**elife**: Introduction; Results; Discussion; Methods; Acknowledgements; References; Figures with the corresponding legend below each one.

**The motor-sensory basis of vision revealed with constrained vision**

**OR**

**Closed-loop motor-sensory strategies of vision revealed with constrained vision**

**OR**

**The closed motor-sensory loop basis of vision revealed with constrained viewing**

**OR**

**Closed-loop viewing: competition between information rate and coding**

**OR**

**Evidence for closed-loop viewing**

**OR**

**Evidence for closed-loop vision**

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**Highlights**

* Vision is currently hypothesized to operate via either open-ended processing of sensory data or closed-loop motor-sensory processing.
* We tested the mode of operation by modulating the available spatial information, changing stimulus size and effective retinal size.
* The modulations of available spatial information were accompanied with significant modulations of oculomotor kinematics and scanning trajectories, indicating closed-loop viewing.
* Viewing kinematics was affected via changes in the trajectories and kinematics of both saccades and drifts.
* Trajectories in tunneling conditions indicated clear closed-loop control of both saccades and drifts.
* Kinematic changes were consistent with the system trying to maintain the rate of spatial information on the expense of the reliability of temporal coding.
* These experiments indicate that both saccades and drifts are controlled in real-time; when the eye seems to drift around randomly during natural viewing it is thus due to a controlled choice, adapting drift scanning to available visual information.

To what extent drifts are controlled is an open question.

 Here we tested the dependency of saccades and drifts on (i) the bandwidth of sensory information and (ii) details of sensory information.

We found that constraining/tunneling vision

* Caused the distribution of visual gaze to move from the center of the images to their contours.
* Caused the majority of saccades to follow the borders of the shapes and the drift between them to be straight in shape.
* Increased the saccadic rate as well as the average drift velocity (while the size of the shape affected the saccadic rate but not drift characteristics).
* Caused the saccadic main sequence as well as the average drift velocity to be less precise and more variant.
* Increased the periodicity of drift velocity and the consistency of the distance traveled by the drift.

**Abstract:**

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. Visual perception is currently hypothesized to operate in either one of two general motor-sensory schemes. In one, open-loop vision, visual perception results from open-ended processing of the sensory data generated by the interactions of these movements with external objects. In the other, closed-loop vision, perception is converged upon via motor-sensory closed-loops that dynamically associate the brain and the environment. The open-loop scheme predicts that perception will depend on the sensory data alone and that eye movements should not be affected by the concurrent sensory data, whereas the closed-loop scheme predicts that perception will depend on motor-sensory dynamics and that that eye movements should be affected by the concurrent sensory data. We tested the mode of operation 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 in tunneled conditions demonstrated clear closed-loop dynamics; the eyes often scanned the borders of the images, both using saccades and drifts, in a manner that necessitates relying on concurrent sensory data. The statistics of eye kinematics showed that when challenged with tunneled vision the visual system compensated the constancy of drift velocity, and hence that of temporal coding, for increasing the acquisition rate. Tunneling also induced increased 10Hz oscillations in drift kinematics. These experiments indicate that vision involves closed-loop viewing in which the kinematics of saccades and drifts are adapted to available external information.

Old abstract version:

Visual scene perception involves abrupt changes of regions of interest (ROIs) using saccades and scanning of these ROIs using drifts. We ask here how these eye movements are affected by the spatial bandwidth of eye-environment interactions, i.e., by the amount of spatial information available to the visual system. We compared natural vision of basic shapes to two modes of “tunneled vision,” in which visual spatial bandwidth was bounded. The main finding was that visual perception with limited sensory spatial bandwidth required strategical changes in the control of eye movements. These changes occurred at three levels. First, the mode of the distribution of visual gaze moved from the center of the images to their contours, and the majority of saccades, were following the contours. Second, saccadic rate as well as drift average velocity significantly increased. Third, more periodicity was found in the drift’s instantaneous velocity and the consistency of the distance traveled by the drift was greater. Moreover, both the main sequence of the saccades and the average velocity of the drift were preserved in the tunneled vision, but were less accurate and greater variance. These results demonstrate the intrinsic role of eye movements in vision at all levels, including both drift and saccades, and their dependency on the sensory spatial bandwidth. These results further demonstrate the different control levels available to the visual system, and suggest motor parameters that are being controlled and manipulated by the system.

Introduction:

The question of perceptual activity control, in EyeM specifically, is frequently studied and can be approached in different ways. One can, for example, discriminate the “where” question from the “how” question. Why do we look *where* we do? (Schütz et al., 2011) versus *how* do we look *the way* we do? (Ahissar et al., 2014). The first question deals with the selection of gaze’s position while viewing and the second question deals with the types of EyeM occurring while viewing- and their motor variables. The selection of gaze position or fixation location was already studied in the classical works of Buswell 1935 and Yarbus 1967, and is still being studied to these days in various fields of study, among them neuroscience, physiology, phycology and computer science (Schütz et al., 2011).

Visual exploration and visual search are characterized by the alternation of saccades and fixation periods. Important to keep in mind, though, that fixation periods are defined somehow arbitrarily because the eyes are never completely still (Yarbus,1967; Otero-millan et al., 2008). Furthermore, the common approach used to discriminate between saccades that happen during these fixation periods, and therefore are naturally smaller in amplitude and involuntary, and saccades that happen between the fixation periods, which are larger in amplitude and could be potentially voluntarily controlled. These saccades were named micro-saccades and macro-saccades, respectively, and were suggested to have different generators and different roles in vision.

More recent studies show that there is a microsaccade–saccade continuum as visual information is discretely sampled with all saccades, large and small (Otero-millan et al., 2008) and that micro-saccades are used to “re-sharpen” the image and improve spatial resolution (Donner & Hemilä, 2007). It seems that micro-saccades also fulfill the same purpose as large saccades – precisely shifting gaze to the most relevant locations in order to achieve the goal of a task (Kowler & Collewijn, 2010). Moreover, the so called ‘voluntary’ saccades can be the same size as micro-saccades, the later can be defined only operationally, as involuntary saccades that are produced while attempting to fixate (Martinez-Conde, 2006). Note that this definition for itself is very controversial; hence we are not usually and continually aware of our EyeM at all. In addition, a growing list of common characteristics to saccades and micro-saccades supports the hypothesis of a shared oculomotor generator (Martinez-Conde et al., 2004; Rolfs et al., 2008).

The second important type of EyeM, which occurs between saccades, during most of the fixation periods, is the drift. The drift is much differentiable from the saccadic movement and its role in vision is very debatable. The role of drift in vision, to these days in some studies, is considered as mainly preventing perceptual fading from happening (McCamy et al., 2014).Yet, a growing list of studies suggests otherwise. One suggestion is that the drift is adapted to an image in order to transform visual signals into an optimized spatiotemporal code for further visual processing (Kagan, 2012). The drift might be unfold already during retinal processing by redistributing the temporal frequency power into a range of increased retinal sensitivity (Kuang et al., 2012). In addition, studies show that drift movements are also suitable for visual detailed sampling (Ahissar et al., 2001, 2012, 2014)**…**

Results:

We found that constraining vision affected the motor strategy of vision at several levels: gaze distribution, spatial trajectories of saccades and drift movements (henceforth “drifts”) and kinematics of saccades and drifts.

Gaze distribution was assessed by computing the visit rates - the fraction of time spent in each pixel of the image during each trial. During natural viewing of large shapes, the gaze was typically directed to the center of the shape (fig2A). In contrast, during tunneled viewing of large shapes the gaze was typically directed to the edges of the shapes (fig2B). Importantly, the gaze was directed to the edge of the shapes also during tunneled viewing of small shapes, where it typically focused on a specific area of interest (fig2D), in contrast to the spread and multi focal gaze distribution during natural viewing of them (fig2C). Interestingly, none of the participants were aware of their tendency to visit these areas, as they all reported that intended eye movements in the small shapes task was extremely challenging. 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).

Unlike gaze distribution, spatial trajectories of saccades and drifts did differ between tunneled viewing of large and small images (Fig. 3). During tunneled viewing of large images a novel type of saccades emerged: border-following saccades (fig3A). Different strategies were used by the participants in the constrained tasks, but the most robust one is directing the saccadic jumps along the borders of the shapes (fig3B). More than 50% of the saccades made by all participants in all “large tunneled” trials were border-following (fig3B). This did not happen during tunneled viewing of small images (fig3B). Furthermore, categorizing the drifts by the shape of their spatial trajectory - strait, circular and curved - revealed that almost all drifts between border-following saccades were strait and hence border-following as well (fig3C). Straight drifts were unique to border-following as when not near the borders drifts were typically not straight (Fig. 3C).

In order to look into the motor characteristics of the eye movement, and test the effect of ‘tunneling’ in a shorter time scale, we analyzed the sequences of saccades and drift under the 4 conditions (natural and tunneled viewing of large and small shapes). Saccadic rates were primarily affected by the tunneling in both shapes sizes (fig4A). Tunneling significantly increased the saccadic rate. A significant increase in saccadic rate was also observed when comparing large shapes with the small shapes in both natural and tunneled vision. While an increased saccadic rate merely infers shorter drift duration, we observed a significant increase in the mean drift velocity – and no significant decrease in its amplitude, as would be expected by the decreased duration (fig4B). This additional effect was observed only when tunneling vision and not when increasing the shape size. I.e., the shape size affected only the saccadic rate, while the tunneling manipulation affected both the saccadic rate and the mean drift velocity. Furthermore, when categorizing drift movements by their location with regards to the shapes, i.e. near the borders or far away from them, we found a significant velocity decrease when the drift was near the borders – as well as a significant duration increase (similar to the tunneled-natural comparison….). [[REPHRASE LATER]]

To further characterize these motor differences, we examined the known “main saccadic sequence” – the linear relationship between saccades maximum velocity and its amplitude (ציטוט). As can be seen in figure 5, the linear relations were generally preserved during the tunneled viewing, as indicated by the high R^2 values of the linear regression. In higher amplitudes, though, the residuals of the linear fit were significantly larger during tunneled viewing. Saccades longer than 6 visual degrees were less tightly paired with a specific maximum velocity during tunneled vision. Similarly, the mean drift velocity, mainly of drifts under 500ms, had larger variance in the tunneled vision conditions (fig5B). The shorter drift durations in the tunneled conditions (which are also more common in this condition, see last paragraph) had a wider range of velocities than short drift in the natural condition. [[REPHRASE LATER]]

For a deeper understanding of drift velocity we then looked into the instantaneous velocity of each movement in the different experimental conditions. We computed the autocorrelations of drift vertical and horizontal instantaneous velocities in order to look for any periodic behavior (fig6A). We found that a significant peak in the autocorrelation can be found much more in trials of the tunneled vision conditions than in trials of the natural vision. The periodicity is stronger, i.e. appears more frequently, in the vertical movements than in the horizontal one. Importantly, in all experimental conditions, the peak, if exist, is at 100ms and in some cases also 200ms (which might be a harmonic). [[REPHRASE LATER]]

We then computed the autocorrelations of the distance “travelled” by the drift in each movement. This distance is, in practice, the cumulative integral of the change in the position of the eye, which is similar to the instantaneous velocity discussed previously. We found that the autocorrelation of the traveled distance decayed faster in the natural vision conditions. The time constant of the exponential that best fit these decays, is about two times longer in the tunneled vision conditions. Tunneling vision, hence, not only entailed more periodicity in drift’s velocity, it also increased the consistency of the distance covered by drift motion (fig6B). [[REPHRASE LATER]]

Discussion:

Whether ocular drifts are controlled by the brain had been a source of enduring debate {refs, Steinemann,…}. Our results demonstrate clearly that ocular drifts are actively controlled by the visual system when vision is tunneled. Our current paradigm did not address the computational basis behind the specific adaptation of drift kinematics, leaving space for speculative accounts, of which we will mention two. In one, drift may be controlled in a way resembling saccadic control, and yielding a main-sequence like dependency between amplitude and velocity. According to this account, the main variable controlled here was the amplitude, for increasing sampling range. The second speculation is that as tunneling decrease the total amount of retinal signals, the visual system try to compensate by increasing the intensity of retinal signals by increasing scanning velocity {ref}.**(need to change – discussion about the temporal vs spatial information rate….)**

These results also support the idea of a closed-loop perception, as new sensory constrains have an immediate effect on the basic motor characteristics of saccades and drift. Though natural elements of the EyeM are kept, their motor profiles are significantly different when receiving different sensory input (Saig, Gordon, Assa, Arieli, & Ahissar, 2012; Gordon & Ahissar, 2012; Mitchinson et al., 2011).

As for the known ‘main sequence’ phenomenon - the expected linear dependency of the saccade maximum velocity and its amplitude were observed in all parts of the experiment. Though the population of saccades amplitudes seemed to change between conditions, as was just mentioned, saccades from all range of amplitudes could be found in each condition (up to 25 deg amplitude). We suggest that the less peripheral vision participants have, the less the saccades velocity is controlled. We hypothesize that whenever one moves his or her gaze to an ‘unseen’ target, the velocity of the saccade is less controlled, either by the inability of the system to calculate the best velocity because of lack of input, or by an intended effort to explore. This suggestion, of course, needs to be further investigated and quantified.

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 (fig2). 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.

*More detailed on the different analysis made for each figure:*

*\** SPECTRAL AND CORRELATION ANALYSIS