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

*Liron Gruber, Amos Arieli and Ehud Ahissar*

Department of Neurobiology, Weizmann Institute, Rehovot, Israel

**Visual perception is based on continuous eye movements, typically yielding abrupt switching between regions of interest (ROIs), using saccades, and scanning of these ROIs, using drifts 1-3. 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 independent of the visual input 1,4. 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. The subjects’ scanning trajectories demonstrated clear closed-loop dynamics of saccades and drifts. First, the eyes often scanned the borders of the images, in a manner that necessitated relying on concurrent sensory data. Second, when challenged the visual system maintained acquisition parameters by modifying saccade and drift kinematics. Third, the system converged to its target kinematics anew during each fixational pause (henceforth “pause”), converging to significantly different kinematics depending on the viewing condition and the visual input. 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 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).

Limiting the available spatial information had a dramatic effect on 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 (**Fig. 1a**). In contrast, during tunneled viewing of Large shapes the gaze was typically directed to the edges of the shapes (**Fig. 1b**). 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, 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.

The overall statistics of saccade rate and drift speed showed that both increased in tunneled conditions compared to natural viewing, for both image sizes (**Fig. 2a,b**). (This was further ensured by comparing 3 seconds time windows from the tunneled trials, to care for the difference in trials length). 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 system 5-7. Open-loop systems do not have this capacity. If visual information is acquired during a pause, then the mean rate of acquisition would be proportional to the mean speed of the drift during the pause (Sp) 3,8 and the total spatial information sampled during a pause would be proportional to the total scanning distance (the length of the gaze trajectory) of a pause (Xp). Pause duration (Tp) is determined by the saccade rate, which in turn determines the number of ROIs sampled per time unit, and might reflect different parameters as the task difficulty and alike (Gao, X., Yan, H. & Sun, H.-J. Modulation of microsaccade rate by task difficulty revealed through between- and within-trial comparisons. *J. Vis.* **15,** 1–15 (2015)).

In our experiment, the tunneling-induced changes in saccade rate and drift speed compensated each other, on average, keeping the total distance scanned by the eye per pause unchanged for each stimulus size (Large shapes: 1.33±0.04 versus 1.40±0.04 deg, p=0.4; Small shapes: 1.77±0.08 versus 1.63±0.08 deg, p=0.2, for natural and tunneled vision, respectively). Thus, when tunneled, the visual system appears to increase the ROI sampling rate while maintaining Xp and compromising Sp. Interestingly, a different strategy appeared with size challenging. When challenged with small sizes, the visual system decreased the ROI sampling rate and here preferred maintaining Sp while compromising Xp (**Fig. 2a,b**).

If the visual system indeed controls the drift speed in a closed-loop manner then it should exhibit a convergence dynamics. Indeed, analyzing the mean within-pause dynamics of drift speed showed that the eye converged to its target drifting speed during the first 50 – 70 ms of the pause. 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**). The dynamics of drift speed is a short increase at the beginning of a pause followed by a decrease until the target speed – while the entire range of speeds is below the thresholds for saccades detection.

If the visual system maintains Sp when challenged with size and compromises it when challenged with tunneling, then the trial-to-trial variability of Sp should reflect that. Indeed, while Sp exhibited relatively little variance during natural viewing [[LIRON, COMPUTE THE CV]], its variance increased significantly when tunneled (**Fig. 2d**). (This was again further ensured by comparing 3 seconds time windows from the tunneled trials, to care for the difference in trials length). for comparison, saccadic kinematics obeyed 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); beyond these amplitudes the main-sequence showed higher variations in tunneled vision (supp\_Fig. X).

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. This loop appears to be influenced by the saccadic rate, which may be determined in another control module or loop (e.g., 9). To analyze the interactions between saccades and drift kinematics in more detail 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 Large-tunneled trials were border-following, and as a result most (59±4%) of the pauses were on borders, compared with 20±7% and 28±4%, respectively, in all other conditions (**Fig. 3b**; see **Methods**). During pauses close to borders drift trajectories scanned differently if vision was challenged or not. When challenged, by tunneling or size, the eye tended to drift in a curvier pattern, remaining closer to their starting location (**Fig. 3c;** see **Methods**). 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 deg/sec versus 5.00±0.07 deg/sec in Large and 3.99±0.10 deg/sec versus 4.92±0.02 deg/sec in Small images, p<0.05).

Whether ocular drifts are controlled by the brain had been a source of enduring debate 1,9-11. The role of drift in vision, to these days in some studies, is considered as mainly preventing perceptual fading from happening (McCamy, M. B., Macknik, S. L. & Martinez-Conde, S. Different fixational eye movements mediate the prevention and the reversal of visual fading. *J Physiol* **592,** 4381–4394 (2014)). Our results demonstrate clearly that ocular drifts are actively controlled by the visual system - drift kinematics depended on the amount of available visual information and on the concurrently-scanned image patterns. Moreover, drift kinematics were 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 reason for such a control is to maintain temporal coding relatively constant at a range suitable for neural processing 9,12. When challenged with small sizes the visual system does not compromise this control and even tightens it [[LIRON, SEE IF THIS IS TRUE]]. However, when challenged with tunneled viewing the system compromises drift speed for maintaining constant scanning distances under an increased rate of ROI switching. In this scheme, ROI switching seems to be controlled at another level, and to influence the functioning of the drift control loop(s) 9. Overall, these data support two major postulations. One is that the fixational pauses are used for visual acquisition, as if they were 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 environment-dependent manner.

**Methods:**

*Participants*. 5 healthy participants with normal vision at the ages 21-28 participated in the experiment (3 females, 2 right-handed with right dominant eye, 3 right-handed 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 dark 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 5 images of basic shapes (square, rectangle, circle, triangle and a parallelogram; see **Fig. 1** for their outlines) was presented – filled gray shape against a black background. 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 trial lasted up to 30 s (except trials with natural viewing which lasted 3 s), 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 5 shapes was presented, received a ‘correct/wrong’ feedback. Success rates were 0.94±0.06 for the Large shapes and 0.60±0.02 for the Small shapes. Only correct trials were used for the analysis. 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, Y. S. *et al.* Motion-induced blindness and microsaccades: Cause and effect. *J. Vis.* **1022,** 1–15 (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.

*Borders analysis*. Saccades or drift pauses that started and ended close to a border (<1.8 deg for Large, <0.15 deg for Small) were classified as “border saccade” or “border drift”, respectively.

*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. [[LIRON, THINK IF WE CAN ALSO ANALYZE the “close-to-border index” – how much it remained close to the border during the pause. It fits better the current text]]

1 Steinman, R. M. & Levinson, J. Z. in *Eye Movements and Their Role in Visual and Cognitive Processes* (ed E. Kowler) 115-212 (Elsevier, 1990).

2 Rucci, M., Iovin, R., Poletti, M. & Santini, F. Miniature eye movements enhance fine spatial detail. *Nature* **447**, 851-854 (2007).

3 Ahissar, E. & Arieli, A. Figuring space by time. *Neuron* **32**, 185-201 (2001).

4 Pitkow, X., Sompolinsky, H. & Meister, M. A neural computation for visual acuity in the presence of eye movements. *PLoS Biol* **5**, e331 (2007).

5 Marken, R. S. You say you had a revolution: Methodological foundations of closed-loop psychology. *Review of General Psychology* **13**, 137 (2009).

6 Ahissar, E. & Assa, E. Perception as a closed-loop convergence process. *eLife* **5**, e12830 (2016).

7 Buckley, C. L. & Toyoizumi, T. A theory of how active behavior stabilises neural activity: Neural gain modulation by closed-loop environmental feedback. *PLoS computational biology* **14**, e1005926 (2018).

8 Rucci, M. & Victor, J. D. The unsteady eye: an information-processing stage, not a bug. *Trends in Neurosciences* **38**, 195-206 (2015).

9 Ahissar, E., Arieli, A., Fried, M. & Bonneh, Y. On the possible roles of microsaccades and drifts in visual perception. *Vision research* **118**, 25-30 (2014).

10 Martinez-Conde, S., Macknik, S. L. & Hubel, D. H. The role of fixational eye movements in visual perception. *nature reviews neuroscience* **5**, 229-240 (2004).

11 Herrmann, C. J., Metzler, R. & Engbert, R. A self-avoiding walk with neural delays as a model of fixational eye movements. *Scientific Reports* **7**, 12958 (2017).

12 Ahissar, E. & Arieli, A. Seeing via miniature eye movements: A dynamic hypothesis for vision. *Frontiers in Computational Neuroscience* **6**, 89 (2012).