

Current Biology

Dissociation between the Perceptual and Saccadic Localization of Moving Objects

Highlights

- Moving stimuli containing internal motion induce large shifts of perceived location
- In contrast, saccades to these stimuli go to their real, not perceived, locations
- Dissociation shows perception is strongly biased by recent sensory history
- Saccades rely principally on current input

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In Brief

Lisi and Cavanagh compare localization of moving objects in perception and saccadic eye movements in humans. They find a striking dissociation: while perception is biased by past sensory signals, saccades rely only on current information. Dependence on past sensory history might be a key difference between processing for perception and action.

Dissociation between the Perceptual and Saccadic Localization of Moving Objects

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SUMMARY

Visual processing in the human brain provides the data both for perception and for guiding motor actions. It seems natural that our actions would be directed toward perceived locations of their targets, but it has been proposed that action and perception rely on different visual information [1–4], and this provocative claim has triggered a long-lasting debate [5–7]. Here, in support of this claim, we report a large, robust dissociation between perception and action. We take advantage of a perceptual illusion in which visual motion signals presented within the boundaries of a peripheral moving object can make the object's apparent trajectory deviate by 45° or more from its physical trajectory [8–10], a shift several times larger than the typical discrimination threshold for motion direction [11]. Despite the large perceptual distortion, we found that saccadic eye movements directed to these moving objects clearly targeted locations along their physical rather than apparent trajectories. We show that the perceived trajectory is based on the accumulation of position error determined by prior sensory history—an accumulation of error that is not found for the action toward the same target. We suggest that visual processing for perception and action might diverge in how past information is combined with new visual input, with action relying only on immediate information to track a target, whereas perception builds on previous estimates to construct a conscious representation.

RESULTS

When a patch of texture seen in peripheral vision moves in one direction and its internal texture drifts in an orthogonal direction (a double-drift stimulus), the apparent orientation of the path can deviate by 45° or more from its actual path [8–10] (with actual or physical path, we will refer hereafter to the path traced by the envelope or patch containing the texture). We used this double-drift stimulus to compare object localization in perception and saccadic eye movements. A number of studies have shown that localizing an object involves more than simply reading out its retinal coordinates (e.g., [12]), and that many different factors including visual motion [13–15], can make the

perceived position of an object deviate from the location corresponding to its retinal stimulation. The double-drift stimulus combines motion within an aperture (“internal” motion) and motion of the aperture itself (“external” motion), with the direction of one motion vector orthogonal to the other. More specifically, our stimuli were Gabor patterns (sinusoidal luminance modulation within a Gaussian contrast envelope) oscillating back and forth on a linear trajectory and reversing the direction of internal motion (the drifting of the internal grating) in synchrony with path reversals (Movie S1). This stabilizes the illusory path and changes its perceived orientation so that a physically tilted path can appear vertical (Figure 1A). In experiment 1, we measured the magnitude of the shift in perceived location along the motion path and investigated whether this is taken into account by saccadic eye movements directed toward the moving Gabor. Protocols for all experiments were approved by the Université Paris Descartes Review Board, in accordance with French regulations and the Declaration of Helsinki.

The experiment comprised two parts: the first part consisted of a perceptual task designed to measure for each participant and condition (left or right physical tilt; Figure 1A) the physical orientations of the Gabor's motion path that were perceived as vertical. We presented the double-drift stimuli moving along trajectories of varying orientation and asked participants to report whether the perceived orientation of the path was left or right of vertical (see Supplemental Experimental Procedures for details). For all the participants ($n = 6$), the orientations that were perceived as vertical (yielding 50% “right tilt” responses) were strongly deviated from 0° (with 0° corresponding to physical vertical; see Figures 1A, 1B, and 1C). The mean right tilt that was perceived as vertical was 49°, 95% confidence interval (CI) [33°, 66°], and the mean left tilt that was perceived as vertical was –52°, 95% CI [–44°, –60°], revealing a dramatic influence of the internal motion on the perceived orientation of the trajectory. In the second part, we asked participants to make interceptive saccades toward the moving Gabor patterns (Figure 1D; see Supplemental Experimental Procedures for details). In this second part, we presented only path orientations that were perceived as vertical by each participant and added a control condition in which the same trajectories were presented without internal motion. This control condition was necessary to get a baseline of saccade landings in the absence of the perceptual illusion. In both conditions, the Gabor pattern was removed from screen as soon as the saccade started so that participants never received feedback about the accuracy of their saccades.

In the analysis of saccade data, we excluded trials with saccade latency shorter than 100 ms or longer than 600 ms (3.5% of total trials; mean latency in the remaining trials,

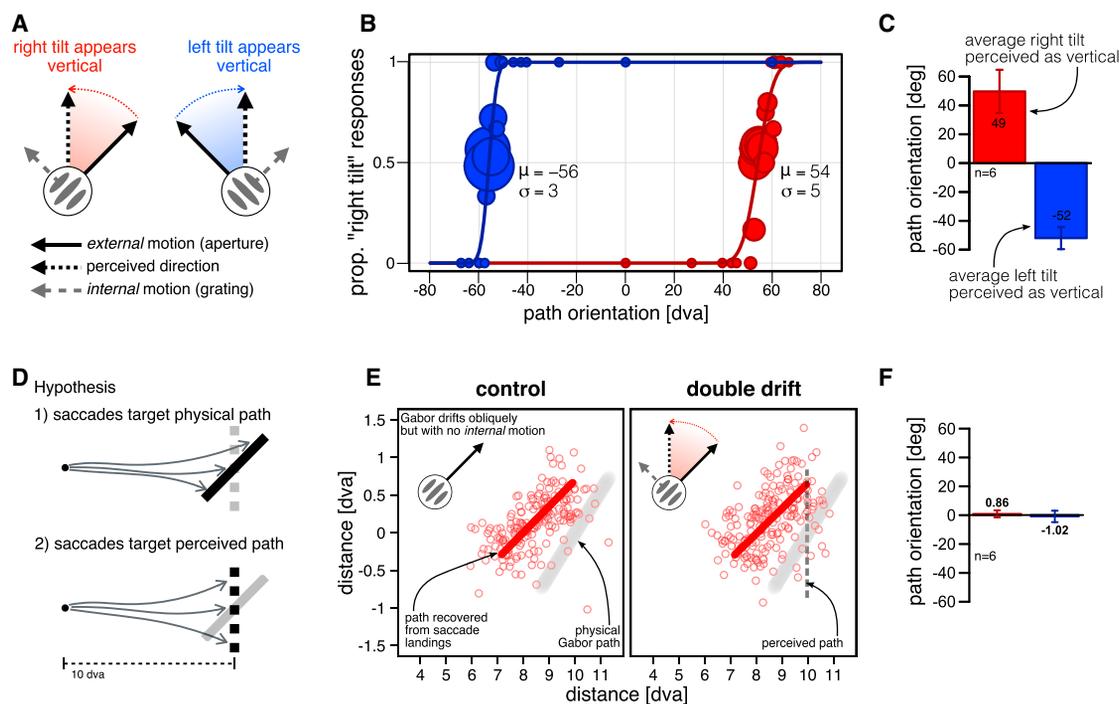


Figure 1. Experiment 1

(A) The two double-drift stimuli with oblique paths that appear vertical.

(B) An individual psychometric function in the perceptual task. The proportion of “right tilt” responses is shown in red for the right oblique stimulus, for various angles of tilt, and for the left tilted stimulus in blue. The mean of the functions, μ , indicates the point of perceived verticality (50% right responses) of the motion path. Data points are represented binned for clarity, with the size of the dot proportional to the number of trial in that bin (480 trials in total).

(C) Average point of perceived verticality across the six participants (error bars represent 95% CI).

(D) In the saccade task, participants fixate a central point and when it disappears, make a saccade to the Gabor target, which is moving back and forth along its path at 10° of visual angles (dva) to the right of the fixation point. The relative landing locations of saccades targeting different points of the path can be used to infer the orientation of the path as “seen” by the saccade system as either the physical path (hypothesis 1) or the perceived path (hypothesis 2).

(E) Landing locations for a representative subject are plotted along with the fitted values of a multivariate linear model (red lines, see Figure S1 and Supplemental Experimental Procedures for details). The control condition (with no internal motion) is represented on the left, and the double-drift condition (where the perceived path is vertical) is on the right.

(F) Average effect of the internal motion on the orientations recovered from the analysis of saccade landings (double-drift minus control) for the six participants (error bars represent 95% CI).

237 ms, SD across participants, 19 ms). Next, we recovered the orientations of the target path as seen by the saccade system from the distributions of vertical and horizontal saccade amplitudes. We analyzed these amplitudes using a multivariate linear model (see Figures 1D and S1 and Supplemental Experimental Procedures). The model was fitted on average with 741 saccades per participant. The mean r^2 of the fits was 0.44 for the horizontal amplitudes (SD 0.12) and 0.50 for the vertical amplitudes (SD 0.13). The difference between the orientations recovered in the control and double-drift conditions gave a measure of the effect of the internal motion (Figure 1F): this difference was not significantly different from zero for either the left ($t(5) = 0.97$, $p = 0.37$) or right ($t(5) = 0.70$, $p = 0.51$) tilts (paired t tests), regardless of the latency of the saccade (see Supplemental Results). This result indicates that saccades did not show the vertical alignment of landing positions expected from the perceived vertical orientation of the double-drift paths. Instead, all participants showed a distribution of saccade endpoints that closely matched the orientation of the physical path (except for the typical saccade undershoot). Across participants, the

path angles recovered in the double-drift condition were oblique and virtually identical to the angles recovered in the control condition ($r = 0.97$, $p = 0.0009$).

The effect measured in the perceptual task suggested an accumulating deviation in apparent location: the perceived location began at the starting point of the trajectory, but then the internal motion of the Gabor moved its perceived location away from its true location. The perceived location at any one point in time is not only shifted in the direction of illusory motion at that moment but that shift is added onto the accumulated shifts of previous locations. This accumulating shift changed the oblique path into a vertical one. Even though this accumulating position shift was not seen in the saccade landings, it is possible that the internal motion of the Gabor did affect saccade landings, perhaps with a constant position deviation at each location as is seen for stationary Gabors with internal motion [13, 16, 17]. We tested this shift by rotating the coordinates of the saccade landing positions to obtain a measure of the landing error orthogonal to the trajectory (see Supplemental Experimental Procedures for details). We analyzed this orthogonal

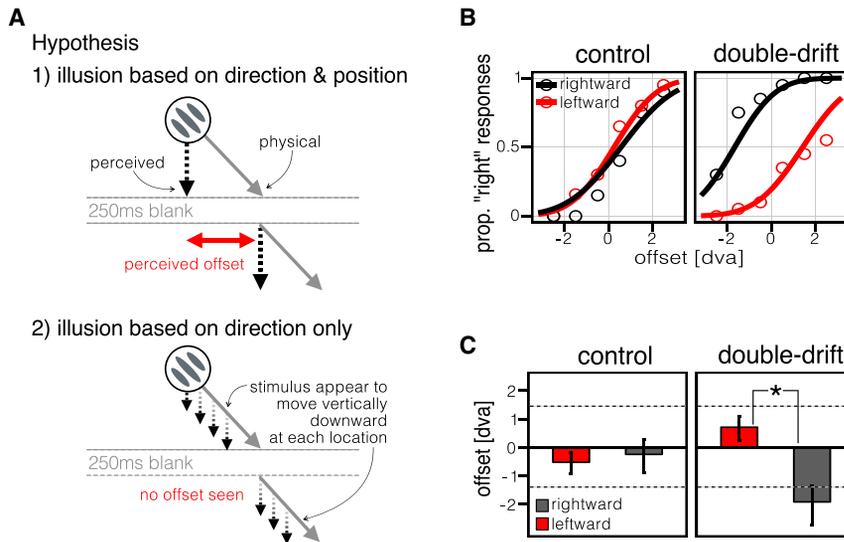


Figure 2. Experiment 2

(A) Schematic representation of the position and direction hypotheses for the illusion and the predicted consequences for the perceived path offset caused by a break in the trajectory. The direction of the aperture motion was always downward, slanted 45° either to the right or to the left. The internal motion was orthogonal to the aperture direction in order to make the path appear nearly vertical. In the example, the Gabor moves downward and rightward and disappears for 250 ms in the middle of its trajectory. If the illusion involves an accumulating shift in perceived position, then the pre- and post-blank segments should appear misaligned when the Gabor reappears in the same exact position (top). On the other hand, if the illusion distorts only the direction of motion, making it appear vertical downward at each location without affecting position, the two segments should appear aligned when the Gabor reappears in the same physical location (bottom). The results of this simple test (B and C) clearly demonstrate that the internal motion contributed to the perceived position of the Gabor.

(B) Psychometric curves for one representative participant in experiment 2. The probability of participant reporting an offset to the right is shown as a function of the amplitude and direction of the offset. The left panel represents the control condition with no internal motion where the horizontal offset is reported veridically with no bias. The right panel represents the double-drift condition: here, the point of subjective equality (PSE), corresponding to 50% of "right offset" responses, is clearly shifted toward the initial horizontal position so that, for example, a small offset to the left is seen as an offset to the right most of the time.

(C) Mean PSEs across participants ($n = 6$); error bars represent bootstrapped 95% CI. A significant difference between downward-leftward and downward-rightward motion was found only in the double-drift condition (right panel) and not in the control condition (left panel). The dotted horizontal lines represent the prediction for the position-based illusion: the end of the first segment and the beginning of the second should appear aligned when initial positions of the two segments are aligned. Note the slight bias toward negative values (i.e., toward fixation, always located on the left), common to both conditions; this reflects a small foveal bias (see Results).

landing error as a function of the direction of internal motion at saccade onset. This analysis showed that the saccade landing positions differed significantly for the leftward versus rightward internal motion (mean difference 0.67 degrees of visual angle [dva], 95% CI [0.49, 0.85], $t(5) = 9.68$, $p = 0.0001$), a shift similar in magnitude to the reported shifts for stationary Gabors in perceptual [13] and saccade [16, 17] experiments. We also found that this error did not change along the path, remaining constant at different locations, and did not depend on the latency of the saccade (Figure S2).

These results indicate clearly that the saccadic system does not process the position of a moving target in the same way as conscious perception. The saccade system appears to track the Gabor and show only a small, local shift in response to the internal motion. This local shift did not change or accumulate over time. In contrast, the perceptual system combines the two internal and external vectors to create an illusory direction, and we have assumed that this drives the accumulation of an illusory position shift. To verify this assumption, we ran a second experiment to determine whether the perceptual effect was simply a result of the illusion of direction or involved a deviation in perceived location as well.

We designed experiment 2 to determine whether the perceived illusion involves only a distortion of the perceived direction of motion [8] or also a shift in perceived position (Figure 2A). We noted in pilot observations that the perceived path appeared to be anchored by its initial position with the position error accumulated from there. In addition, an interruption in the motion path appeared to reset this initial position so that after the interruption, the path appeared to begin from the new starting point, not

from the previous illusory position. If these pilot observations held up, it would indicate that the illusion indeed affected perceived position as well as direction. We therefore used an interruption in the motion path to differentiate between a direction-based and a position-based illusion (Movie S2).

We presented a Gabor moving down to the left or down to the right, with a trajectory that deviated 45° from vertical, but with an internal motion that made its trajectory appear approximately vertical. A brief (250 ms) temporal gap was introduced halfway between the top and bottom locations. During the gap, the Gabor was removed from the screen, and it reappeared shifted horizontally to the left or right of where it had disappeared. The task of the participant was to report the direction of this horizontal jump (see Supplemental Experimental Procedures). We reasoned that if the illusion involved only an illusory distortion of direction and not of position, then participants would judge the new position as aligned with pre-gap position when it was in fact physically aligned (Figure 2A). On the other hand, if the illusion involved an accumulating deviation in position, participants would judge the new position after the gap relative to the illusory position at the end of the first half of the trajectory. The illusory position at the end of the first segment should be approximately vertically aligned with the initial start location of the trajectory, whereas the second segment would be perceived to begin at its new physical location, as there would not yet be any accumulated position shift.

The results clearly supported the position-based effect. The point of perceived vertical alignment (Figure 2B) in the condition with leftward internal motion (external motion downward-rightward) was -1.92 dva (95% CI $[-2.72, -1.36]$), whereas with

rightward internal motion (external motion downward-leftward), it was 0.71 dva (95% CI [0.26, 1.09]). Both of these shifts were significantly different from 0 and from each other, and the amplitude of the shifts was quite close to the physical horizontal offset between the top and bottom locations (1.41 dva) as would be expected if the illusory position shift was accumulating linearly from the beginning of the trajectory. The shifts that seemed aligned when there was no internal motion (control) both differed significantly from the apparently aligned shifts when there was internal motion: -0.25 dva (95% CI $[-0.89, 0.28]$) for the left and downward trajectory and -0.52 dva (95% CI $[-0.92, -0.18]$). Finally, the position matches both with and without the internal motion in the Gabor showed an average shift toward the left (double-drift, -0.61 dva; control, -0.39 dva). These mean biases are toward fixation and may reflect the foveal bias typically seen for brief targets [18]. In our case, the final position of the first segment is remembered as closer to fixation than it really was, causing the shift common to all alignment judgments.

The pattern of motion-dependent alignments indicates that the illusion did indeed involve the buildup of position offset from the initial starting position: participants judged the new position of the Gabor relative to the previous illusory position rather than the physical one. Most importantly, since the illusory effect seems to be position based, any simple explanation based on a position versus direction distinction [19] cannot account for the absence of an effect in the saccade condition of the first experiment. The saccade system, which targets locations not direction, should be equally affected if perception and action share the same map of locations. Clearly, they do not.

DISCUSSION

We have found a large dissociation between the perceived path of a moving target and the action toward it. We used moving Gabor patterns whose perceived and physical direction were dissociated by making the internal sinusoidal pattern drift in a direction orthogonal to the direction of its displacement in space. When viewed in the periphery, motion signals coming from the displacement of the Gabor and from the drifting pattern inside it are erroneously combined [8–10], leading to a shift in its perceived direction that we measured here as up to a 50° change of orientation, corresponding to a shift in perceived position of over 1.5 dva (measured at the endpoints). Despite the striking perceptual effect, saccades clearly targeted the physical rather than the perceived path, and the trajectories recovered from the distribution of saccade landings showed no difference between the double-drift stimulus that induced the illusion and a control condition where the Gabor had no internal motion and there was no illusion.

One interpretation of the results could have been that the perceptual judgments are not based on the perceived position of the Gabor but only on its perceived direction. However, the results of experiment 2 clearly rule out this possibility: we showed that when a brief temporal gap (250 ms) is introduced in the Gabor's trajectory (oblique but perceived as vertical), the pre- and post-gap segments appear misaligned. Observers perceived the new starting position after the gap as beginning at its physical location, whereas last perceived position before the gap had been shifted in the direction of the internal motion.

This finding demonstrated that the perceived position of the Gabor in the double-drift stimulus is constructed by integrating the initial position with the illusory direction vector over time to produce new position estimates that increasingly deviate from the physical location. The temporal gap resets the integration so that subsequent position trace, starting at the new physical location, seems offset from the perceived end location of the position trace before the gap.

Despite the absence of the accumulating position shift in the saccade responses, there was a small, constant offset of about 0.3 dva, less than the width of the Gabor, in the direction of the target's internal motion at saccade onset, in agreement with previous reports of saccades made toward a static but drifting Gabor [16, 17, 20]. Importantly, this shift in saccade landings did not increase over time but remained constant along the motion path.

What causes the perceptual illusion and why is there such a dramatic difference between the perception of the target and the motor response toward it? The original studies of the double-drift stimulus [8, 9] focused on the direction as opposed to the position of the target describing how the external and internal motion vectors are integrated to produce the illusory perceived direction. Both of these studies noted that the perceived difference in direction might also influence perceived location but did not measure this. The results here showed that the combined motion vectors do act directly on perceived position and that this position error can accumulate across up to 1s of the target's trajectory (temporal interval between the onset of the target and the blank in experiment 2).

A recent study explicitly modeled the integration of velocity information into perceived position [10]. The model is a Kalman filter that optimally weights the sensory signals based on their reliability. When the precision of incoming position information is low, as it is here for a Gabor pattern presented in peripheral vision on a background of the same mean luminance, the estimates of object position are strongly influenced by the prediction based on past visual information. The model predicts a number of results in the motion-induced position shift literature and explains how the persisting influence of past visual information can produce growing position shifts in the curveball illusion and our double-drift stimuli.

In contrast with this evidence for strong dependence on past visual information in perception, our data here suggest that the saccadic system uses only the current visual input to extrapolate the target position in order to intercept it [21–23]. We found evidence of the small, constant position shift that this would produce rather than the accumulating position shift seen for perception. In particular, the shift in saccade landing position was independent of the location of the target along its path and therefore independent of the previous history of sensory signals. However, other factors may have contributed to the difference between perception and saccades. If the saccadic system, like the perceptual system, uses a velocity-integrating mechanism to track target location [10], then one possibility is the presence of a smaller amount of noise (less position uncertainty) in the location information available, perhaps as a consequence of additional visual input from the subcortical retino-collicular pathway [24–26]. It is also possible that the processing of motion signals is different between perception and saccadic

eye movements: previous studies have shown different parameters for motion integration in action and perception, although these were limited to smooth pursuit eye movements [27–29] or reflexive ocular following responses [30–32].

To conclude, we provide compelling evidence of a difference between perceptual and saccadic localization of a moving object. Other studies have compared perception and eye movements [25], although only a few focused on saccades, and these have provided conflicting evidence of similarities [17, 33–36] and differences [37–39]. However, these studies examined saccades directed to static targets where the information provided by prior sensory history was negligible. Here, we used a moving stimulus that drifts in one direction with an internal pattern that drifts in the orthogonal direction. For this stimulus, perception shows not only a deviation in the apparent direction of motion but also a large, accumulating shift in perceived position that generates a new trajectory based on prior sensory history. In contrast, saccade landings show a small, constant shift that depends only on the instantaneous direction of the internal motion just before saccade onset. More generally, our results highlight a fundamental difference between perception and action, suggesting that while our perceptual experience builds upon the history of previous sensory signals, motor control seems to use only the most recent information available.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Results, Supplemental Experimental Procedures, two figures, and two movies and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2015.08.021>.

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