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Dissociation between the perceptual and saccadic localization of moving objects

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Abstract

Visual processing in the human brain provides the data both for conscious perception and for guiding motor actions. It seem natural that our actions would be directed toward the consciously perceived locations of their targets but it has been proposed that perception and action rely on different visual information and this provocative claim has triggered a long lasting, active debate. Here, in support of this claim, we report a remarkably large dissociation between perception and action. We studied saccadic eye movements directed to a moving Gabor patch whose perceived trajectory deviated by 45° or more from its physical trajectory. Surprisingly, saccades targeted the physical target path not the perceived path. We show that this perceptual illusion is based on the steady accumulation of target position error over at least 500 ms – 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.

Introduction

Visually guided behaviors such as picking up a cup of coffee from the table or shifting our gaze to an approaching car, require many computational steps, ranging from the sensory acquisition of the target to the generation of the appropriate motor command. Intuitively, it seems natural that the planning of motor actions toward visible objects would use the same visual representation that allows us to perceive those objects. However, many experimental findings have challenged this idea, suggesting instead that visual information undergoes independent processing when used for perception as opposed to action [1–4] (but see also opposing results [5–10]). For healthy subjects, the action-perception dissociation is based on a reduction of illusions when tested with actions rather than perception (see [4]). For example, in their original study, Aglioti et al [11] reported that probe circles surrounded by smaller vs larger circles show a perceptual size shift about 5% (the classic Ebbinghaus illusion), which is approximately the same as the just noticeable difference for size judgments (6%, [12]). When subjects grasped the same probe circles, however, the effect of the illusion on grasp preparation decreased to about 3%. This was significantly smaller than the perceptual illusion but still significantly greater than 0. The illusion was present in action, but reduced.

In contrast, we report here an action–perception dissociation in healthy subjects that is far larger and remarkably robust. When a patch of texture 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 [13–15]. The shift in apparent orientation is several times larger than the typical discrimination threshold for motion direction (about 5° [16, 17]). We used this double-drift stimulus to compare object localization in perception and action. A number of studies have shown that localizing an object involves more than simply reading out its retinal coordinates (e.g., [18]), and that there are many different factors that can make the perceived position of an object deviate from the location corresponding to its retinal stimulation, including but not limited to: attention [19], eye movements [20], masking [21, 22] and visual motion [23–26]. 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, as in the infinite regress illusion of Tse and Hsieh [13] or the curveball illusion [14]. In our new version, the aperture oscillates back and forth on a linear trajectory, reversing the direction of internal motion in synchrony with path reversals (see Movie S1). This stabilizes the illusory path and produces large differences between perceived and real *positions* as well as directions. We measured the magnitude of the shift in perceived location along the motion path and investigated whether this is taken into account during saccade planning. Surprisingly, despite the dramatic perceptual effects, saccades clearly targeted the real rather than the apparent path. Indeed, the path orientations recovered from saccade landing positions were indistinguishable from a control condition where the target had no internal motion.

In addition to demonstrating the perception vs action dissociation with this double-drift stimulus, we also examined whether the effect was based on the perceived position of the target as compared to its perceived direction. In a second experiment, we started with an obliquely oriented motion path that appeared vertical because of the internal motion. We introduced a brief gap in the target's apparently vertical trajectory at around the mid-point. We found that the pre-and post gap segments showed a strong horizontal offset even though their apparent directions remained vertical. This result shows that the internal motion vector contributed to the build up of position offset from the initial starting position. The gap reset this start point, producing a pair of parallel but offset motion segments (see Movie S2). Since the internal motion contributes directly to the perceived position, 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.

Results

Experiment 1

Experiment 1 comprised two parts; the first part consisted in a perceptual task designed to measure for each participant and condition (left/right physical tilt; see fig. 1A) the physical orientations of the Gabor's motion path that were perceived as vertical. This was followed by a second part in which participants were asked to saccade toward the moving target (fig. 1D). In the saccade task only the physical orientations yielding a perceived vertical path were presented. The saccade task included also a control condition where the internal grating remained static: this condition served as a baseline to measure the effect of the drift of the grating on saccade targeting.

Perceptual task. For all the participants, the orientation of the motion path that was perceived as vertical was dramatically different from 0° (with 0° corresponding to physical vertical; see fig. 1A, B, and C). The mean right tilt that was perceived as vertical was 49° [95% CI 33°, 66°], and the mean left tilt that was perceived as vertical was -52° [95% CI -44°, -60°], indicating that the internal motion heavily influenced the perceived direction of the aperture and the orientation of the trajectory.

Saccade task. For each participant, the orientation of the motion path that appeared to be vertical in the perceptual task was then used as the target path for the saccades and here, surprisingly, the saccade landing locations toward the moving target showed no effect of the illusion. The same orientations were also used in trials with the Gabor having no internal motion (controls) to get a baseline of saccade landings in the absence of the perceptual illusion. In the following analysis, we excluded trials with saccade latency shorter than 100ms or longer than 600ms (3.5% of total trials; mean saccadic latency in the remaining trials, 237ms, standard deviation across participants, 19ms). The first step in our analysis was to recover the orientations of the target path seen by the saccade system from the distributions of vertical and horizontal saccade amplitudes. We analyzed these amplitudes using a multivariate linear model (fig. 1D, see Methods for details). The mean r^2 of the fits was 0.44 for the horizontal amplitudes (standard deviation across participants 0.12), and 0.50 for the vertical amplitudes (standard deviation 0.13). The difference in recovered orientations of saccade landings between the control and double-drift conditions gave a measure of the effect of the internal motion (fig. 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). 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). In particular, across participants, the path angles recovered for both directions in the double-drift condition were again oblique and virtually identical to the angles recovered in the control condition where there was no perceptual illusion [$r=0.97$, $p=0.0009$].

Local, motion-induced effects on saccade landing. The effect measured in the perceptual task indicated an accumulating deviation in apparent location: the perceived location began at the starting point of the trajectory but then moved increasing far away, changing an oblique path into a vertical one. This accumulating position shift did not show up in the saccade landings, which followed the physical path. Nevertheless, there is the possibility that the stimulus motion did affect saccade landings with a constant position deviation at each location that did not accumulate over time. Specifically, the saccade landing might shift orthogonally to the target's path as a consequence of the internal motion of the Gabor. The effects of the internal motion of the Gabor have been shown for saccades to stationary Gabors with internal motion [27]. In this case, the effect is typically a fraction of the Gabor envelope size and does not accumulate over time, after the initial 100ms [27]. 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 Analysis section for details). We analyzed this orthogonal 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 vs. rightward internal motion (mean difference 0.67dva, 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 [23] and saccade [8, 27] 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 (see 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 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 if the perceptual effect was simply a result of the illusion of direction or involved a deviation in perceived location as well.

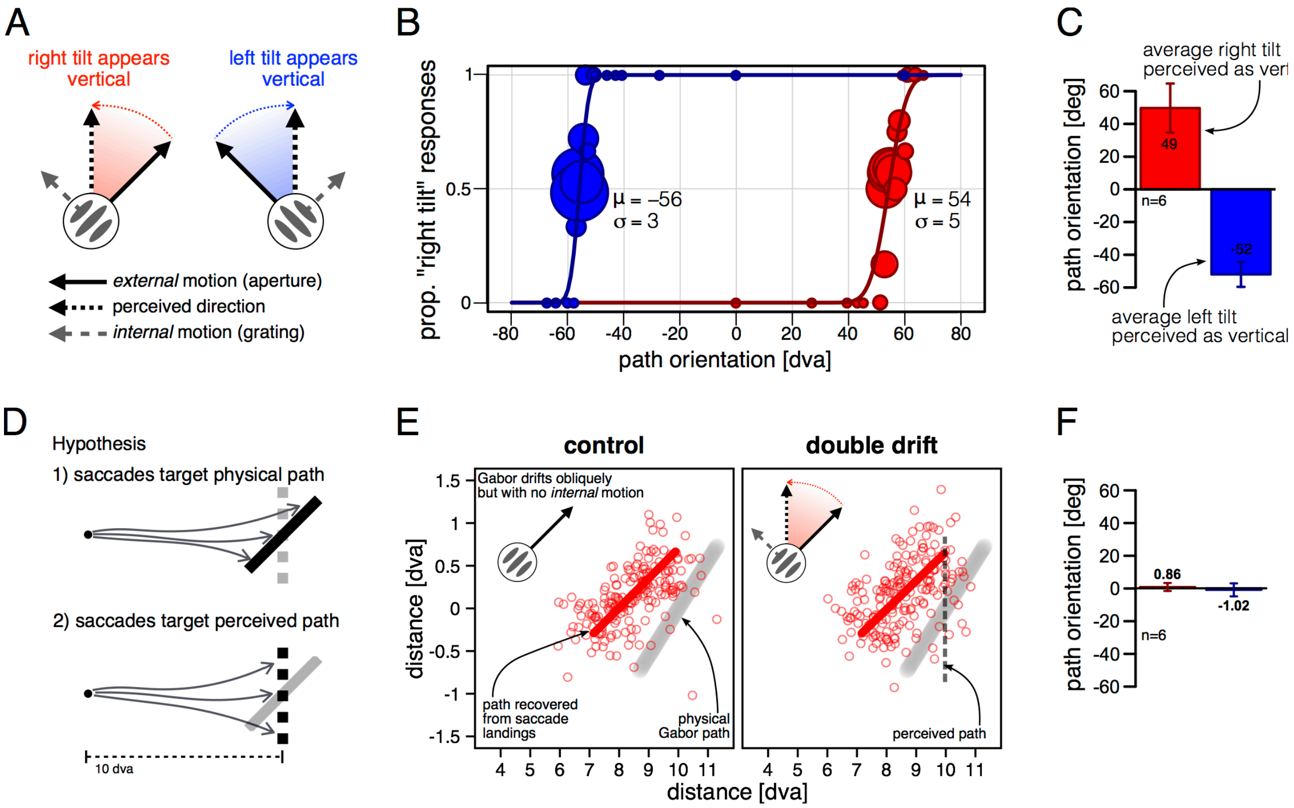

Figure 1. Experiment 1. **A.** The two double drift stimuli with oblique paths that appear vertical. **B.** An individual psychometric function in the perceptual task. The proportion of "right tilt" responses is shown right oblique stimulus for various angles of tilt and for the left tilted stimulus 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 6 participants (error bars represent 95% confidence interval). **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 10dva 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 Analysis 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 6 participants (error bars represent 95% confidence interval).

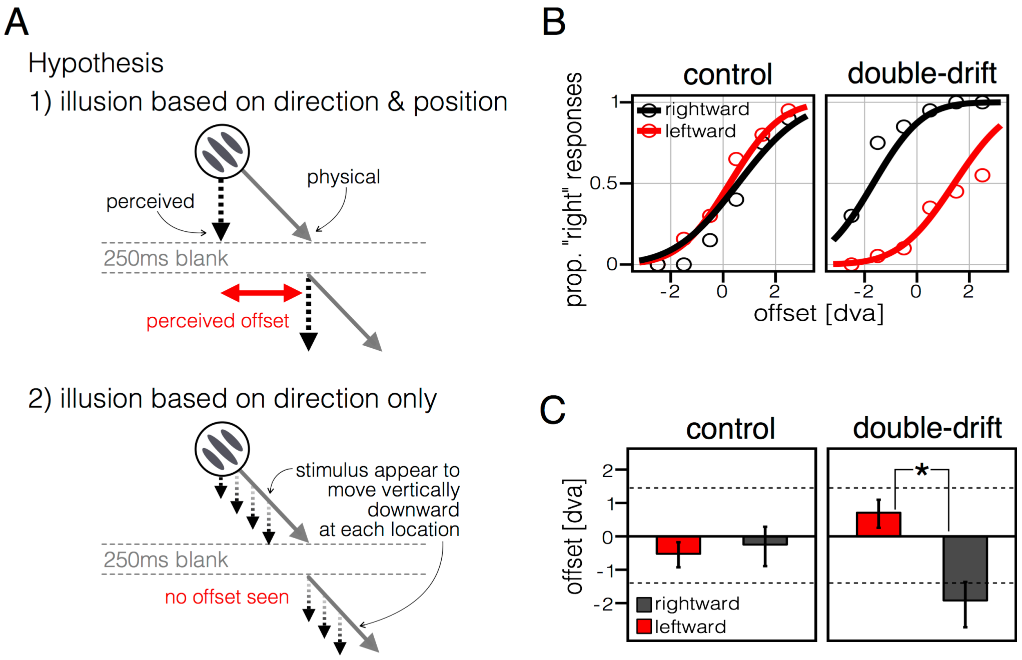

Figure 2. Experiment 2. **A.** Schematic representation of the position and direction hypotheses for the illusion and the predicted consequences for the perceived path offset caused by a break in the trajectory. The direction of the aperture motion was always downward, slanted 45degree either to the 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 250ms 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 (panel 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 alignment (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% confidence interval. 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).

Experiment 2.

In this experiment we investigated the characteristics of the illusory perceptual effect to determine whether it involves only a distortion of the perceived direction of motion [13], or also a shift in perceived position (fig. 2A). We designed a test based on pilot observations that the perceived path appear 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.

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 (based on results from the first experiment). A brief (250ms) temporal gap was introduced after 1 second from motion onset, exactly 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. 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. 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 (see fig. 2A) 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 two alternatives thus give very different predictions for the shift that should appear vertically aligned across the gap: if the illusion is based on direction without any perceived position shift, the segments will appear aligned when they actually are; if the illusion also includes an accumulating shift in perceived position, then the segments will appear aligned when they are shifted by approximately the horizontal offset between the physical top and bottom locations, to the left or to the right depending on the direction of motion (Fig. 2A).

The results clearly supported the position-based effect. The point of perceived vertical alignment in the condition with leftward internal motion (external motion downward-rightward) was -1.92dva [95% CI -2.72, -1.36] whereas with rightward internal motion (external motion downward-leftward) it was 0.71dva [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 (1.41dva) 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 both differed significantly from the apparently aligned shifts when there was internal motion: -0.25dva [95% CI -0.89, 0.28] for the left and downward trajectory and -0.52dva [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. The average shift was -0.61 dva with internal motion and -0.39 dva without internal motion. These mean biases are toward fixation and may reflect the foveal bias typically seen for brief targets [28]. 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 perception of position with a shift that accumulated over time: participants judged the new position of the Gabor relative to the previous illusory position, rather than the physical one. Moreover, since the illusory effect seems to be position-based, any simple explanation based on a position vs. direction distinction cannot account for the absence of an effect in the saccade condition of the first experiment.

Discussion

We have found a dramatic 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 [13–15], leading to a shift in its perceived direction that we measured here as up to 50° of rotation, corresponding to a shift in perceived position of over 1.5 degrees of visual angle (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. Overall, the present results reveal a fundamental difference between perceptual and saccadic localization of a moving object, a finding that adds the most striking example yet that oculomotor and perceptual responses can be dissociated [29–33].

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 (250ms) 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 degree of visual angle, 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 [8, 27, 34]. 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 [13, 14] 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 500 ms of the target's trajectory.

A recent study explicitly modeled the integration of velocity information into perceived position [15]. 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 intercept it [35–37]. 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, then 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 [33, 38, 39]. It is also possible that the processing of motion signals is different between conscious perception and saccadic eye movements: other studies have shown different parameters for motion integration in action and perception, as well as for different perceptual tasks [29, 30, 32, 40], although the effects were on a smaller scale than that reported here.

To conclude, we provide compelling evidence of a dramatic difference between perceptual localization and saccadic targeting of a moving object. The difference arises when the moving target has also an internal pattern that drifts orthogonally to its direction of motion. Perception shows a dramatic shift of over 45° of the apparent direction of motion and a position deviation that grows along the motion path to over 1.5° of visual angle (for the conditions of our stimuli). In contrast, saccade landings show only a small, constant shift of about 0.3° of visual angle. Previous reports of dissociation between perception and saccadic eye movements have been far smaller than the effects reported here [8, 41–44], and to our knowledge this is the first evidence of such a large and clear difference between saccadic targeting and perceived position. 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.

Experimental Procedures

Participants

6 observers (4 female, 1 author; mean age 32, standard deviation 3) participated in the experiment 1 (both perceptual and saccade task) and 6 observers (4 female, 1 author; mean age 29, standard deviation 4) participated in experiment 2. All observers 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 Review Board, CERES, in accordance with French regulations and the Declaration of Helsinki. All participants were experienced psychological observers, and (except the author) all were naïve to the specific purpose of the experiments.

Setup

Participants sat in a quiet, dark room. We recorded the right-eye gaze position with an SR Research Eyelink 1000 desktop mounted eye tracker, at a sampling rate of 1 kHz. Participant's head was positioned on a chin rest, with adjustable forehead rest, at 60 cm in front of a gamma-linearized Compaq P1220 CRT screen (vertical refresh rate 120Hz) that was used to present stimuli. An Apple computer running MATLAB (Mathworks) with the Psychophysics and Eyelink toolboxes [45–47] controlled stimulus presentation and response collection.

Stimuli

Experiment 1. In experiment 1 the stimulus was a Gabor pattern (a sinusoidal luminance modulations within a Gaussian contrast envelope) with a spatial frequency of 2 cycles/dva (cycles per degree of visual angle) and 100% of peak contrast. The standard deviation of the contrast envelope was 0.1dva. The Gabor was moving back and forth along a linear path of length 3dva, with a speed of 2dva/sec (*external* motion). The sinusoidal grating had the same orientation of the motion path, and drifted in an orthogonal direction with a temporal frequency of 3Hz (*internal* motion), reversing its direction in synchrony with path reversals at the two endpoints, every 1.5 seconds. The combination of internal and external motion can make a tilted path appear vertical (see fig. 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 (see Movie S1). The stimulus was presented on a uniform gray background (5.3 cd/m^2) and the midpoint of the trajectory was placed at 10dva from fixation to the right on the horizontal midline.

Experiment 2. In experiment 2 the stimulus was similar to experiment 1, with the following differences: the length of the trajectory was 4dva, and its orientation was fixed at either -45/+45. Additionally the stimulus was presented only for half a cycle every trial, always starting from the top position, with a brief gap (250ms blank) at the midpoint of the trajectory (1/4 of a cycle).

Procedure

Experiment 1.

Perceptual task. In the first part we presented Gabor patterns moving along paths with different orientations, and participant were asked to judge the left/right tilt of the motion path. The stimulus was displayed until participants provided the response by pressing on the left or right arrow key. Gaze position was recorded and monitored online with the eyetracker, and trials in which 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 was adjusted by means of multiple interleaved QUEST staircases [48] that converged to a 50% proportion of “right” tilt responses. Each participant performed two sessions of 240 trials each, divided in 6 blocks.

Saccade task. In the second part, participants were presented only the orientations of the motion path that corresponded to perceived verticality of the motion path. Each trial started when participant fixated a black dot (a circle of 0.2dva diameter) in the center of the screen. After a random interval, of duration uniformly distributed within the interval 400-600 ms, the Gabor appear in the central position of its motion path and started moving. Participants were instructed to make a saccade to the Gabor as soon as the fixation point disappeared. The fixation point could disappear at one out of six points in time equally spaced along a full cycle of motion, starting from the first path reversal. As soon as the gaze position was detected outside a circular area with 2dva of radius around fixation, the Gabor was removed so that participants received no feedback about the accuracy of their saccades. Participants made 2 session of the task, each comprising 384 trials divided in 12 blocks. Gaze position was recorded at 1Khz 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. Experiment 2 was designed to discriminate between direction-based and position-based illusions. Each trial began when the participant fixated a small black dot (diameter 0.2dva) placed at a position drawn from a 2D isotropic Gaussian distribution with a standard deviation of 0.2dva and centered 4dva to the left from the center of the screen (the chinrest was shifted by the same amount so that the participant was fixating straight ahead). This shift to the left allowed presenting the drifting Gabor to be presented closer to the center of the screen, in order to minimize the use of monitor frame as a reference; the jitter in fixation (and consequently stimulus) position served again to discourage any strategy based on other visual landmarks. After a random interval, uniformly distributed within the interval 400-600, the Gabor appeared at the top position, and started moving downward, either toward the left or to the right with an orientation of 45° from vertical (see fig. 2, panel A). The direction of the internal motion was always orthogonal to the direction of the aperture and downward, in order to create a perception of a vertical, or close to vertical, path. As soon as the Gabor reached the midpoint of its trajectory (at 10dva to the right from fixation, along the horizontal midline) it was removed from the screen for 250ms, and then reappeared at the same height but at a shifted horizontal position (-2.5, -1.5, -0.5, 0.5, 1.5, 2.5 dva); immediately after reappearing the Gabor continued moving with the same direction from the new position. The duration of motion before and after the 250 ms blank was 1 second. After the Gabor reached the final bottom position and completed its trajectory, participants were required to report the direction of the horizontal jump that occurred during the gap, by pressing the left or right arrow keys. A control condition with no internal motion was included, randomly interleaved, as a comparison. Gaze position was recorded and monitored online with the eye tracker, and trials in which participant shifted gaze away from the fixation point or blinked before giving the response were aborted and repeated. Each participant completed 480 trials of the task in total, divided in 6 blocks.

Analysis

Experiment 1.

Perceptual task. For each participant and condition the point of subjective verticality of the motion trajectory was computed as the orientation corresponding to the 0.5 level of a cumulative Gaussian psychometric function, fitted by maximum likelihood on the proportion of “right” tilt responses (i.e., the orientation that would yield 50% “left” and 50% “right” tilt responses).

Saccade task. First, we detected saccades onsets and offsets offline with an algorithm based on two-dimensional eye velocity [49]. Next, we analyzed horizontal and vertical saccade amplitudes (the differences in the horizontal and vertical coordinates of saccade offset and onset positions) to recover the orientation of the motion trajectory targeted by the saccades in each condition. For each participant we fitted a multivariate linear model with the horizontal and vertical saccade amplitudes as dependent variables (see Figure S1). The models included as linear predictors the horizontal and vertical coordinates of the Gabor at the moment of saccade onset, together with the condition (control, with no internal motion, vs. double-drift, where the internal motion made the path of the Gabor appear vertical) and the interactions between condition and the Gabor's coordinates. We fitted a multivariate model for each participant, and then used the fitted model to predict saccade amplitudes for each of the positions along the Gabor's path. Finally, we computed a linear regression of the vertical on the horizontal predicted saccade amplitudes, and derived the angle of deviation from vertical from the regression slope. The difference between the orientation angle of the recovered path in the control and double-drift condition was taken as a measure of the effect of the internal motion on the orientation of the trajectory targeted by the saccades. We used this two-step approach because by separating noise in the vertical vs. horizontal dimension it allows to account better for the typically larger variability of saccade landings along the radial than tangential axis [50, 51].

We also analyzed the landing error as a function of the direction of the internal motion measured at the time of the saccade onset (double-drift condition only). The direction of the internal motion was always at 90° from the direction of the aperture, and thus it varied according with the participant, the left/right tilt, and the phase of the motion cycle. To compensate for these differences, we rotated the 2D saccade landing positions to a common vertical axis to determine the deviations in saccade landing orthogonal to the common axis (see Supplemental figure 2).

Experiment 2. Participants reported the direction of the mid-trajectory jump and we analyzed the proportion of "right jump" responses (that is the proportion of trials in which participants reported a rightward horizontal offset) as a function of the horizontal offset and horizontal direction of the aperture (leftward vs. rightward) to determine a PSE where the pre- and post-gap trajectories appeared aligned. We used a generalized linear mixed-effects model [52], with a probit linking function, fitted with R [56] and the *lme4* library [54]. By including random effects grouped according to the participant, the model allowed for both random location and scale parameters (respectively the mean and the standard deviation of cumulative Gaussian psychometric functions) for each participant in all conditions.

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Supplemental information

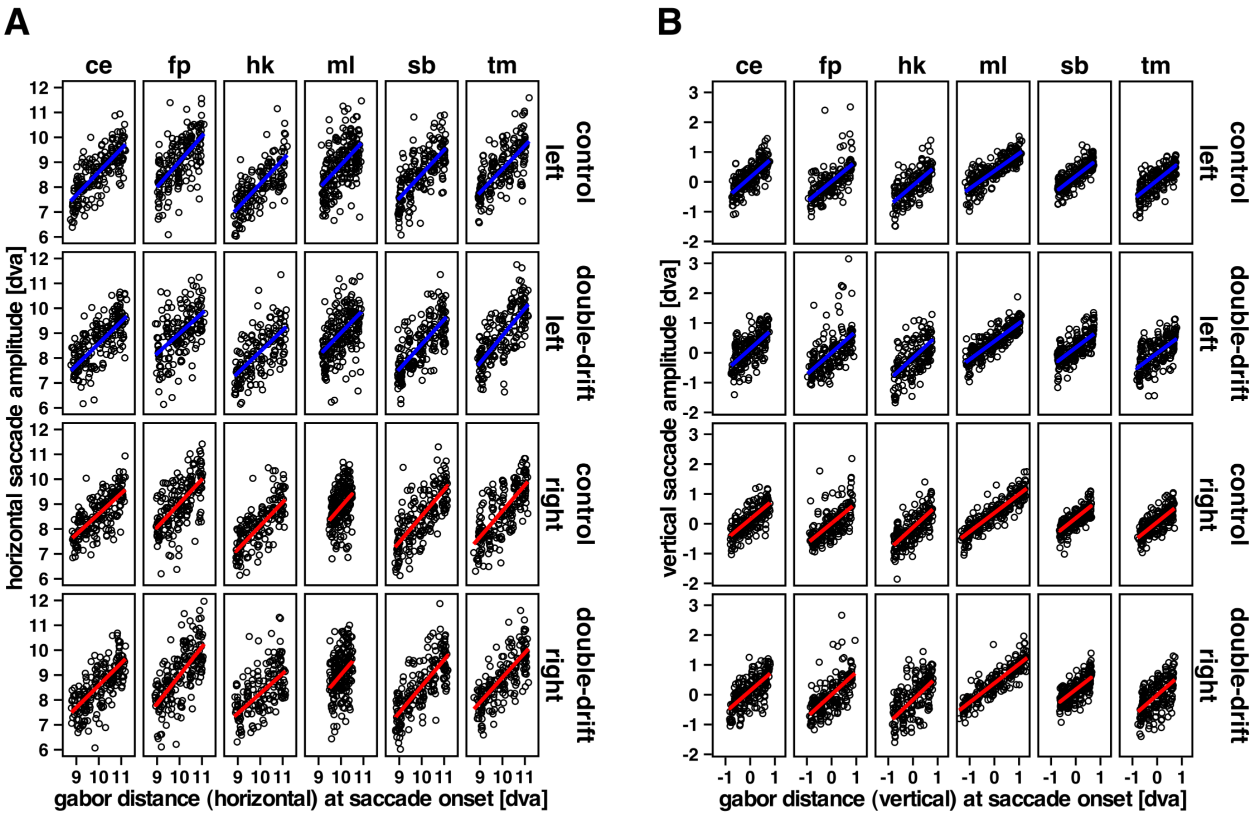

Figure S1. Multivariate analysis of saccade amplitudes. Each column in the panels represent a participant, with horizontal components represented in **A** and vertical components in **B**. The X axis represents the position of the Gabor (horizontal or vertical) at the moment of saccade onset, and the Y axis the saccade amplitude. Horizontal and vertical amplitudes, and left and right tilt, are represented in separate panels for clarity, although they were fitted within a single multivariate model for each participant. Thick lines represent the predicted values (blue for left tilt and red for right tilt).

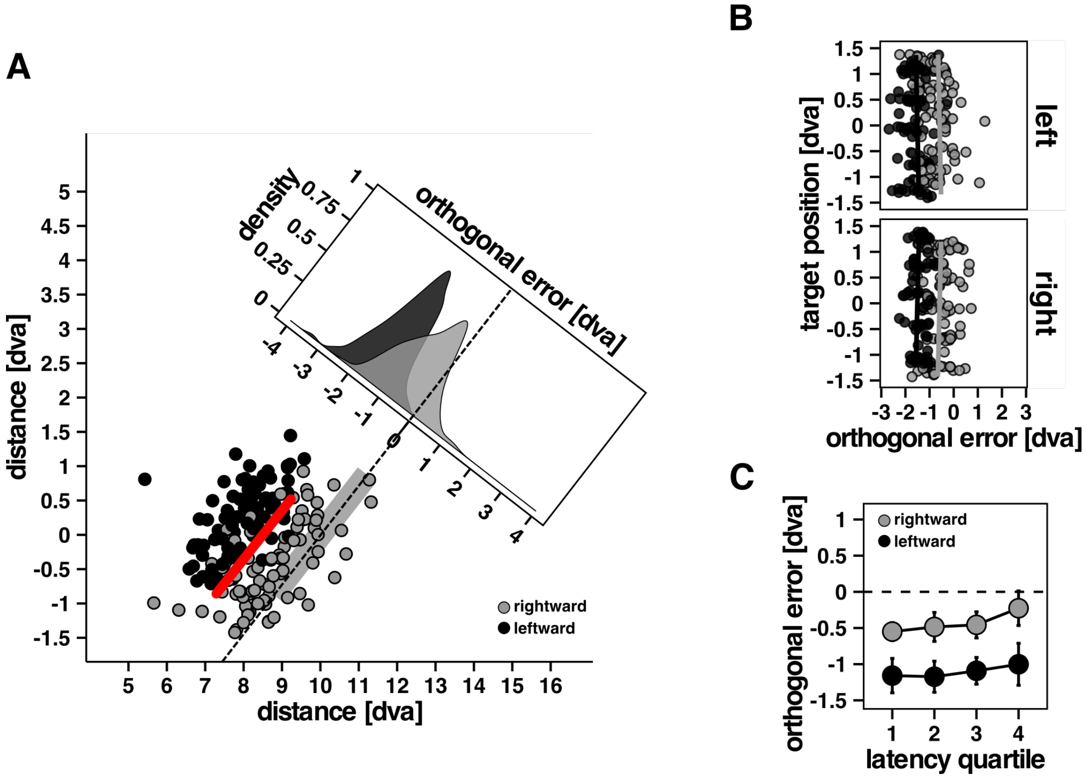

Figure S2. Analysis of orthogonal landing error. **A.** The orthogonal landing error is the perpendicular distance of each landing position from the physical path of the Gabor (represented by the thick gray line in the background). The red line represents the predicted values of the multivariate fit for this particular subject. **B.** In order to investigate whether the orthogonal errors remained constant along the path, we fitted for each participant a linear model with the orthogonal landing error as dependent variable; the independent variables were the position of the Gabor along the path, in interaction with the tilt (left/right), and the direction of the internal drift at saccade onset (leftward/rightward). If the shift in landing positions varied as a function of the Gabor position along the path (similar to perception) the regression slopes would have been significant and with opposite sign in the left vs right tilt; instead the slope were not significant for either the left tilt, mean $\beta = -0.07$, 95% CI [-0.17, 0.03], or the right tilt, mean $\beta = 0.08$, 95% CI [-0.02, 0.19]. The only significant parameter was the one coding for the difference between leftward and rightward internal motion, mean $\beta = 0.73$, 95% CI [0.49, 0.96], which indicated a significant difference in the marginal means between leftward and rightward. The regression is represented in panel B (same subject as panel A); note that the dependent variable is on the X-axis. **C.** The orthogonal landing error did not change as a function of saccade latency: a repeated-measures ANOVA was used to test the effect of the individual latency quartile on the difference between leftward and rightward drift, and did not reveal a significant effect [$F(3,15)=2.44$, $p=0.10$] (error bar represents 95% CI across participants).

Movie S1. This movie shows an example of the stimuli used in experiment 1. The motion trajectory of the Gabor in this example is tilted to the left by 45 degree from vertical. However, when viewed in peripheral vision (with gaze directed to the black fixation dot on the left), the motion vector of the internal drifting pattern is erroneously integrated with the aperture motion and makes the perceived motion trajectory of the Gabor appear near vertical.

Movie S2. This movie shows an example of the stimuli used in experiment 2. The motion is directed down to the right (45 degree of deviation from vertical). The Gabor disappears at the midpoint of its trajectory, and reappears in the same position after 250 ms. When observers view this stimulus in peripheral vision (with gaze directed to the black fixation dot on the left) they report instead that the initial position of the Gabor after the blank appears shifted to the right with respect to its last position before the blank (Fig. 2 B and C), resulting in the perception of two parallel but misaligned segments. This result supports the hypothesis that double-drift stimuli induce illusory distortions of both perceived direction and position of motion (Fig. 2A).