**Tunneled vision reveals closed-loop signatures of vision**

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**Visual scene perception is based on continuous eye movements, typically yielding abrupt changes of regions of interest (ROIs), using saccades, and scanning of these ROIs, using drifts {Steinman, 1990 #1203;Rucci, 2007 #2683;Ahissar, 2001 #1830}. Whereas saccades are commonly considered to result in part from closed-loop dynamics related to scene analysis, drifts are commonly considered to function in an open-loop scheme – their kinematics are commonly assumed independent of the visual input {Steinman, 1990 #1203;Pitkow, 2007 #2945}. We tested this dependency in human subjects perceiving basic geometrical shapes by modulating the spatial information that is available to them and assessing their motor interactions with the environment. We modulated the available spatial information by changing stimulus size and by changing the effective retinal size – the latter was achieved by real-time tunneling of the gaze to a limited window around its center. Scanning trajectories demonstrated clear closed-loop dynamics of both using saccades and drifts. First, the eyes often scanned the borders of the images, in a manner that necessitates relying on concurrent sensory data. Second, the visual system increased saccade rate and drift speed when challenged with tunneled vision. Third, the system decreased drift speed when scanning borders. Drift speed converged to its target value anew during each fixational pause (henceforth “pause”), on average within 50-70 ms from pause onset. Importantly, within the same trial the speed converged to significantly different values depending on whether the eye landed on a border or not. Analysis of these controlled variables suggest that when challenged with tunneled vision the visual system compromised the constancy of drift speed, and hence that of temporal coding, for increasing the acquisition rate. Overall, these results reveal clear indications for vision being based on closed-loop mechanisms through which the kinematics of saccades and drifts are adapted on-line to the characteristics of available external information.**

Five participants were asked to identify an image on a screen as one of five options (square, rectangle, circle, triangle and a parallelogram) after viewing it either naturally or through tunneled vision (during which spatial information was exposed only around the center of their gaze, which was continuously tracked). Two image sizes were presented (Large, 10.80±0.15x10.80±0.15 deg; small, 0.90±0.03x0.90±0.03 deg) and two tunneling windows were used (2.90±0.15x1.90±0.15 deg for Large images and 0.24±0.03x0.16±0.03 deg for Small images).

Limiting the extent of spatial information had a dramatic effect of the distribution of gaze centers, visualized by their visit rates (the fraction of time spent in each pixel of the image during each trial) (**Fig. 1**). During natural viewing of large shapes, the gaze was typically directed to the center of the shape (fig1a). In contrast, during tunneled viewing of large shapes the gaze was typically directed to the edges of the shapes (fig1b). Limiting spatial information by size reduction yielded patchy distribution of gaze centers, typically closer to shape borders (Fig. 1c). Tunneled viewing of small shapes yielded more focused distributions, clearly preferring borders (Fig. 1d). Interestingly, none of the participants was aware of their tendency to focus on borders, although they all reported awareness to the challenge in gaze direction during tunneled viewing, especially of the small shapes. To quantify the similarity between the tasks, we focused on the most visited areas in the four maps of each shape (top 10% of each map). We calculated all the Euclidian distances between them in the different tasks (6 differences for each shape). The distances between the two tunneled tasks were found to be significantly smaller (One-way ANOVA, p<0.001). ~~To quantify the similarity between the tunneled tasks, we compared the Euclidian distances between the most visited areas (top 10%) in the four experimental conditions. Differences between each same shape in the two tunneled vision tasks were found to be significantly smaller than the differences between any tunneled vision and natural vision tasks (One-way ANOVA, p<0.001).~~

Next, we examined the spatiotemporal trajectories of eye movements (saccades and drifts) during individual trials (Fig. 2). Tunneled vision of large images induced a novel type of movements: border-following saccades and drifts (fig2a). XX% of the saccades made by all participants in all large-tunneled trials were border-following, and as a result XX% of the pauses were on borders, compared with XX% and XX%, respectively, in all other conditions (fig2b; see Methods).

The overall statistics of saccade rate and drift speed showed that both increased in tunneled conditions compared to natural viewing, for each image size (**Fig. 3A,B**). Assuming that the rate of acquisition of visual information during a pause increases with increased drift speed {Ahissar, 2001 #1830;Rucci, 2015 #3625}, and observing that the total distance travelled by the eye during a pause did not change between conditions (XX vs XX), these adaptations of eye movement kinematics are consistent with increasing the overall acquisition rate in tunneled conditions. The effect of reducing the available spatial information by reducing image size had a different effect; participants reduced their saccade-rate while keeping drift speed roughly unchanged (**Fig. 3a,b**). This adaptation is consistent with increasing the amount of information acquired in each pause.

We then asked whether drift speed is controlled on slow time scales or on a pause-by-pause manner. As individual trials contained both border and no-border fixations, we compared drift speeds across these pauses. Drift speed was significantly lower when drifting along borders than otherwise (4.8±xx vs 5.36±xx in large and 4.62±xx vs 5.18±xx in small images, p<XXX). To further analyze the control dynamics we looked at the within-pause dynamics of drift speed. This analysis showed that the visual system converged to the target drifting speed during the first 50 – 70 ms of the pause. While starting the pause with speeds around 7 deg/s on average, the eye then converged to speeds around 5 deg/s in natural viewing and to speeds around 6 deg/s in tunneled viewing (**Fig. 3c**). Similar dynamics characterized border and no-border drifts, converging to lower speeds in border pauses (**Fig. 3d**).

In closed-loop systems, some of the variables are controlled and some are compromised for that control {Marken, 2009 #3858;Ahissar, 2016 #3772;Buckley, 2018 #3859}. We analyzed the variance of the relevant variables in order to see which variables the system tries to keep invariant in each condition. Saccadic kinematics obeyed a main-sequence pattern to the same extent in natural and tunneled conditions for low saccadic amplitudes, amplitudes that were in the scale of the image size (up to 7 deg for large and 2 deg for small images); beyond these amplitudes the main-sequence showed higher variations in tunneled vision (XX vs XX … in residuals, sup figX). Drift speed, on the other hand, exhibited larger variance throughout the fixational pauses during tunneled viewing (**Fig. 4a**). The data is consistent with the relatively constant drift speed in natural conditions being compromised during tunneled viewing (individual examples in **Fig. 4a**).

Whether ocular drifts are controlled by the brain had been a source of enduring debate {Steinman, 1990 #1203;Martinez-Conde, 2004 #2044;Ahissar, 2014 #3699;Herrmann, 2017 #3860}. Our results demonstrate clearly that ocular drifts are actively controlled by the visual system. This is demonstrated by the drift trajectories being dependent on the concurrently-scanned image patterns (border versus no-border fixational pauses, Fig. XX/NUMBERS), drift speed being increased during tunneled viewing, and drift target-speed being converged upon anew in each fixational pause. When controlled, variables are subject to many kinds of manipulations by the system, depending on the overall system needs. Our data are consistent with the visual system trying to increase information rate under tunneled vision, while compromising the quality of information acquisition. This is conjectured from the observed kinematic changes. When tunneled, the visual system increased saccadic rate, and at the same time increased the drift speed such that the scanning distance per pause remained unchanged (Fig. 3). Increasing the drift speed may by itself reduce acquisition quality as retinal temporal coding is shifted to a narrower range. Our data show that in addition the system compromises temporal coding constancy when tunneled as the variance of drift speed increased significantly in this condition (Fig. 4).

Overall, these data support two major assumption. One is that the fixational pauses are used for visual acquisition, as if they would not then there was no sense in wasting energy for controlling the drift kinematics. The second is that vision is based on closed-loop mechanisms, as both saccades and drift, the two kinematic variables dominating visual acquisition, are controlled by the visual system in an input-dependent manner. Drift speed was adapted to the available spatial information on a pause-by-pause basis, converging anew to condition- and image-dependent values during each pause.

**Methods:**

*Participants*. 5 healthy participants with normal vision at the ages 21-28 participated in all different parts of the experiment. 3 females, 2 right-handed with right dominant eye, 3 right-handed with left dominant eye. All participants were given full and detailed explanation about the eye tracker device and the behavioral task, and were paid for their participation. Informed consents were obtained from all the participants, in accordance with the approved Declaration of Helsinki for this project.

*Experimental Setup*. The experiment took place in a dark and quiet room where the participants sat in front of a high-resolution, fast response time computer screen (VPixx, 1920x1080, 120Hz) and their EyeM were recorded and used for manipulation in real-time using an eye-tracker device (EyeLink II). Throughout each trial only the dominant eye of the participant was opened and tracked (at 100Hz sampling rate) – the other eye was blindfolded. The participants sat 1 meter away from the screen and placed their chin on a chinrest to reduce head movements.

*Stimuli and gaze windows*. Two kinds of images were created: ‘Large’ and ‘Small’, and each were associated with a specific gaze window – a horizontal rectangle centered on the participant’s gaze at each sample and through which the image was exposed. The Large shapes occupied 10.80±0.15x10.80±0.15 deg (720±10x720±10 pixels), and the large gaze window was 2.90±0.15x1.90±0.15 deg (190±10x130±10 pixels). The Small shapes occupied 0.90±0.03x0.90±0.03 deg (60±2x60±2 pixels) with a gaze window of 0.24±0.03x0.16±0.03 deg (13±2x9±2 pixels). The ratio between image and window size was the same in both conditions.

*Experimental Design*. We tested the performance of participants in a five forced choice shapes recognition tasks. Images of 5 basic shapes were used: Square, rectangle, circle, triangle and a parallelogram (see **Fig. 1**). These images were presented in two forms, Large and Small, as described above. Participants were tested during five days. During days 1-3 they performed two tunneled vision sessions, the first one with Large images and the second one with Small images. On day 4 they performed two tunneled vision sessions, both with Small images. On day 5 they performed 4 sessions of natural viewing, 2 repetitions with each image size: Large, Small, Large, and Small. Each trial lasted up to 30 seconds, there were at least two repetitions of each shape in each session (10-12 trials per session, only the first two repetitions of each shape were used for analysis), and hence each session lasted up to 12 minutes. At the end of each trial participants reported which of the 5 shapes was presented, got a ‘correct/wrong’ feedback and a second chance if needed. In cases of 2 wrong answers, participants were presented with the right answer before starting the next trial (only correct trials were used for the analysis, success rates were 0.94±0.06 for the Large shapes and 0.60±0.02 for the Small shapes).

In the Tunneled vision sessions, participants had to identify a shape that was “hidden” on the screen and exposed only through the gaze window (see above). In the Natural vision sessions, participants had to identify the same shapes, naturally viewing them with no constrains.

*Eye movement processing*. A velocity based algorithm (modified from Engbert and Kliegl, 2003 and Bonneh et al., 2010) was used for detecting all saccades and drift. We used the following threshold parameters for saccades detection: 16 deg/sec minimal peak velocity and 0.3 deg minimal amplitude. Each detected saccade was visually examined to verify the quality of saccadic detection. Fixation periods between saccades were labeled drift only if they exceeded 3 samples, a 30 ms minimum duration.