Anticipating the three-dimensional consequences of eye movements

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Rapid eye movements called *saccades* give rise to sudden, enormous changes in optic information arriving at the eye; how the world nonetheless appears stable is known as the problem of *spatial constancy*. While two-dimensional direction constancy has received extensive study, three-dimensional spatial constancy, on the other hand, has been neglected. For example, when the gaze moves from one surface patch to another on the same plane, the surface in the retinal frame undergoes a rotation in depth; instead of perceiving this rotation, however, we perceive the two surfaces as coplanar in space. Here I show that even before the eyes begin to move, the brain anticipates 3D rotations due to saccades. Because this anticipation is absent when subjects fixate while experiencing optically simulated saccades, it must be evoked by extraretinal signals. Such anticipation could provide a simple mechanism for three-dimensional spatial constancy and trans-saccadic integration of depth information.

Directional or two-dimensional spatial constancy holds insofar as the uniform, two-dimensional shifts of the retinal image accompanying each eye movement (see Fig. 1(a)) do not lead to perceptions either of motion or of change in direction. This type of spatial constancy has been studied since the nineteenth century [1, 2] (see references 3–7 for reviews). Distortions in spatial vision in the temporal vicinity of saccades are considered as signs of processes that give rise to constancy. For example, the threshold for perceiving motion rises just before a saccade [8, 9], which may be why motion is usually not perceived following saccade-induced retinal shifts, and may allow for optimal trans-saccadic integration of information [10]. Furthermore, points flashed around the time of a saccade are systematically mislocalized in a way that suggests slow build-up of compensation for retinal shifts [11–17]. The dynamic properties of neurons that remap their receptive fields in the anticipation of saccades may be closely connected with these distortions and contribute to spatial constancy [6]. Such neurons have been found in posterior parietal cortex [18–20], in superior colliculus [21], and in the frontal eye field [22] of monkeys; recently, neuroimaging has demonstrated similar spatial updating in human parietal cortex [23].

An aspect of the spatial constancy problem that has received little or no attention is the *three-dimensional* stability of the world during eye movements. Vision serves not only for detecting the directions of points, but also—and at least as importantly—for extracting the three-dimensional layout of the environment, and in particular the orientations of surfaces [24]. Almost every eye movement brings about a change in the orientation of the surface at the point of fixation, relative to the orientation of the eye. These orientation changes are due to two components, *extrinsic* and *intrinsic*. The extrinsic component is the change in the spatial or allocentric surface orientation at the new point of gaze, as when making a saccade to a different plane, or to a different point on a curved surface. The intrinsic component is due to the rotation of the eye itself with respect to the environment. The extrinsic-intrinsic distinction is a

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useful way of decomposing the problem, since the extrinsic component depends on the three-dimensional layout of the environment, while the intrinsic component depends only on the eye movement.

However, in a significant fraction of our saccades the gaze moves from one point to another on a surface that is planar, or nearly so. This happens, for example, when we perform saccades between two points on a flat ground, or on a wall, or on a printed page or computer monitor, as you are doing now. In these saccades (let us call them 'planar saccades'), the extrinsic component of surface orientation change is absent, or at least greatly reduced, compared to the intrinsic component: the change in the relative orientation of the surface to the eye is due to the rotation of the eye, not the rotation of the surface. An example of such a saccade and its consequences for the retinal image are shown in Fig. 1(b). While the spatial orientation of the surface remains the same, the rotation of the eye relative to the surface brings about a change in the retinal image. After the saccade, all available depth cues will reflect, at the new point of fixation, a surface that has undergone a rotation in depth equal-and-opposite to that of the eye, as shown in see Figs. 1(c), 1(d). Nevertheless, this surface rotation is not perceived as such, no more so than the simultaneous uniform two-dimensional shift in the retinal image. Instead, under normal circumstances, the observer perceives that the surface patches at the starting and end-points of the saccade are coplanar in space. However, if the pre- and post-saccade retinal images (the bottom panels in Fig. 1(b)) were to be presented *without* the intervening saccade (e.g., while the observer fixates some point), the depth rotation *would be* perceived as such.

This is the problem of three-dimensional spatial constancy: when we fixate successive patches lying in the same plane, how do we perceive them as coplanar in space in spite of intrinsic, egocentric depth rotations accompanying each eye movement? The problem can of course be generalized to the case of non-planar saccades, which are accompanied by both intrinsic and extrinsic orientation changes: how does spatial vision discount the intrinsic orientation changes due to eye rotation, and perceive only the extrinsic changes in the three-dimensional geometry?

Since the intrinsic surface rotation depends on eye movement variables alone, it can be predicted—in principle, even before the eyes begin to move. The case is analogous to the uniform, two-dimensional shift in the retinal image (Fig. 1(a)), where an efference copy of the oculomotor signal [25–27] is at least partly responsible for the maintenance of spatial constancy, and can be detected as the mislocalization of points flashed immediately before the saccade [11, 28]. In the three-dimensional case, the brain may also take advantage of the geometry by predicting the intrinsic effect of eye rotations on egocentric surface orientation. This prediction would have to involve three-dimensional rather than two-dimensional transformations, and would therefore be considerable more complex. In the psychophysical experiments presented here, I show that while planning a saccade, the brain makes precisely such a prediction, detected as a distortion in the perception of three-dimensional motion.

Methods

The technique used to probe distortions in three-dimensional motion perception was based on ambiguities in the perception of 3D shape and motion. The stimulus consisted of two frames of a structure-from-motion sequence [29–33]. We can perceive three-dimensional shape and motion from two-dimensional optic flow alone, as shown by Wallach [29] and Rogers [32]; the fact that motion parallax can serve as an independent depth cue is analagous to the case of binocular parallax, as demonstrated by Julesz [34]. The ambiguity in this perceptual process is partly broken by the a priori hypotheses of rigidity (minimal relative motion [31]) and stationarity (minimal absolute motion [33]). However, as in the case of the Necker cube or the Mach book, there remains some ambiguity, leading to simultaneous reversals of depth and direction of motion.

An example movie very similar to one of the stimuli is given in the Supplementary Materials. Each frame was composed of a cloud of dots with a uniform or nearly uniform density in the image plane [32], and therefore offered only trivial static depth cues. This can be seen by pausing the movie: either frame by itself produces no impression of depth. The displacement of the dots between the first and second

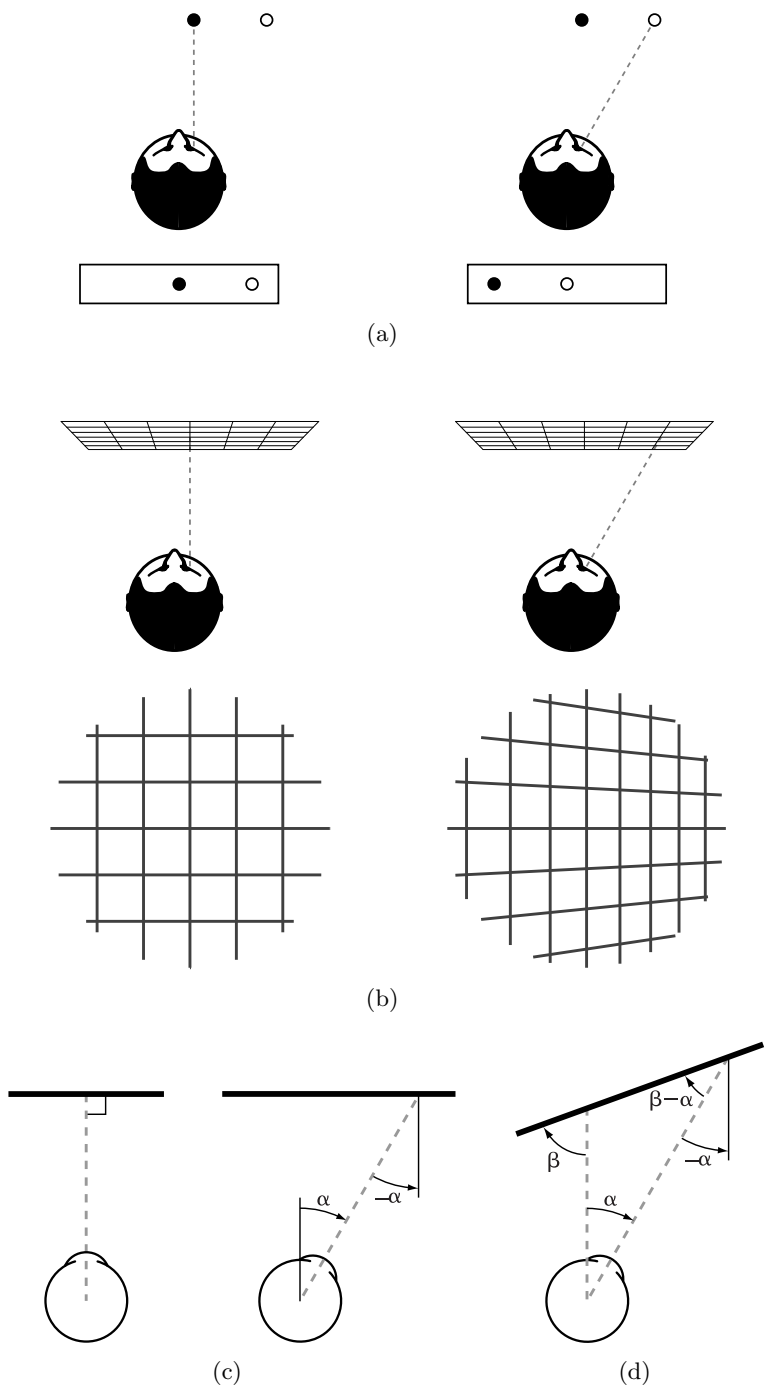

Figure 1: The two- and three-dimensional consequences of saccades. **(a)** The two-dimensional effect of saccades. The top diagrams show the direction of gaze, the bottom ones the corresponding change in the retinal image. The retinal image undergoes a uniform two-dimensional displacement that is equal-and-opposite to that of the direction of gaze. **(b)** The intrinsic three-dimensional effect of saccades, here in the case when the observer looks from one point to another on the same vertical plane. The top diagrams show the direction of gaze, the bottom ones the corresponding retinal image, assuming that the surface is painted with a regular grid. Relative to the eye, the surface undergoes a rotation in depth equal-and-opposite to that of the eye. However, as in the two-dimensional case, this egocentric rotation is not perceived as such. **(c)** In the case of a frontal plane, when the eye rotates by angle α and the gaze falls on the same plane after the eye movement, the surface undergoes the opposite rotation $-\alpha$ relative to the eye. The two rotations are about the same spatial axis. **(d)** The same is true for surfaces with arbitrary orientation.

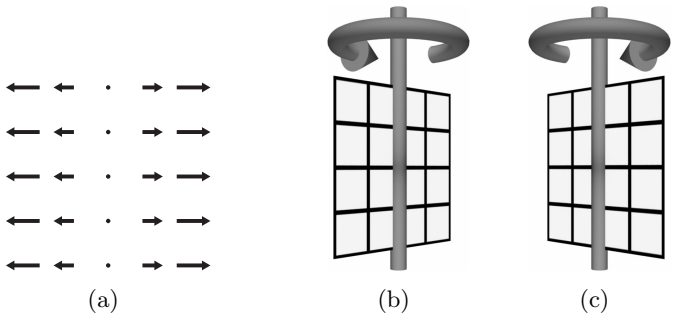

Figure 2: An explanation of the ambiguous stimuli used to probe distortions in three-dimensional motion perception. The optic flow shown in **(a)** and in the movie in the Supplementary Materials is ambiguous, and can have either **(b)** or **(c)** as interpretation, each of which is a combination of three-dimensional structure and motion. The two solutions have opposite tilts and directions of rotation. A similar ambiguity holds for arbitrary tilts and axes of rotation, and it is exact in the limit of small stimuli, or in orthographic projection (as in the stimuli in this study).

frames, on the other hand, gives rise to simultaneous perception of 3D structure and motion, as can be seen in the example. The stimuli were chosen to be compatible with a plane slanted in depth, undergoing a small depth rotation about a vertical axis. However, since the sign of relative depth is completely ambiguous (Fig. 2 offers an explanation of the ambiguity), the stimulus can be perceived as rotating in either direction about the vertical axis [35, 36]. The two solutions are oriented in opposite directions, and therefore have tilts that differ by 180°.[1] The subjects' task was to report the perceived surface tilt, from which the perceived direction of rotation can be inferred. For instance, if an observer who is presented with the stimulus in Fig. 2(a) perceives a surface whose with a tilt to the right, we can conclude that he perceives a three-dimensional rotation such as in Fig. 2(b)—without inquiring about motion directly. Similarly, a surface tilted to the left goes with the rotation depicted in Fig. 2(c). The opposite combination of three-dimensional structure and motion would violate the rigidity hypothesis, known to be closely followed in depth vision [31]. The closer the reported tilt to one of the two possible tilts for a given stimulus, the more we can be certain of the perceived direction of rotation. The advantage of this indirect way of measuring the perception of three-dimensional motion by asking about structure is to make the task cognitively opaque and therefore safe from any decision bias.

Subjects viewed this ambiguous rotation about a vertical axis immediately before, during, or after performing a horizontal saccade, in which the eye also rotated about a vertical axis. The hypothesis was that if the visual was engaged in a predictive three-dimensional transformation related to the saccade, it would interfere with the concurrent perception of three-dimensional motion. In particular, of the two possible directions of perceived rotation for a given stimulus (e.g., Figs. 2(b) and 2(c)), the one rotating opposite to the eye (e.g., Fig. 2(b) for saccades to the right and Fig. 2(c) for saccades to the left) is compatible with the intrinsic surface rotation due to the eye movement. Does this compatibility influence the perceptual choice between the two solutions, and if so, at what point during the preparation and execution of the saccade?

Procedure The time course of a saccade trial is summarized in Figure 3. Subjects first fixated a central fixation point (FP), initially accompanied by an arrow indicating saccade direction. The signal to perform the eye movement was the simultaneous appearance of a peripheral saccade target (7.5° to the left or right), the dimming of the central FP, and a brief tone. At the same time, the first frame of the structure-from-motion (SfM) sequence appeared around the central FP. After a variable delay (calculated so that

[1] *Slant* and *tilt* are a common way of parametrizing the orientation of a plane [37]. Slant is magnitude of the plane's inclination from the frontoparallel; tilt is the direction of that inclination. For example, the surface in Fig. 2(b) has tilt 0°, while the one in Fig. 2(b) has tilt 180°, and the two have equal slant.

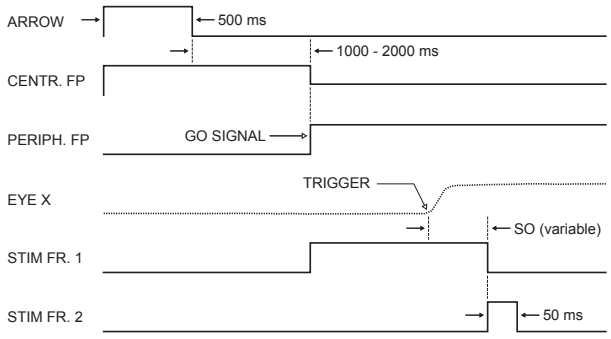

Figure 3: The time course of a trial, showing stimuli and eye movement (see Methods).

stimulus onset would be ideally at -100, 0, or $+100$ ms with respect to predicted saccade onset, the latter calculated from the previous 4 trials), the first stimulus frame was replaced by the second, which was displayed for 50 ms. In data analysis, stimulus onset time with respect to actual saccade onset was used as an independent variable in the analysis.

Ocular trajectories were tested on-line (see below). Trials that did not meet the criteria were aborted and later repeated. On trials that passed, after the disappearance of all stimuli subjects used a joystick to adjust the 3D tilt of a visual probe (centered on the saccade target) to match the average perceived tilt of the SfM stimulus.

The *fixation condition* was identical to the saccade condition (same stimuli with respect to the display monitor), except that subjects were required to continue fixating the central FP throughout. Stimulus onset was timed as if the reaction time had been 250 ms. In the *simulated saccade* condition, subjects fixated a central FP while receiving the same retinal stimulus as in a previous saccade trial (i.e., stimuli directions rotated about the eye in the opposite direction as the saccade). In both conditions, any trial that had a saccade was repeated.

Visual stimuli The visual stimulus consisted of two frames. The first frame was a texture of random dots with uniform density in the image plane. The second frame was generated by (1) parallel-projecting the first frame onto an inclined plane with slant 45° and tilt chosen from $15°, 45°, \ldots, 345°$ (see ref. [37] for definitions); (2) rotating this object by 7.5° about a vertical axis through its center; (3) parallel-projecting it onto the screen. The two rigid interpretations have opposite rotations and tilt that differ by 180°. The dots had a mean density of 5 dots/deg^2, were displayed on the screen as white circles (size: 0.03°), and only those dots falling within a circle of radius 2.5° were shown. The two-frame animation in the Supplementary Materials closely reflects an actual stimulus with tilt 0° (or 180°). The only difference, other than the timing, is the size of the dots, which has been increased to make them easier to see.

The fixation points were displayed as red dots of radius 0.1°, and the arrow that previewed the saccade direction had length 2°. The probe used for the tilt response was the perspective projection of a flat object with irregular, star-shaped edges (radius 2.5° face-on, width 0.5°). The probe always had slant 45°, and its tilt was controlled by a joystick.

Stimuli were displayed on a computer monitor, with pixel size 1.7 arcmin and a refresh rate of 100 Hz. The experiment was performed in darkness, with the monitor and its edges covered by an attenuating filter, so that nothing other than the stimuli could be seen (including the edges of the monitor).

Eye movement recording Eye movements were monitored using a Skalar Iris infrared limbus eye-tracker. The horizontal position of the left eye (the right eye being occluded) was digitally sampled at 100 Hz $\times$ 12 bits. Head movement was restrained using a chinrest, the eyetracker was calibrated prior to each block, and the initial FP on each trial was used for drift correction.

Saccade criteria were as follows: eye speed had to attain 100°/s, and saccadic onset and offset were

defined as the samples at which speed went above or fell below 20°/s. Additionally, saccadic onset had to occur between 50 and 600 ms following the "go" signal, and its amplitude had to be between 0.5 and 1.5 times the 7.5° jump in the FP.

Subjects Eight subjects (six naïve) participated in the saccade condition of the main experiment. Subjects with no experience with SfM tasks performed a preliminary simplified training block. Subjects then performed 4 blocks in the normal condition, each with 72 trials. Four of the subjects later performed a single block (72 trials) in the fixation condition. Seven subjects (5 new) participated in the simulated saccade experiment (4 blocks, as in saccade condition); the subjects who had participated in the saccade condition received their own previous optic flow, while the new subjects received optic flow from randomly chosen previous subjects.

Results

Real saccades

In a first experiment, subjects were shown the ambiguous 3D stimulus while they were planning, executing, or had just executed a horizontal saccade, either to the left or right. Some subjects also participated in a fixation control condition, in which stimuli were the same relative to the computer monitor, but gaze was kept fixed.

The results are shown in Figure 4. The time variable for each trial is defined so that $t = 0$ corresponds to saccade onset. Figure 4(a) shows mean horizontal eye trajectories. The crucial results will be given in terms of *bias*, defined as the fraction of trials in which subjects reported a tilt compatible with the 3D rotation opposite to that of the eye on that trial (i.e., counter-clockwise surface rotation (as seen from the top) for rightward saccades and clockwise rotation for leftward saccades). Figure 4(b) shows mean bias in the saccade condition as a function of stimulus onset time (relative to saccade onset), and also in the fixation condition. In order to reduce noise, this analysis was carried out on trials with accurate responses, defined as having tilt error below 45°. Chance level for bias is 0.5, which corresponds to the two solutions being chosen equally often. Three points differ significantly from chance ($p < 0.05$, Bonferroni-corrected binomial test), with $t = -150$, -100 and -50 ms. For these points, stimulus onset occurred on the average 190 ms after the go signal. Bias did not differ significantly from chance level for any other stimulus onset times, nor for the fixation control condition. Individual subject data are shown in Figure 4(c), with data in the saccade condition grouped into before- and after-saccade bins. There is a significant difference between biases in the before-saccade and fixation conditions (t test, $p < 0.001$), and between the before- and after-saccade conditions ($p < 0.01$), but not between the after-saccade and fixation conditions.

In order to check that subjects actually performed the 3D task, *tilt error* was defined as the absolute value of the angular difference between the tilt response and the closest of the two tilts in the stimulus. Thus defined, tilt error is orthogonal to bias, and ranges between 0° and 90° with chance level at 45°. Mean tilt error as a function of stimulus onset time is given in Figure 4(d), which shows that performance is better than chance level (45°) before and after the saccade, but drops close to chance during the eye movement—evidence for saccadic suppression of perception of structure from motion. This is confirmed by error distributions (Figure 4(e)). Before and after the saccade the error distribution peaks at 0, and Kolmogoroff-Smirnov tests show that it is non-uniform ($p < 0.01$ in both cases); on the other hand, for trials with stimulus onset during the saccade, the same test shows that the distribution does not differ significantly from uniform.

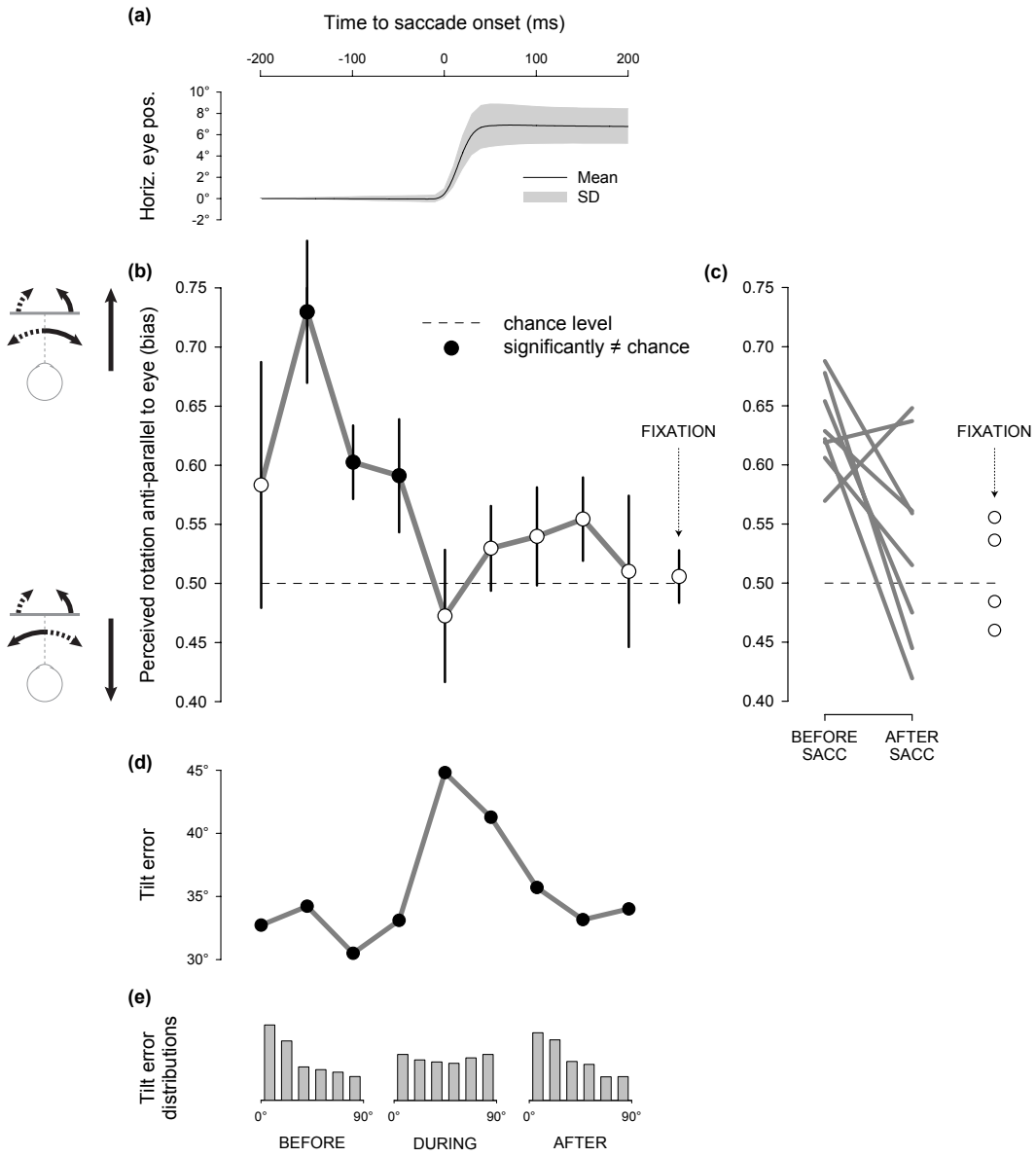

Figure 4: Results of the main experiment. **(a)** Mean horizontal eye trajectory (relative to initial position, with leftward saccades multiplied by -1) and standard deviations. Time $t = 0$ corresponds to saccade onset. **(b)** Mean bias in 3D rotation perception as a function of stimulus onset time (relative to saccade onset, binned by 50 ms). Time scale same as in (a), so that negative values of the abscissa correspond to stimulus onsets *before* the saccade. The point on the right shows data for the fixation condition. Error bars denote between-subject standard errors. **(c)** Individual bias data for subjects in the main experiment: before the saccade (means of the -150, -100 and -50 ms bins), after the saccade (the 100, 150, and 200 ms bins), and in the fixation condition. **(d)** Tilt error as a function of stimulus onset time. Time scale and bins as in (b). **(e)** Distributions of tilt errors for stimulus onsets before (200 ms), during, and after (200 ms) the saccade.

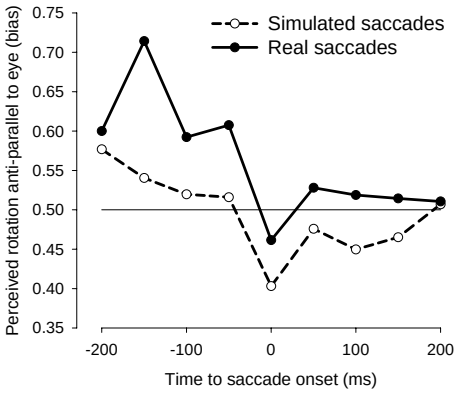

Figure 5: Simulated versus real saccades. Curves show anti-parallel rotation bias as a function of stimulus onset relative to saccade onset (as in Fig. 4(b)) in the two conditions.

Simulated saccades

The bias demonstrated here could have been due to either retinal or extra-retinal signals associated with the saccade. The fact that it occurs *before* the saccade points to an extra-retinal origin [25, 26, 38], but a role for retinal flow and smear due to the saccade cannot be excluded, since, even for trials with stimulus onset before the saccade, some retinal signals (e.g., due to the saccade target) were present, and could have resulted in a retroactive bias. In order to probe the origin of the bias, an additional control experiment was performed with optically simulated saccades [39, 40]. Subjects maintained central fixation (as in the fixation condition above), while experiencing approximately the same flow on the retina as in previous saccadic trials. The results (Fig. 5) show that the bias curve is very different in the simulated case than in the case of real saccades: in the case of simulated saccades, although there is a small bias towards anti-parallel rotations for stimuli presented before the saccade, it is nowhere significantly different than chance. (The only point that approaches significance is $t = 0$, where there is a bias towards *parallel* rotations.) Thus, the control experiment shows that optic flow in simulated saccades is insufficient to induce anti-parallel bias, and lends strong support to the hypothesis that the bias is induced by extra-retinal signals.

Discussion

It has been shown that during the planning but $150 - 50$ ms prior to the onset of a saccade, the visual system develops a bias in its perception of 3D rotation, in favor of rotations opposite to the impending rotation of the eye. Because of saccadic suppression it is not possible to determine whether this effect persists during the saccade. The bias may reappear immediately after the end of the saccade, but here it is weaker and not statistically reliable. The absence of bias in the fixation condition shows that the origin of the effect is not cognitive: simply knowing the saccade direction induces no bias. Nor is the bias due to subsequent retinal flow and smear: its absence in the simulated saccade condition shows that extra-retinal eye movement signals are involved in its generation.

As discussed in the Introduction, a saccade usually changes the three-dimensional orientation of the surface at the point of gaze, and this change has two components. The extrinsic component arises when, after the saccade, one is looking at a surface oriented differently in space. The intrinsic component is due to the rotation of the eye itself with respect to any stationary surface. While the extrinsic component is hard to predict, since it depends on the layout of the environment, the intrinsic component depends on motor variables alone, with the surface rotation being equal-and-opposite to that of eye (Fig. 1). The bias that has been found in the perception of three-dimensional motion matches the direction of the intrinsic component of surface rotation. The occurance of the bias immediately prior to the saccade

strongly suggests that the visual system predicts the intrinsic component of surface rotation during the preparation of saccades.

The time course of the bias found here is similar to that of perisaccadic mislocalization (PSML) [11,41]. One differences between the two is that the bias demonstrated here is a three-dimensional rather than two-dimensional effect, and that it concerns motion rather than localization. The three-dimensional bias is also unlikely to be directly caused by PSML, because PSML is absent for stimuli without temporal gaps [14], such as the ones used here; and because the three-dimensional bias is predictive (in favor of the post-saccadic retinal image), whereas PSML is compensatory: errors occur in the opposite direction of retinal image change (a more complicated error pattern has also been reported [16], but it only seems to hold in the case of a visible background [17], unlike the experiments reported here); and because the sign of PSML reverses after the saccade, while no trace of this reversal is found here. Thus, the three-dimensional bias is probably caused by mechanisms at least partly independent of PSML. The time course of the three-dimensional bias also seems to differ from that of a bias in two-dimensional motion perception [42].

The three-dimensional bias shares at least two characteristics with anticipatory re-mapping of neuronal receptive fields [18–22]: they are both predictive (rather than compensatory), and they both operate before saccades. Recently, a population of neurons has been discovered in area CIP of the intraparietal sulcus of monkeys that codes the three-dimensional orientation of surfaces [43]. It would be interesting to test whether the three-dimensional coding in this population (situated close to area LIP, the location of saccade-predictive neurons) also shifts in anticipation of eye movements. One can predict that shifts will occur in the direction opposite to the eye rotation.

The results presented here suggest that the visual system effectively assumes that the end-point of a saccade will lie on the same spatial plane as the starting point, and that three-dimensional spatial constancy is based on this assumption. For instance, while planning a saccade in which the eyes will undergo rotation R, the three-dimensional orientation of the surface at the starting point, expressed as a normal vector $\mathbf{n}_s$, would be transformed by a rotation opposite to that of the eye: $\mathbf{n}' = R^{-1}\mathbf{n}_s$. If the surface normal at the end-point of the saccade, $\mathbf{n}_e$, matches the anticipated normal $\mathbf{n}'$, the two surface patches are perceived to lie in the same plane and no rotation is seen. According to this hypothesis, the three-dimensional motion bias that has been found, in the direction R^{-1}, is the result of interference between this anticipatory transformation and the process of structure-from-motion. Even when the assumption of coplanarity is false, the prediction process would be useful, insofar as a mismatch between the predicted and perceived orientations at the saccadic endpoint could serve as a simple criterion of gaze falling on a new surface.

Finally, the anticipatory bias that has been found could be used in trans-saccadic integration of three-dimensional information. Results on trans-saccadic integration have been mixed, with reports of no integration [44–46], as well as evidence for integration of two-dimensional shape and motion across saccades [10, 47–49] (see reference 50 for a possible reconciliation of these results). Given the particular slowness of three-dimensional vision [51–53] compared to the typical time between saccades, trans-saccadic integration of three-dimensional information would be especially useful. The difficulty in integrating three-dimensional information across fixations is precisely the egocentric rotation of surfaces with eye movement (Fig. 1(b)). The anticipatory rotation that has been demonstrated here would keep egocentric surface information up-to-date, provided the gaze remains on roughly the same plane in space. Updating three-dimensional egocentric representations in anticipation of saccades could thus provide a mechanism for both three-dimensional spatial constancy and trans-saccadic integration of depth information.

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