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On the possible roles of microsaccades and drifts in visual perception

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ABSTRACT

During natural viewing large saccades shift the visual gaze from one target to another every few hundreds of milliseconds. The role of microsaccades (MSs), small saccades that show up during long fixations, is still debated. A major debate is whether MSs are used to redirect the visual gaze to a new location or to encode visual information through their movement. We argue that these two functions cannot be optimized simultaneously and present several pieces of evidence suggesting that MSs redirect the visual gaze and that the visual details are sampled and encoded by ocular drifts. We show that drift movements are indeed suitable for visual encoding. Yet, it is not clear to what extent drift movements are controlled by the visual system, and to what extent they interact with saccadic movements. We analyze several possible control schemes for saccadic and drift movements and propose experiments that can discriminate between them. We present the results of preliminary analyses of existing data as a sanity check to the testability of our predictions.

1. Introduction

Saccades (Ss) are rapid eye movements that shift the line of sight ("visual gaze") of both eyes simultaneously. Large saccades (LSs) have amplitudes >2 deg, peak velocities of up to >500 deg/s, and durations of 20–100 ms. Within their primary natural working range (<10 deg) (Dorr et al., 2010) LSs obey the "main sequence" relationship: the ratio between their amplitude and peak velocity is constant (Bahill, Clark, & Stark, 1975; Findlay & Walker, 2012). Therefore, saccade durations are confined to smaller modulations; for perceptual relevant saccades, when amplitudes change by 20 folds (from 0.5 to 10 deg), durations change only by 2-fold (from 20 to 40 ms) (Bahill, Clark, & Stark, 1975).

Microsaccades (MSs) are small saccades; they exhibit all characteristics of LSs described above, but their amplitudes are smaller than the diameter of the foveal region, i.e., typically less than 2 deg (Engbert, 2006). During free viewing LSs occur several times per second, typically 2–4 times. Each LS shifts the gaze rapidly to a new target, where the eye dwells for several hundreds of millisecond before jumping to the next target (Fig. 1A). Each dwelling period (e.g., Fig. 1B) is termed a "fixational pause" (Barlow, 1952) and its duration is affected by global planning as well as by the visual information acquired during the pause (Sereno & Rayner, 1992). The sequence of saccadic targets, which forms the scanning path of the entire scene, is also affected by global planning as well as visual information acquired during the scan of the scene (Noton & Stark, 1971; Walker-Smith, Gale, & Findlay, 1977). MSs' occurrence rate depends on the task (e.g., Bonneh et al., 2014; Bonneh et al., 2010; Fried et al., 2014; Rolfs, Kliegl, & Engbert, 2008; Siegenthaler et al., 2014; Stampe & Reingold, 2002). In fixation tasks, where subjects are instructed to fixate at one point, MSs occur at rates similar to, though a bit lower than, LSs (Otero-Millan et al., 2008). During free viewing they occur at much lower rates as described below.

2. Microsaccades function

Several functions had been suggested along the years for MSs. Two such functions assign to MSs a central role in the perception of external objects. In one, it is suggested that MSs are not different in function from LSs, and as such they redirect the visual gaze to new locations within the foveal region (Cunitz & Steinman, 1969; Ko, Poletti, & Rucci, 2010; Zuber, Stark, & Cook, 1965). In the other it is implied that MSs are used to directly encode visual details while gaze shifts are determined by LSs (e.g., McCamy et al., 2014). Encoding by MSs can be done in principle in two ways: by scanning during movement or by "flashing" (i.e., resetting photoreceptors and reactivating them according to the new spatial configuration) upon landing (Rolfs, 2009a). "Flash" encoding by

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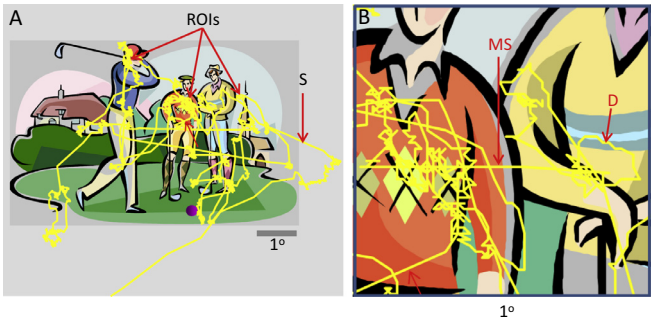

Fig. 1. (A) Example of ocular scanning of an image. The trajectory of a human subject's gaze (of one eye) during free viewing of an image presented on a computer screen is depicted. ROIs, regions of interest; S, saccade. Courtesy of Shira Ozana. (B) Zoom-in into a 1° × 1° area in the middle ROI of A. MS, microsaccade; D, drift.

MSs was examined and found to be a plausible mechanism for improving near-threshold visual detection (Elsner & Deubel, 1986). However, such a mechanism cannot underlie encoding of fine visual details because there is simply not enough information in the spikes generated at the retina upon MS landing and before smearing due to drift begins (Appendix 2 in Ahissar & Arieli, 2012).

We examined the plausibility of MS encoding by scanning. The suggestion is that the retinal slip (i.e., the shift of the visual image across the retina) induced by a MS activates photoreceptors and as a result visual details are encoded at the output of retinal ganglion cells. Critically, however, MS velocities are too fast for fine retinal encoding. Regular visual acuity can reach the limit of receptor granularity: spatial frequencies of about half of the receptor frequency can be perceived (Hirsch & Curcio, 1989). As the spacing between neighboring image peaks equals to the width of only two retinal receptors, a pre-requisite for the perception of this image is that the activities of two neighboring receptors are distinguishable. Visual encoding by MSs thus requires that activities of neighboring receptors should be distinguishable when the eye traverses a stationary grid during a MS (Fig. 2).

MS velocities obey the main sequence ratio and vary between ~20 and 90 deg/s for MSs of 0.1–1 deg (McCamy et al., 2014). The diameter of the smallest foveal receptors in typical human subjects is about 1/3 of an arcminute (or 1/180 of a deg). A retinal slip induced by such MS induces inter-receptor-delay (IRD) of about 0.06–0.3 ms. Evidently, these temporal delays are too brief for any significant retinal coding: First, single receptors will be hardly activated during such brief exposures even at very high contrasts (Vuong, Chabre, & Stryer, 1984). Second, if antagonistic (e.g., center-surround) RFs exist in the fovea, then their inhibitory and excitatory zones will be activated virtually simultaneously, likely preventing any meaningful retinal response (Amthor & Grzywacz, 1993). Third, even if retinal responses would be generated at these temporal intervals it is not conceivable that downstream stations could phase lock to them or decode them because synaptic and conduction temporal variances are an order of magnitude larger (Faisal, Selen, & Wolpert, 2008). Thus, if MSs are used for visual encoding this could work only for coding of much lower spatial frequencies.

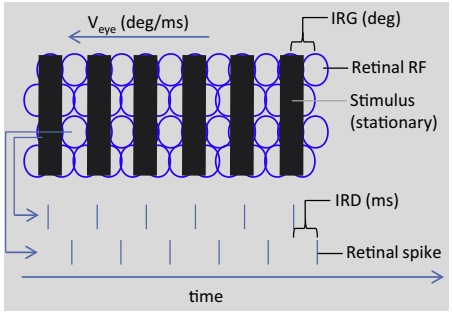

Fig. 2. A schematic illustration of scanning of a stationary spatial grid. The moving retinal receptor mosaic is illustrated by an array of blue circles, each representing a single receptive field (RF), which moves to the left at a velocity V_{eye}. The spikes generated via two single RFs are illustrated by two rows of vertical blue lines at the bottom, each row representing spikes of one RF (arrows). Inter-receptor-delay (IRD) is determined by inter-receptor-gap (IRG) divided by the velocity of the eye (V_{eye}).

However, MSs do not seem to be good candidates for encoding coarse vision either. Their occurrence rate is too low for any meaningful coding during free viewing. Free viewing is dominated by LSs. MSs occur only once per 3 to10 LSs, and when they occur they occur late in the fixational pause – typically later than 250 ms into the pause (McCamy et al., 2014). With such sparse occurrence it is not clear how any meaningful coding can be based on MSs. On the other hand, these data are consistent with a gaze-redirection role of MSs – more frequent redirections are expected to occur within more informative regions of the scene.

The conclusion from these considerations is that the role MSs play in vision is similar to that of LSs, only for within-fovea targets (Ko, Poletti, & Rucci, 2010; Poletti, Listorti, & Rucci, 2013), as originally suggested by Zuber, Stark, and Cook (1965) based on their similar kinematics. Thus, LSs and MSs initiate a new acquisition period, outside or within the current ROI, which lasts, typically, a few hundreds of milliseconds. This is consistent with the control mechanisms of LSs and MSs being shared (Hafed & Krauzlis, 2012), as originally suggested by Rolfs, Laubrock, and Kliegl (2006) and Rolfs, Kliegl, and Engbert (2008) based on theoretical considerations and supported by kinematic analysis (Otero-Millan et al., 2008). One interesting prediction of this suggestion is that during free viewing of natural scenes the clear preference for horizontal and vertical MS directions that is shown in artificial conditions (Rolfs, 2009a) should significantly decrease, or even disappear, as gaze redirection is expected in all possible directions.

3. Drift function

Acquisition of the visual details of stationary external objects can only be done via eye movements (eyeM) (Ahissar & Arieli, 2001). As MSs cannot be used for such acquisition, the only remaining candidate is the ocular drift (D). During every fixational pause the eye drifts around in a random-walk manner (Ahissar & Arieli, 2001; Barlow, 1952; Bengi & Thomas, 1972; Eizenman, Hallett, & Frecker, 1985; Ratliff & Riggs, 1950) (Fig. 1B). This drift motion is associated with high-frequency (>30 Hz) low-amplitude (<1′) fluctuations of the eye called 'tremor'. Tremor is often assumed to reflect the operation of an independent motor source, superimposed on the drift motion. However, a more parsimonious interpretation would assume that the tremor fluctuations reflect the fundamental 'steps' of the random-walk-like process underlying the drift motion. D mean velocities are in the order of 10–100 arcmin/s, and they typically cover areas of about ten to a few tens of arcminutes in diameter during a fixational pause (Cherici et al., 2012; Engbert, 2006). Importantly, D mean velocities translate to IRD values of ~3–30 ms at the smallest receptors of the fovea. Such temporal delays can be reliably decoded by neuronal circuits (Ahissar, 1998; Ahissar & Arieli, 2012). D occurs at all directions and thus can sample all visual details in a given image. Moreover, temporal encoding via D preserve all details required for perceiving shapes, textures, locations and motions of external objects (Ahissar & Arieli, 2012).

We thus propose the following scheme of visual encoding at the retina. Saccades (Ss, including LSs and MSs) shift the fovea from

one region of interest (ROI) to another, and each ROI is encoded during the fixational pause using drift motion. MSs, thus, reflect relocations of the fovea within the current ROI. Encoding of fine visual details is based on temporal coding whereas encoding of coarse details can be based on both temporal and spatial coding (Ahissar & Arieli, 2012). This is in line with studies that demonstrated the benefits of the drifts, and not microsaccades, for the encoding and perception of fine spatial detail (Kuang et al., 2012; Rucci et al., 2007). This scheme does not exclude possible effects of MSs (as well as LSs) in initiating neuronal processes in the visual system (Gilad et al., 2014; Meirovithz et al., 2012), perhaps via specifically tuned neurons (Kagan, Gur, & Snodderly, 2008). Importantly, however, these effects cannot be considered as components of a continuous processing because during long fixation periods MS only perturb cortical representations (in V1), which has to be recomputed (during >100 ms) after each MS (Gilad et al., 2014; Meirovithz et al., 2012). Resetting processing in V1 by MSs (and likely also LSs) suggest that V1 is involved primarily in the processing of local visual details within each ROI during each fixational pause and less in global scene processing.

4. Saccade and drift control schemes

The scheme presented above entails two control tasks for the visual system. It has to control the shift of gaze from one ROI to another, using saccadic (S) movements, and it has to control visual acquisition in each ROI, via drift (D) motion. There is no doubt that LSs are controlled by the visual system, and the accepted notion is that this control is a retino-motor control (Fig. 3A); that is, the control is based on ex-afferent (i.e., visual) retinal information obtained at the retina during the current or previous fixational pauses (Findlay & Brown, 2006; Sereno & Rayner, 1992; Shen & Paré, 2014; Zangemeister, Sherman, & Stark, 1995). In principle, MSs may be controlled via their motor behavior per se, for example, by the amount of integrated ocular motion conveyed via re-afferents (e.g., muscle proprioceptors; Fig. 3B), or, similar to LSs, by retina-acquired visual details (Fig. 3A). In agreement with our analysis above, and with the conclusion that MSs are simply small saccades, experimental evidence indicate that LSs and MSs are controlled by the same mechanism, and the mechanism is based on a retino-motor control scheme (Engbert & Mergenthaler, 2006; Ko, Poletti, & Rucci, 2010). The LS–MS common loop is referred to here as a saccade-loop (Fig. 3C–F, S-loop). Importantly, we use here a single 'conceptual' loop to describe the control of Ss; in practice, however, retino-motor control is likely to be implemented via more than one neuronal loop (Shen & Paré, 2014).

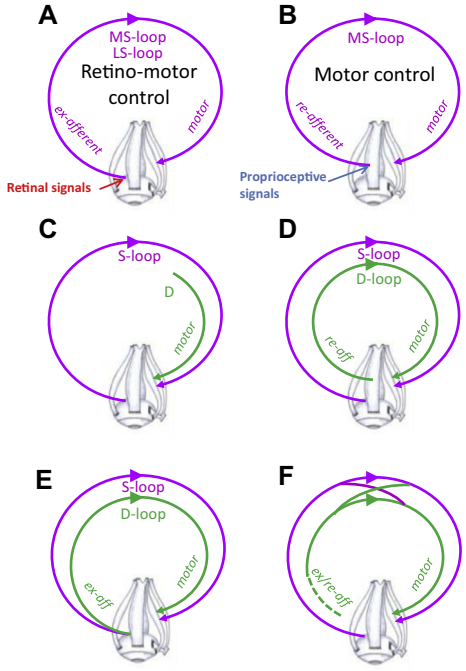

Fig. 3. Control schemes for LSs, MSs and Ds. (A) Retino-motor control scheme for LSs or MSs. The sensory pathways of the loop originate at the retina and convey ex-afferent (visual) information. The motor pathways innervate the ocular muscles. (B) Motor control scheme for MSs. The sensory pathways of the loop originate at the ocular muscles and convey re-afferent (proprioceptive) information. (C–F) Saccades (S; LSs and MSs) are controlled in the same retino-motor scheme. (C) Ds result from an uncontrolled random walk process, driven by muscular or neuronal noise (open-loop scheme). (D) Ds are controlled within a motor control loop. (E) Ds are controlled in a retino-motor control loop. (F) Ds are controlled in motor or retino-motor loop. The two control loops, D and S, interact in the brain.

The control of the D is an open question. Three schemes had been suggested. In one, D results from an uncontrolled random walk process, driven by muscular or neuronal noise (Fig. 3C, green) (Carpenter, 1988). In the second scheme D is controlled by motor variables (Fig. 3D), possibly for maintaining predetermined movement statistics (Engbert & Mergenthaler, 2006). In the third scheme D is controlled by retinal information (Fig. 3E), possibly for tuning D's velocity and direction according to visual details (Ahissar & Arieli, 2012). The two (conceptual) control loops, S-loop and D-loop, may be interacting (Fig. 3F) such that D is affected by S variables and S by D variables (Engbert & Mergenthaler, 2006). Note that the schemes described above are not mutually exclusive; for example, D can be controlled by both motor and visual variables.

Although all these schemes are plausible, the interaction scheme (Fig. 3F) is currently probably the leading candidate. Accumulated evidence indicate that while the gaze is known to be actively maintained within an ROI, once it reached there, there is no clear direction in the cause-and-effect relations between MSs and D during this process; in some contexts MSs respond to D processes and in other contexts it is the opposite (Rolfs, 2009a). Moreover, based on accumulated behavioral and neuronal data, the superior colliculus had been proposed as one neuronal station in which these bidirectional interactions occur, as part of one process aiming at keeping the gaze within the ROI (Rolfs, 2009b). According to the framework we propose here, the interacting control of S and D aims at optimizing the scanning of visual details (by D) and redirecting the gaze (by both MS and LS) according to, among other factors, the scanned details. Naturally, also in our scheme the interactions between D and MS will be stronger than those between D and LS, given the overlap of the ROIs before and after an MS, and the lack of such overlap with LSs.

5. Testable predictions of the alternative control schemes

Which of the plausible control schemes is consistent with empirical data can be tested by specific predictions of each. A list of such predictions, for specific experiments, is presented in Table 1. In experiment A, the temporal interval between a given MS and its preceding S (LS or MS) is measured while the amount of information acquired during this interval is manipulated and measured. This can be done using protocols similar or analogous to the reading and comprehension protocol (Sereno & Rayner, 1992). Inverse dependency between the two (Table 1, result 2) would indicate a retino-motor control scheme of MSs, and thus a common mechanism for S (LS and MS) control (Fig. 3A, C–F). In experiment B, a motion-induced blindness (MIB) like protocol is used, in which background dots move coherently (Bonneh, Cooperman, & Sagi, 2001), and their speed is manipulated. A retino-motor control loop of D predicts that D speed should be

Table 1
Predictions of specific experiments. ISI-S, inter-saccadic-interval from any S to any S (LS or MS to LS or MS); ISI-MS, inter-saccadic-interval to MS (from MS to MS or LS to MS). A–F (two right columns), schemes in Fig. 3.

	Experiment	Results		Consistent	Inconsistent
A	Measure ISI-MS dependence on acquired visual information	1	No dependence	B	A, C–F
		2	Inverse dependence	A, C-F	B
B	MIB protocol, manipulate background mask speed, measure dependence of D speed on mask speed	3	No dependence	C, D	E
		4	Inverse dependence	E, F	C, D
C	(only if Result #4 is obtained) MIB protocol, manipulate D speed by changing mask speed, measure dependence of ISI-S on D speed, everything else being equal	5	No dependence	C–E	F
		6	Inverse dependence	F	C–E
D	Measure dependence of D speed on acquired visual information	7	No dependence	C, D	E
		8	Dependence	E	C, D

determined according to retinal slip speed. Thus, an inverse dependency between dot's and D's speeds is predicted (assuming that the loop tries to maintain the retinal speed at a certain range). If such a dependency is not found, control of D may be implemented within an open-loop (Fig. 3C) or a motor-loop (Fig. 3D) scheme.

Experiment C can be conducted only if result 4 is obtained for experiment B, namely, that D speed reacts to dots' speed. If this is the case, the interactions between the D and S loops can be tested by manipulating dots' speed. An inverse relation between D speed and ISI (between any two Ss) is consistent with the existence of interactions between the D and S loops: with everything else being equal, increasing D speed (within its natural working range) will speed up the acquisition of visual details and this ISI should shorten.

Note that the loops schematized here are 'conceptual' loops. That is, in practice each loop may be implemented by several, interconnected loops. Also, note that not all components of each scheme are tested in every prediction and thus consistency or inconsistency in one test is not sufficient for characterizing the comprehensively consistent scheme or the entirely inconsistent scheme. A comprehensively consistent scheme should be consistent with all tests.

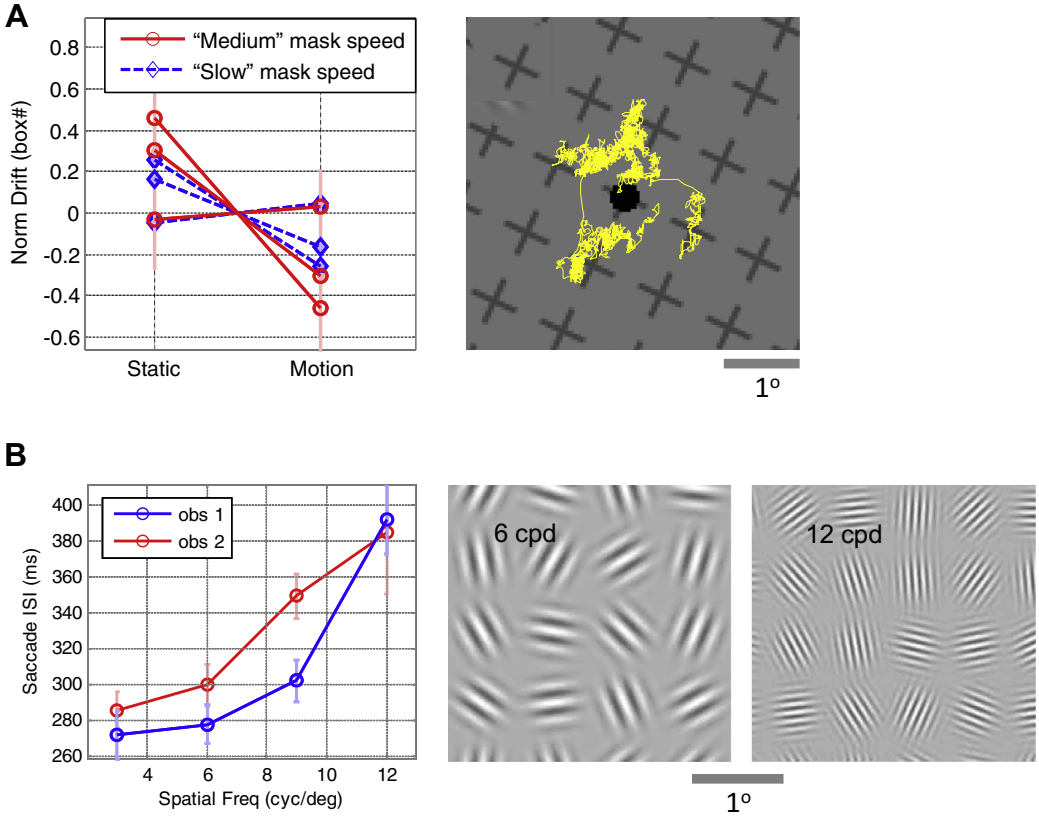

Fig. 4. Preliminary tests of predictions of different control schemes. (A) The effect of stimulus motion on drift during continuous fixation. Observers ($N = 6$) fixated on a small fixation point for 2 min periods, repeated 4 times, with a background of either a static uniform luminance (gray, 30 cd/m^2) or a rotating square grid mask (right panel; 7 × 7 elements, ~6°×6° see (Bonneh et al., 2010) experiment 1). The left panel depicts the individual data of the normalized box-counting drift, averaged across 1 s bins, after strictly removing and adjusting for all traces of saccades (0.01° boxes, sliding window of 100 ms; (Engbert & Mergenthaler, 2006). Data for "slow" (blue, 3 observers) and "medium" (red, 3 observers) motion speeds are shown (see main text for details). (B) Preliminary results for the effect of spatial frequency on inter saccade interval during free viewing. In each trial a Gabor array similar to that shown on the right was presented for 10 s for free viewing. Spatial frequency (Gabor wave length, fixed envelope) was randomly varied across trials. The left panel show the average and SEM ($n = 12$ trials) of inter-saccade interval (ISI-S) as a function of spatial frequency, for two observers. The work was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki); informed consent was obtained from each participant.

6. Preliminary tests of the candidate control schemes

A retino-motor control of D is supported by preliminary data showing that D speed is affected by visual onsets in a similar time course as S rates and with a similar dependency on contrast and previous events (Bonneh et al., 2014; Rolfs, Kliegl, & Engbert, 2008; Stampe & Reingold, 2002).

As a sanity check for the more specific predictions presented here, we re-analyzed existing data from our on-going and previous experiments. To address the predictions suggested by Experiment-B we analyzed data from experiments in which observers had to fixate on a black dot (0.3°) surrounded by either a blank screen or a rotating mask of crosses (Fig. 4A, right panel) (Bonneh et al., 2010). Three observers were tested on two mask speeds: "slow" (maximum of 1.1 deg/s, ~0.25 deg/s at the region covered by the ocular traces around fixation, Fig. 4A right panel) and "fast" (maximum of 26.5 deg/s, ~6.5 deg/s around fixation). Three additional observers were tested on one mask speed, "medium" (maximum of ~16 deg/s in the image, ~4 deg/s around fixation). We compared the speed of D in these conditions. We assessed D speed at two time scales: (1) mean speed per 100 ms, using the box-counting method (Engbert & Mergenthaler, 2006), which ignores repetitions through the same geometrical location and filters out very small fluctuations, and (2) instantaneous speed between two adjacent samples, which measures speed more directly, but might be more susceptible to measurement noise. Using box-counting we found that the "fast" mask motion produced no consistent effects (3 observers). However, the "slow" and "medium" speed masks (Fig 3A, blue and red, respectively) reduced the amount of drift significantly in 4 observers (*t*-test across bins, $p < 0.05$ for each of these observers), while 2 observers (one from each group) showed no difference between conditions. Similar results, but with a smaller magnitude, were obtained for the instantaneous drift speed measure. These preliminary data suggest that stimulus motion usually reduces drift motion speed when its speed is not too distant from the drift speed range, and has a non-consistent effect otherwise.

We also used our preliminary data to address the experiment suggested in Experiment-C. We analyzed the dependency of ISI-S on the spatial frequency of the image. A full field array of 20×15 Gabor patches with random orientation (Fig. 4B) was presented for 10 s trials of free viewing, while the spatial frequency was varied (3–12 cyc/deg) randomly between trials by modulating the Gabor wave length, keeping a constant envelop ($\sigma = 0.4°$) and spacing (1.2°). Our preliminary analysis (data from two observers shown in Fig. 4B) shows that, on average, ISI-S increases with the spatial frequency, suggesting that ISI-S might indeed increase with the amount of information acquired in each fixational pause.

Modulation of ISIs and MS amplitudes, as a function of the visual stimulus, were also observed previously. Deubel and Elsner found that when subjects had to detect static near-threshold low frequency gratings under unconstrained viewing conditions, their detection was preceded by a larger probability for a MS; the amplitudes of the MSs were affected by the spatial frequency of the stimulus (Deubel & Elsner, 1986). These results suggest that MSs add transients to retinal illumination and thus, when in the appropriate kinematic regime, can facilitate detection of near-threshold contrasts. Similar MS-induced transients may be involved in the reappearance of scene components, such as in Troxler fading (Martinez-Conde et al., 2006) or motion-induced blindness (Bonneh et al., 2010). While these results are not directly relevant to the way supra-threshold visual details are encoded at the retina, the dependency of MS amplitude on visual details further supports the closed-loop control of MSs, likely together with LSs (Hafed & Krauzlis, 2012; Rolfs, 2009b).

During free viewing of natural scenes MSs tend to prefer consistently-fixated (presumably informative) regions (McCamy et al., 2014). These results may be considered inconsistent with our preliminary results showing that longer ISIs (i.e., less MSs on average) occur when viewing high frequency images, which may be considered conveying more information compared with lower frequency images (Fig. 4B). However, direct comparison between the two studies is not possible at this stage because "informativeness" was defined by McCamy et al. by the frequency of LSs to that region and not by the visual details contained in the region. On the other hand, McCamy's results are consistent with the suggestion that LSs and MSs serve the same purpose – redirection of the gaze. In that sense, MS-redirection should indeed obey the same principles (and rates) as LS-redirections, regardless of the nature of local processing in each ROI.

To summarize, our preliminary analysis suggests that the predictions we listed are testable. Future experiments thus can discriminate between potential control schemes of saccades and drift and suggest specific algorithm for the implementation of active vision in humans.

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