal.pone.0013296.

Souto, D., Gegenfurtner, K. R., & Schütz, A. C. (2016). Saccade adaptation and visual uncertainty. *Fron-*

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tiers in Human Neuroscience, *10*, 227, doi:10.3389/fnhum.2016.00227.

Translucent Technologies, Inc. (2012). Technical specifications of PLATO spectacles. Retrieved from http://www.translucent.ca/home/technical-specifications/

Tse, P. U., & Hsieh, P.-J. (2006). The infinite regress illusion reveals faulty integration of local and global motion signals. *Vision Research*, *46*(22), 3881–3885, doi:10.1016/j.visres.2006.06.010.

Whitwell, R. L., & Goodale, M. A. (in press). Real and illusory issues in the illusion debate (why two things are sometimes better than one): Commentary on Kopiske et al. (2016). *Cortex*, in press, doi:10.1016/j.cortex.2016.06.019.

Wyart, V., & Tallon-Baudry, C. (2008). Neural dissociation between visual awareness and spatial attention. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *28*(10), 2667–2679, doi:10.1523/JNEUROSCI.4748-07.2008.

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