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

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**Visual perception is based on continuous eye movements, yielding abrupt switching between regions of interest (ROIs), using saccades, and scanning of these ROIs, using drifts1-3. 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 assumed to be independent of the visual input2,4. We tested this dependency in human subjects perceiving basic geometrical shapes. We modulated the spatial information that is available to them 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. Recording of the subjects’ eye movements revealed clear signatures of closed-loop vision in the kinematics of both saccades and drift. When challenged, the visual system modified its motor variables in one of two manners, maintaining either scanning speed or scanning distance per fixational pause (henceforth “pause”). Importantly, the system dynamically converged to its target drift speed anew during each fixational pause, stabilizing at significantly different speeds depending on the viewing condition. Furthermore, saccade and drift trajectories often locked to the borders of the shapes, in a manner that necessitated relying on concurrent sensory data. [[?something about the Keplerian assumption?]] Overall, these results reveal clear indications for vision being based on closed-loop mechanisms through which the kinematics of saccades and drifts, which determine visual acquisition, 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 continuously-tracked gaze. Two image sizes were presented (large, 10.80x10.80 deg; small, 0.90x0.90 deg) and two tunneling windows were used (2.90x1.90 deg for large images and 0.24x0.16 deg for small images). Success rates were 100% for natural viewing, 94±6% for the tunneled-large shapes and 60±2% for the tunneled-small shapes. Only correct trials were used for the analysis reported here.

Limiting the available spatial information had a dramatic effect on the distribution of gaze centers5, visualized by their visit rates (the fraction of time spent in each pixel of the image during each trial, mainly reflecting pause location) (**Fig. 1**). During natural viewing of large shapes, the gaze was typically directed to the center of the shape (**Fig. 1a**), while during tunneled viewing of large shapes the gaze was typically directed to the borders of the shapes (**Fig. 1b**). Decreasing image size yielded patchy distribution of gaze centers, typically closer to shape borders (**Fig. 1c**) and tunneled viewing of small shapes yielded more focused distributions, clearly preferring borders (**Fig. 1d**). Interestingly, during tunneled viewing of the small shapes, none of the participants was aware of their tendency to focus on borders, although they all reported awareness to the challenge in gaze direction.

Both saccade average rate and drift averaged speed increased in tunneled conditions compared to natural viewing, regardless of image size (**Fig. 2a,b; Extended Data Table 1).** Such changes may reflect reactions to input changes, as may be expected in open-loop systems, or may reflect active changes of the visual system, if operating in a closed-loop framework and trying to adapt to the environmental changes. Closed-loop adaptation must involve a set of variables, “controlled variables”, whose values are maintained by the loop within a certain range that allows the current functioning of the system6-8. Open-loop systems do not have this active capacity although their variables may remain unchanged if not disturbed.

The mean rate of visual acquisition during a pause should be proportional to the mean speed of the drift during that pause (*Sp*)3,9 and the amount of visual information collected during that pause should be proportional to the integrated distance scanned by the eye (the length of its trajectory) during the pause (*Xp*). Mean pause duration is inversely proportional to the mean saccadic rate, which reflects the number of ROIs sampled per time unit. The increased saccade rate observed here in tunneled conditions is consistent with its dependency on task difficulty10. Importantly, however, the tunneling-induced changes in saccade rate and drift speed compensated each other, on average, keeping *Xp* unchanged for each stimulus size (**Fig. 2c**). As these changes cannot be attributed to changes in saccade rate (**Fig. 2c**, *Rs*), these results are consistent with a parallel control of saccades and drift. Accordingly, when tunneled, the visual system appears to increase the ROI sampling rate while maintaining *Xp* and compromising the control of *Sp*. Interestingly, a different strategy appeared with size changes. When viewing small sized images, the visual system decreased the ROI sampling rate while maintaining *Sp* and compromising the control of *Xp* (**Fig. 2a-c**). These results are also not consistent with open-loop vision. If the observed changes were affected by the visual stimuli in a strict bottom-up manner, then consistent changes in system behavior would be expected for consistent changes in the visual stimuli. This was not the case (**Fig. 2c**). Thus, either a specific mapping between specific visual stimuli to specific values of system variables is implemented in an open-loop manner, or a different organizational principle is underlying the observed changes. Closed-loop vision provides such a possible scheme. In one plausible closed-loop scheme, which is consistent with these data, the visual system maintained optimal acquisition speed11 in natural conditions but compromised its control for more information when tunneled.

If the visual system controls the drift speed in a closed-loop manner then it should exhibit a convergence dynamics7. Indeed, analyzing the mean within-pause dynamics of drift speed showed that the eye converged to its target drifting speed during the first 50 – 150 ms of the pause, following an initial increase and a gradual decrease of the speed. While starting the pause with speeds ~7 deg/sec on average, the eye then converged to ~5 deg/sec in natural viewing and to ~6 deg/sec in tunneled viewing (**Fig. 2c**). These speed values should be considered as upper bounds of the actual drift speed, as recording noise was not filtered out in order to preserve maximal temporal sensitivity11. Indeed, filtering the drift records removes the fast within-pause changes but preserves the general convergence dynamics (**Extended Data Fig. 2e**). As the recording noise in our system could be biased by pupil size or saccade kinematics12, we verified that the drift speeds we measured did not depend on the pupil size or on the amplitudes or speeds of the saccades preceding them (r2 < 0.01 for all cases), and that these variables were not significantly different across viewing conditions (**Extended Data Fig. 2**). Given these independencies, the fact that the drift speed stabilized on different values in different viewing conditions indicate that the stabilization dynamics do not stem from a passive adaptation process such as ocular muscle fatigue.

If the visual system maintains *Sp* $ I think you defined Sp as drift speed?$ across image sizes and compromises its control when challenged with tunneling $ not clear- what is compromised? The closed loop aspect?, then the trial-to-trial variability of *Sp* should reflect that. Indeed, while *Sp* exhibited relatively small coefficient of variance (CV) during natural viewing (0.88 and 0.55 for large and small, respectively), its CV increased significantly when tunneled (1.22 and 1.05 for large and small, respectively; **Fig. 2d; Extended Data Table 1**). Interestingly, the kinematics of the saccadic jumps, which are often considered open-loop ballistic movements, also appeared to be under closed-loop control; while obeying a main-sequence pattern to the same extent in natural and tunneled conditions for low saccadic amplitudes, (amplitudes that scaled with the image size - up to 7.5 deg for large and 3 deg for small images); saccade kinematics showed higher variations in tunneled vision beyond these amplitudes (**Extended Data Fig. 1**).

The analysis thus far suggests that drift kinematics are controlled in a closed-loop manner, in which the amount of the available visual information affects *Sp* and *Xp*, which in turn determine the acquisition of visual information. To analyze the relations between the concurrently-scanned visual details and the kinematics of eye movement we examined the spatiotemporal trajectories of eye movements during individual trials (**Fig. 3**). tunneled vision of large images induced a novel saccadic pattern - border-following (**Fig. 3a**). Most (55±7%) of the saccades made by all participants in all tunneled-large trials were border-following (**Fig. 3b**; see **Methods**). This border-following behavior, observed here for the first time, is consistent with a closed loop control of saccadic target selection (as saccadic target is determined by concurrent sensory data and its execution will modify the sensory data), and is not based on target-saliency models5,13, since the target is not visible in most cases of saccadic jumps under tunneled viewing.

During pauses that were close to borders drift trajectories scanned the image differently if vision was challenged or not. When challenged by tunneling or a small image size, the eye tended to drift in a curvier pattern14, remaining closer to their starting location. The distributions of the curvature index (see **Methods**) differed between border and non-border drifts in all conditions (p<0.05, two-tailed t-test) except for the natural-large condition (p=0.7) (**Fig. 4**). Drift speed was also affected by the concurrently-scanned visual details - *Sp* was significantly lower when drifting along borders than otherwise (4.48±0.07 versus 5.00±0.07 deg/sec with large and 3.99±0.10 versus 4.92±0.02 deg/sec with small images, p<0.05). These differences indicate that drift behavior, which selects the sensory data, is also affected by the sensory data.

Whether ocular drifts are controlled by the brain had been a source of enduring debate2,15-19. Our results demonstrate clearly that ocular drifts are actively controlled by the visual system - drift kinematics depended on the amount of visual information available and on the concurrently-scanned image details. Moreover, drift kinematics were gradually converging to their target values, a reliable signature of closed-loop dynamics. Our data suggest that under normal conditions the visual system controls its drift speed such as to maintain it within a specific range. One plausible reason for such a control is to maintain temporal coding relatively constant at a range suitable for neural processing16,20,21. When viewing small-size images the visual system does not compromise this control and even tightens it, possibly for increasing the reliability of sensory data. However, when challenged with tunneled viewing, which decreases the amount of available spatial information, the system compromises the control of drift speed, allowing its increase, for maintaining constant scanning distances under an increased rate of ROI switching (shorter fixational pauses), thus increasing total spatial information on the expense of its reliability. In this scheme, ROI switching seems to be controlled at another level, influenced by scene- and task-related factors1,5,22-25, and to influence (in an open- or closed-loop manner) the functioning of the drift control loop(s)16. Overall, these data support two major postulations. One is that the fixational pauses are used for visual acquisition, since if they were not then there was no sense in controlling the drift kinematics during the pause. The second is that vision is based on, although not completely dependent on, brain-environment closed-loop mechanisms, not only when selecting ROIs, but also while acquiring visual information within these ROIs.

**Methods:**

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

*Experimental Setup*. The experiment took place in a darkened and quiet room where participants sat in front of a high-resolution, fast computer screen (VPixx, 1920x1080, 120Hz). The movements of the dominant eye were recorded at 100Hz (EyeLink II) while the other eye was blindfolded. 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 was 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 for both image sizes.

*Experimental Design*. We tested the performance of participants in a five forced choice shapes recognition tasks. In each trial, one out of five filled gray basic shapes against a black background was presented (square, rectangle, circle, triangle and a parallelogram; see **Fig. 3a**). These images were presented in two forms, large and small, as described above. Participants were tested during 5 days. During days 1-3 they performed 2 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 tunneled trial lasted up to 30 s, mean trial duration for tunneled large was 9+2 s and for tunneled small 20+4 s (trials with natural viewing lasted 3 s, hence all comparative analyses were further verified using only the first 3 s of all tunneled trials, to control for trial length confounds, **Extended Data Table 1**). There were at least 2 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 five shapes was presented, and received a ‘correct/wrong’ feedback. 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 Bonneh et al.26) 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.

*Borders analysis*. Border-following movements during tunneled viewing were those movements in which the border of the shape was visible to the participant during the movement. This was determined by the window size: saccades or drift pauses that started and ended at less than 1.8 deg (for large), or 0.15 deg (for small) from a border, were classified as “border saccade” or “border drift”, respectively. During natural viewing border-following movements were defined using the same distance criteria.

*Curvature index*. We defined an index for drift curvature, where *Xp* equals the length of the drift trajectory and *Dp* equals the linear distance between its starting and ending points. Hence, *c*=0 represents a straight line and *c*=1 represents a closed curve.

*Statistical analyses.* Two-tailed t-tests were used to evaluate the significance of differences in the mean values of motor variables (Sp, … [[LIST ALL]]) [[JUSTIFY WHY WE ASSUME NORMAL DISTRIBUTION]]. Non-parametric Wilcoxon rank sum tests were used to evaluate the significance of differences in saccade rates and drift speeds for individual participants [[ONLY THOSE?]], where normal distributions could not be assumed. Variances were compared via the corresponding coefficients of variation (CV = var/mean). Data are expressed as mean ± s.e.m [[ARE THERE OTHER CASES?]]. Shape presentation was randomized using a uniform distribution. No blinding was done during analysis and none of the data points was excluded.

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**Author contributions**. L.G. conducted the experiments and analyzed the data. L.G., A.A. and E.A. conceived the project, designedh the experiments and wrote the paper.

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**Figure Legends**

**Figure 1. Gaze visit rates.** The distribution of gaze locations, measured in each sample, normalized (min-to-max) per trial and averaged across trials and subjects, for large shapes with natural viewing (**a**; 5 participants x 4 trials); large shapes with tunneled viewing (**b**; 5 participants x 6 trials); small shapes with natural viewing (**c**; 5 participants x 4 trials) and small shapes with tunneled viewing (**d**; 5 participants x 10 trials). Color maps were normalized for each panel. Movies demonstrating the visual stimuli presented during tunneled viewing of large and small images appear in **Extended Data Video 1,2**).

**Figure 2. Kinematics of saccades and drifts.** **(a)** Changes in mean saccadic rates between natural and tunneled viewing for large (blue) and small (magenta) image sizes. Data for each participant (left) and their mean (right most) are presented (\*, p<0.05, t-test). **(b)** Distributions of mean drift speeds per trial in the four experimental conditions; data as in (a) (\*, p<0.05, Wilcoxon rank sum tests). **(c)** Mean within-trial instantaneous drift speeds presented for large (1st & 3rd plot) and small objects (2nd & 4th plot) and in two time scales. Color code as in (b); error-bars denote SEMs. **(d)** Mean drifts speeds versus pause durations in the four experimental conditions (variances and SEMs: in the right most figures).

**Figure 3. Eye trajectories.** **(a)** Example of eye trajectories in single trials with natural (left) and tunneled large viewing. Saccades, lighter blue; fixational pauses, dark blue; traces, horizontal and vertical components as a function of time next to each example. Movies of these examples are in **Extended Data Video3-7**). **(b)** Fractions of border-following saccades in the two large conditions for each subject (small dots) and their means (large colored dots).

**Figure 4. Drift curvature indices**. Distributions of curvature indices (see Methods) of border drift trajectories (brown) and non-border drifts, in the four experimental conditions **(a-d)**. The vertical dashed lines depict the mean values of curvature indices across all pauses and subjects (mean±SEM): 0.52±0.01 vs. 0.48±0.01, respectively, for tunneled-large; 0.65±0.05 vs. 0.55±0.02 for natural-small; 0.60±0.03 vs. 0.53±0.01 for tunneled-small; 0.48±0.04 vs. 0.49±0.01 for natural-large.

**Extended Data**

**Extended Data Movies 1-2. Demonstrations of tunneled viewing.** Movies of tunneled viewing of large (Movie 1) and small (Movie 2) shapes. In each movie, the right panel shows the entire shape with the tunneling window superimposed and the left panel shows what was presented on the screen.

**Extended Data Movies 3-7. Demonstrations of the eye trajectories presented in Fig. 3.** Movies are slowed down by 2.4.

**Extended Data Table 1. Control for trial duration differences.** The analyses described in **Fig. 2a,b,d** were repeated for the first 3 s of the tunneled conditions, a time period equal to the duration of natural viewing trials. P values represent the probability that the values measured in the relevant tunneled condition were drawn from the same distribution as those measured in the natural viewing conditions.

**Extended Data Table 2. Emerging controlled variables.** Mean ± SEM of visual scanning variables during each viewing condition. Values marked with the same or different color show p > 0.15 or p < 0.05, respectively (Wilcoxon rank sum tests).

**Extended Data Figure 1. Variability of the saccadic main sequence.** The maximum velocity of a saccade linearly depends on its amplitude in all experimental conditions (R2 = 0.66 (natural-large); 0.69 (natural-small); 0.70 (tunneled-large) and 0.74 (tunneled-small). The figure shows the residuals of the linear fit of the main sequence in each condition. Dashed line denotes the saccade amplitude above which the difference was significant. Shaded areas represent the SEMs.

**Extended Data Figure 2. Dependencies between kinematic variables. (a)** Each data point represents a single pause (mean pause speed versus the amplitude of the preceding saccade). No correlation was found between these two variables across the entire data set (R2 = -0.04, p = 0.12; colors as in Fig. 2); similarly, no correlation was found for the maximal saccade speed (R2 = XX, p = XX) **(b)** The mean amplitude of the preceding saccades of all pauses in each of the four experimental conditions; no significant difference was found (p > 0.05, t-test); similarly, no significant difference was found for the maximal saccade speed (p > 0.05, t-test). **(c)** Mean within-pause instantaneous pupil size **(d)** Mean within-pause instantaneous drift speed (no correlation with pupil size, R2 = 0.02, p = 0.55) **(e)** Mean within-trial instantaneous drift speed, calculated from filtered data (a third order Savitzky-Golay filter with window size of 3 samples14)