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

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**Vision is traditionally considered to be an open-loop process, in which visual stimuli trigger a sequence of brain computations much like in computer vision1,2. Accordingly, ocular kinematics are considered to either not affect or not be affected by visual acquisition, except for slow updates of motor plans for sampling regions of interest (ROIs) in the scene using ocular saccades3,4. We tested the dependency of saccades and drifts (the slow scanning motion in each ROI5,6) on the visual input 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 drifts. When challenged, the visual system modified its motor variables in one of two manners, maintaining either scanning speed or scanning distance per ROI. Typical to closed-loop but not to open-loop systems, the visual system dynamically converged to its target scanning speed anew in each ROI, 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. The dependency of ocular kinematics on visual acquisition entails closed-loop vision since visual acquisition depends on ocular kinematics. Our results further suggest that the visual system can adapt its closed-loop strategy according to the availability of visual data.**

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 centers7, visualized by their visit rates (the fraction of time spent in each pixel of the image during each trial, mainly reflecting the location of fixational pauses, henceforth “pauses”) (**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, typically near 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 (*Rs*) and drift averaged speed per pause (*Sp*) 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. With closed-loops, adaptive changes are part of a process in which the values of a set of variables, the “controlled variables”, are actively maintained within a certain range that allows the current functioning of the system8-10. Open-loop systems do not have this active capacity and depend on a-priori mapping between environmental and internal variables. We examined whether the behavior of perception-relevant oculomotor variables is better explained in the light of open- or closed-loop dynamics.

We assume here that visual information is acquired during fixational pauses 11-14 and that photoreceptors are activated by illumination changes. Consequently, the mean rate of visual acquisition (during a pause) should be proportional to *Sp*6,15 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 *Rs*, which reflects the number of ROIs sampled per time unit. The increased *Rs* observed here in tunneled conditions is consistent with its dependency on task difficulty16. Importantly, however, the tunneling-induced changes in *Rs* and *Sp* compensated each other, on average, keeping *Xp* unchanged for each stimulus size (**Fig. 2c**). Thus, 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 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 each input manipulation, tunneling and size change. This was not the case (**Fig. 2c**). Moreover, each combination of tunneling and size induced a specific combination of kinematic variables. A sequential open-llop scheme in which the visual input affects *Rs and Rs* affects the drift variables is also ruled out; the mean values of *Rs* did not systematically change along with either *Sp* or *Xp* (**Fig. 2c)** and the pause-by-pause correlations between each *Sp* or *Xp* and its preceding instantaneous *Rs* (i.e., the inter-saccadic-interval) were negligible (R2 < 0.06). Thus, either a specific mapping between specific combinations of visual stimuli to specific sets of 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 an organizational principle. In one plausible closed-loop scheme, which is consistent with our data, the visual system maintained optimal acquisition speed17 in natural conditions but compromised its control while attempting to acquire more information when tunneled.

If the visual system controls *Sp* in a closed-loop manner then it should exhibit a convergence dynamics9. 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/s on average, the eye then converged to ~5 deg/s in natural viewing and to ~6 deg/s 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 sensitivity17. Indeed, filtering the drift records removes the fast within-pause changes but preserves the general convergence dynamics (**Extended Data Fig. 2g**). As the recording noise in our system could be biased by pupil size or saccade kinematics18, 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 at different values in different viewing conditions despite similar initial values upon pause initiation, indicate that the stabilization dynamics did not stem from a passive adaptation process such as ocular muscle fatigue.

If the visual system maintains *Sp* across image sizes and compromises its control when challenged with tunneling, then the trial-to-trial variability of *Sp* should reflect that. Indeed, while *Sp* exhibited relatively small coefficient of variance (CV) during natural viewing (0.90 and 0.57 for large and small, respectively), its CV increased significantly when tunneled (1.22 and 1.02 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 certain 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 not based on peripheral target-saliency models7,19, since the target is not visible in most cases of saccadic jumps under tunneled viewing (mean saccadic amplitude was significantly larger than window size, 3.45±0.07 vs 2.90 deg; p<0.05 , n= 4648, one-tailed t-test). Border-following here must depend on the visual information acquired during the pause preceding the saccade, expressing scene-level closed loop dynamics of saccades and drifts20.

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 pattern21 when scanning a border, 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/s with large (n=1405,757) and 3.99±0.10 versus 4.92±0.02 deg/s with small images (n=66,2723), p<0.05, two-tailed t-tests). 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 debate5,20,22-25. 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 processing20,26,27. 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 factors3,7,28-31, and to influence the functioning of the drift control loop(s)20. 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, as demonstrated by the perception of flashed stimuli9) 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.32) was used for detecting all saccades and drift. We used the following threshold parameters for saccades detection: 16 deg/s 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 kinematic variables (*Rs*, *Sp*, *Xp*, *c*), all of which exhibited normal distribution for all subjects. N’s for *Rs* statistics in TL,NL,TS,NS were: Sub1 (30,19,30,20); Subj2 (29,20,30,19); Subj3 (27,20,28,18); Subj4 (30,20,30,19); Subj5 (25,20,30,20); N’s for *Sp* and *Xp* statistics in TL,NL,TS,NS were: Sub1 (1756,229,2392,154); Subj2 (534,110,2626,45); Subj3 (723,129,2108,101); Subj4 (409,104,1288,46); Subj5 (1085,203,2775,136); Variances were compared via the corresponding coefficients of variation (CV = variance/mean), using two-sample F-tests. Data are expressed as mean ± S.E.M. Shape presentation order was randomized using a uniform distribution. No blinding was done during analysis and none of the data points was excluded.

*Data availability Statement*. All analyses were done using MATLAB. All data is available upon request.

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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, designed 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, two tailed t-tests). **(b)** Distributions of mean drift speeds per trial in the four experimental conditions; data as in (a) (\*, p<0.05, two tailed t-tests). **(c)** 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 (two tailed t-tests). **(d)**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. **(e)** Mean drifts speeds versus pause durations in the four experimental conditions. See Methods for N’s.

**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 (n=1405,757); 0.65±0.05 vs. 0.55±0.02 for natural-small (n=23,270); 0.60±0.03 vs. 0.53±0.01 for tunneled-small (n=66,2723); 0.48±0.04 vs. 0.49±0.01 for natural-large (n=192,374). P-values in (a-d) are of two tailed t-tests.

**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 (two tailed t-tests for means and two tailed f-tests for variances).

**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)** 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, two-tailed t-test); similarly, no significant difference was found for the maximal saccade speed (p > 0.05, two-tailed t-test). **(b-d)** Each data point represents a single pause (mean pause speed versus (b) the amplitude of the preceding saccade, (c) the maximal speed of the preceding saccade (d) mean pupil size during the pause). R2 < 0.01 in all cases. Colors as in Fig. 2. **(e)** Mean within-pause instantaneous pupil size **(f)** Mean within-pause instantaneous drift speed (no correlation with the mean within-pause instantaneous pupil size, R2 = 0.02, p = 0.55) **(g)** Mean within-trial instantaneous drift speed, calculated from filtered data (a third order Savitzky-Golay filter with window size of 3 samples21).