Current Biology

Supplemental Information

Dissociation between the Perceptual and Saccadic Localization of Moving Objects

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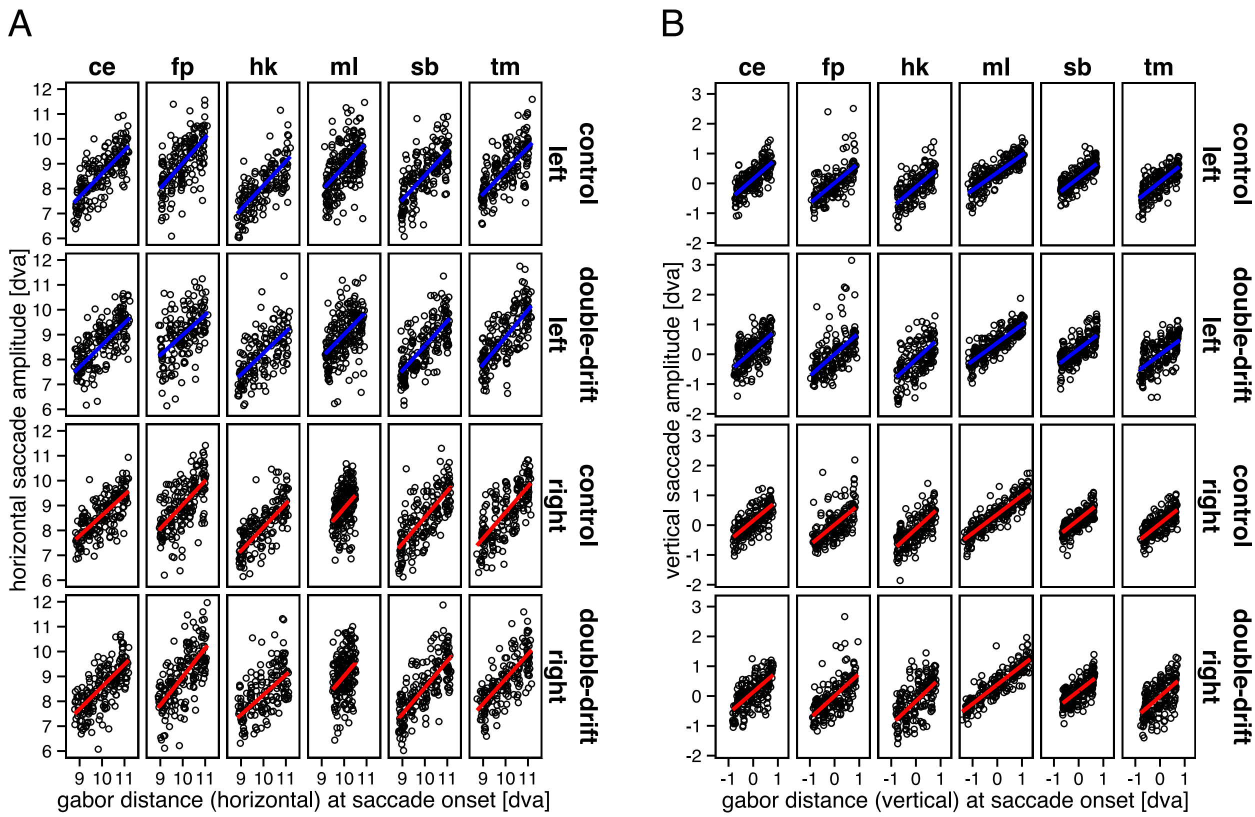

Figure S1, Related to Figure 1, Multivariate analysis of saccade amplitudes.

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).

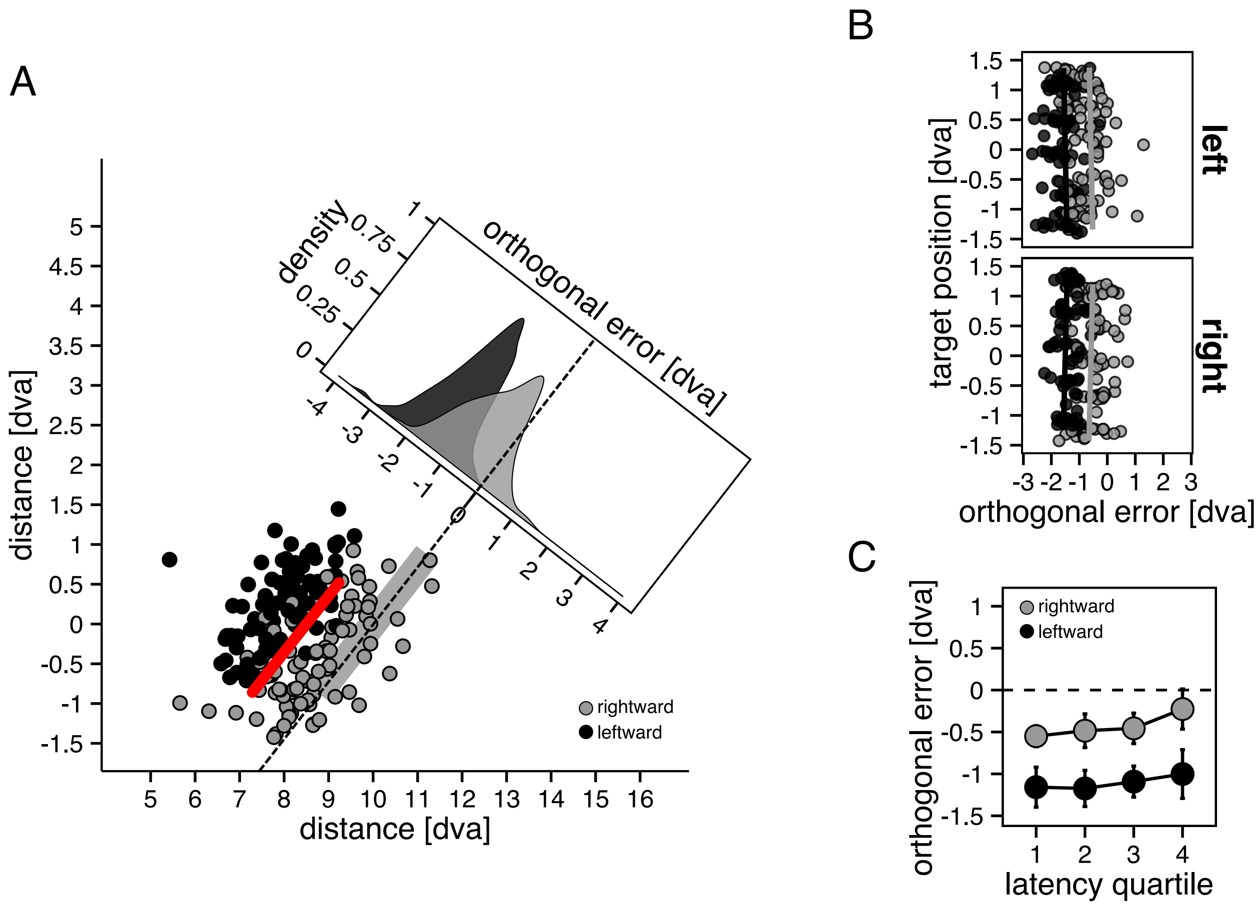

Figure S2, Related to Figure 1, Analysis of orthogonal landing error.

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 β = -0.07, 95% CI [-0.17, 0.03], or the right tilt, mean β = 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 β = 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).

SUPPLEMENTAL 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 60cm 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 [S1–S3] 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 2cycles/dva (cycles per degree of visual angle) and 100% 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 (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 (see Movie S1). The stimulus was presented on a uniform gray background (5.3cd/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; see Movie S2).

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 [S4] that converged to a 50% proportion of "right" tilt responses. Trials with left and right tilt were randomly interleaved. Each participant performed 2 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 400-600ms, 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 400-600ms, 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 (Figure 2A). 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 250ms 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 [S5]. 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 [S6, S7].

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 Figure S2).

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 [S8], with a probit linking function, fitted with R [S9] and the *lme4* library [S10]. 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.

Supplemental Results

Experiment 1

Our main analysis showed that saccades directed toward double-drift stimuli target the real envelope location and are minimally affected by the internal motion (the drift of the sinusoidal pattern). Specifically, the internal motion induced a small shift in saccade landing that was orthogonal to the trajectory and in striking contrast with the change in orientation of the Gabor trajectory found in perceptual judgments. We found also that the small shift in saccade landing is independent of the latency of the saccade. Here we report additional analyses showing that the orientation of the trajectory computed from the saccade landings did not depend on saccade latency, and that the internal motion did not have a detectable effect on eye position after the saccade.

We divided the trials according to individual latency quartiles, and for each quartile we repeated the analysis (as reported in Results section) in order to infer the orientation of the Gabor's trajectory from the saccade endpoints. On average there were 190 trials in each latency quartile and for each participants, with small deviations due to trials excluded according to the criteria reported in the main text (Results section). For each participant and latency quartile we computed the difference between the orientation recovered in the control condition and the orientation recovered in the double-drift condition, and we analyzed these differences with a repeated-measures ANOVA with saccadic latency quartile and tilt (left/right) as predictors. The effect of saccadic latency quartile was not significant [$F(3,15)=1.28$, $p=0.32$], nor was the effect of tilt [$F(1, 5)=0.42$, $p=0.54$] or the interaction between tilt and latency quartile [$F(3,15)=1.97$, $p=0.16$]. The mean differences between trajectory orientations recovered in control and double-drift trials were not significantly different from zero for any combination of saccadic latency quartile and tilt (all confidence intervals included 0).

Saccades were directed to targets in motion, so we examined the post-saccadic gaze position traces searching for signs of pursuit immediately after the saccade. We fitted eye position traces from 10 to 80ms after saccade landing with a line, and we took the direction of that line as a measure of pursuit direction. Next for each participant, condition, and tilt we computed the angular difference between the direction of gaze movements and the direction of motion of the Gabor's (envelope). We performed a set of Rayleigh's tests to assess whether these angular differences were concentrated along one direction or were uniformly distributed: the null hypothesis of circular uniformity was rejected (at the Bonferroni-corrected level $p=0.0083$) in 8 cases out of 12 (6 subjects and 2 tilts, left and right) in the double-drift condition, and 7 out of 12 in the control condition. This indicates that post-saccadic gaze movements were often concentrated along one direction, relative to the envelope, and not just random shift in gaze position due to eye drift, or an artifact due to eyetracker noise. We performed another set of Rayleigh's tests that revealed that post-saccadic gaze movements in the double-drift condition were neither in the external (all $p>0.1$), neither in the internal motion direction (all $p>0.1$), and also not in the perceived direction (all $p>0.1$). Finally, we compared the direction of the post-saccadic movements with the direction angle of the saccade itself, and found a significant correlation (Jammalamadaka-Sarma correlation coefficient for circular data), that was significant at the Bonferroni corrected level in 10 out of 12 cases in both the double-drift and control conditions (mean correlations: $r=0.58$, double-drift; $r=0.39$, control condition). This indicates that the gaze movements after the saccade were on average in the same direction as that of the saccade, and thus likely a result of the momentum caused by the fast rotation of the eyeball during the saccade. The average distance covered by the gaze in the post-saccadic interval was quite small, 0.22dva on average, corresponding to a speed of about 3dva/sec. Although pursuit is normally planned concurrently with saccades to a moving target, and occasionally observed even before the saccade onset [S11, S12], we didn't find any clear evidence of pursuit immediately after the saccade in our data, but only an inertial effect in the same direction of the saccade. This could be due to the relatively low speed of the moving target used here (2dva/sec), but also to the repeated intra-saccadic disappearances of the target in our paradigm, which might have caused an inhibition of the pursuit response. It remains a question for future studies to clarify the relationship between pursuit response (to a peripheral moving target) and the visual signals available after the saccade.

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