

Presaccadic motion integration drives a predictive postsaccadic following response

Sunwoo Kwon

Brain and Cognitive Sciences, University of Rochester,
Rochester, NY, USA
Center for Visual Science, University of Rochester,
Rochester, NY, USA



Martin Rolfs

Department of Psychology,
Humboldt-Universität zu Berlin, Berlin, Germany
Bernstein Center for Computational Neuroscience,
Humboldt-Universität zu Berlin, Berlin, Germany



Jude F. Mitchell

Brain and Cognitive Sciences, University of Rochester,
Rochester, NY, USA
Center for Visual Science, University of Rochester,
Rochester, NY, USA



Saccadic eye movements sample the visual world and ensure high acuity across the visual field. To compensate for delays in processing, saccades to moving targets require predictions: The eyes must intercept the target's future position to then pursue its direction of motion. Although prediction is crucial to voluntary pursuit, it is unclear whether it is an obligatory feature of saccade planning. Saccade planning involves an involuntary enhanced processing of the target, called presaccadic attention. Does this presaccadic attention recruit smooth eye movements automatically? To test this, we had human participants perform a saccade to one of four apertures, which were static, but each contained a random dot field with motion tangential to the required saccade. In this task, saccades were deviated along the direction of target motion, and the eyes exhibited a following response upon saccade landing. This postsaccadic following response (PFR) increased with spatial uncertainty of the target position and persisted even when we removed the motion stimulus in midflight of the saccade, confirming that it relied on presaccadic information. Motion from 50–100 ms prior to the saccade had the strongest influence on PFR, consistent with the time course of perceptual enhancements reported in presaccadic attention. Finally, the PFR magnitude related linearly to the logarithm of stimulus velocity and generally had low gain, similar to involuntary ocular following movements commonly observed after sudden motion onsets. These results suggest that presaccadic attention selects motion features of targets predictively, presumably to ensure

successful immediate tracking of saccade targets in motion.

Introduction

Saccade planning is associated with a perceptual enhancement of the saccade target, called presaccadic attention (Deubel & Schneider, 1996; Kowler, Anderson, Doshier, & Blaser, 1995; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011; White, Rolfs, & Carrasco, 2013). The orientation sensitivity and perceived contrast for targets immediately before saccades are increased (Rolfs & Carrasco, 2012). The tuning for stimulus orientation has also been found to sharpen specifically at the saccade target (Ohl, Kuper, & Rolfs, 2017), and there is an enhancement for high spatial frequency features (Li, Barbot, & Carrasco, 2016). The enhancement associated with presaccadic attention is involuntary and occurs even when contrary to task demands. For example, presaccadic enhancement is unavoidable even when it would be beneficial to deploy attention to other locations in the scene (e.g., by cueing a nontarget location before the saccade; Deubel, 2008; Montagnini & Castet, 2007). The timing of presaccadic enhancement is brief, peaking 50–100 ms before saccades (Deubel, 2008; Li et al., 2016; Ohl et al., 2017; Rolfs & Carrasco, 2012; Rolfs et al., 2011). In the current study, we asked what role presaccadic attention might play in

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selecting the motion features of saccade targets and if that would influence slow eye movements that are sensitive to motion.

When saccades are planned to moving targets, the resulting smooth eye movements for postsaccadic tracking can be predictive (Heinen, Badler, & Ting, 2005; Kowler, 1989; Kowler, Aitkin, Ross, Santos, & Zhao, 2014; Spering, Schütz, Braun, & Gegenfurtner, 2011). Voluntary tracking of moving targets typically involves smooth eye movements that nearly match the direction and velocity of the target (Lisberger & Westbrook, 1985; for review, see Lisberger, Morris, & Tychsen, 1987). Humans are able to track targets with a linear dependence on speed that has gain close to unity for speeds up to 45° of visual angle (dva) per second (Buizza & Schmid, 1986; Tychsen & Lisberger, 1986). But tracking targets across visual scenes typically involves a combination of both saccadic and smooth pursuit movements (Kowler, 2011; Lovejoy, Fowler, & Krauzlis, 2009; Zhao, Gersch, Schnitzer, Doshier, & Kowler, 2012). The interaction between saccades and pursuit is of particular interest because it can be predictive. When a saccade is made to a moving target, there is a postsaccadic enhancement of eye velocity to match target velocity even against competing motion from distractors and even from the first moments after the saccade offset (Case & Ferrera, 2007; Gardner & Lisberger, 2001; Lisberger, 1998; Schoppik & Lisberger, 2006). The ability to match target velocity from saccade landing reflects that the computation of target velocity must bypass the visual latency that would be necessary if the motion were estimated from the foveal view of its motion after the saccade and rather that it must rely on information gained peripherally before the saccade. Thus, during voluntary tracking, the visual system can select peripheral target motion to predictively guide pursuit movements. However, it is unclear to what extent predictive smooth eye movements would occur when there is no task demand to track motion, for example, if a saccade were simply made to a stationary aperture that contained motion. If it did, this would mean that presaccadic attention not only enhances perception for saccade targets, but automatically engages prediction for their future locations based on motion.

Smooth eye movements also occur involuntarily as is the case during ocular following for wide field motion stimuli (Gellman, Carl, & Miles, 1990; Hietanen, Price, Cloherty, Hadjimitsakis, & Ibbotson, 2017; Miles, Kawano, & Optican, 1986). Whereas pursuit movements can track target motion over a wide range of speeds, ocular following movements typically exhibit much lower gain ranging from 5% to 30%, and they show a shallow dependence on speed, being related to the logarithm of speed rather than to linear speed (Miles et al., 1986). But despite the lower gain, ocular

following responses (OFR) can be highly indicative of what stimulus was observed (Simoncini, Perrinet, Montagnini, Mamassian, & Masson, 2012). Recent studies also show that wide field stimuli are not necessary to drive responses, and in fact, OFR pools motion preferentially from more foveal locations (Quaia, Sheliga, FitzGibbon, & Optican, 2012) and can be driven even by stimuli only 4 deg² in size (Quaia et al., 2012). Further, recent studies show that OFR is not purely reflexive, but can be influenced by higher-level factors, such as selective attention (Souto & Kerzel, 2014). These findings raise the question of whether or not an involuntary selection of motion features, as we might expect during presaccadic attention, could influence OFR.

In the current study, we tested whether the presaccadic attention during a saccade to a stationary aperture containing motion would influence predictive following movements. Human participants performed a center-out saccade to one of four peripheral-motion apertures. The net motion in the visual field was balanced, on average, by selecting, at random, for each aperture independently, motion that was either clockwise or counterclockwise relative to the center-out saccade. Because following responses are known to have latencies as short as 70 ms in humans (Gellman et al., 1990) and can be driven by foveal motion (Mukherjee, Liu, Simoncini, & Osborne, 2017; Quaia et al., 2012), we included a subset of trials in which the target disappeared during saccade flight. In these trials, the target motion never appeared at the fovea, and thus, we could isolate the presaccadic contribution of target motion to any postsaccadic following responses (PFR). We found that slow eye movements before the saccade were not influenced by the target, but there was a low-gain PFR that aligned with target motion and was present immediately from saccade offset across a range of experimental conditions. To better quantify this effect, we first examined how the spatial certainty of the stimulus aperture, ranging from high certainty when marked by a high-contrast outline to low certainty when Gaussian windowed, constrained following responses. We also considered to what extent the temporal window for integration of motion that drove the PFR was consistent with the brief (50–100 ms) timing of presaccadic attention. Last, we examined the dependence of PFR on stimulus velocity to consider to what extent the following responses are consistent with pursuit or ocular following.

Material and methods

Complete data sets were obtained from a total of eight participants (18–22 years old, four females and

four males) who had normal or corrected-to-normal vision and participated in exchange for monetary payment. The data of an additional three participants who required frequent recalibration of eye position due to head movement throughout the first experimental session were excluded from analysis. All participants were naïve as to the research aims, and all provided written informed consent. All procedures were approved by the research subjects review board at the University of Rochester.

Apparatus

Stimuli were generated using the Psychophysics toolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) in MATLAB 2015b (MathWorks, Natick, MA) on a PC computer (Intel i7 CPU, Windows 7, 8 GB RAM, GeForce Ti graphics card). They were presented on a gamma-corrected display (BenQ X2411z LED monitor, resolution: $1,920 \times 1,080$ p, refresh rate: 120 Hz, gamma correction: 2.2) that had a dynamic luminance range from 0.5 to 230 cd/m^2 at a distance of 95.25 cm in a dark room. Brightness on the display was set to 100 and contrast to 50, and additional visual features of the monitor, such as blur reduction and low blue light, were turned off. Gamma corrections were verified with measurement by a photometer. Eye position was recorded continuously at 220 Hz using an infrared eye tracker (USB-220, Arrington Research, Scottsdale, AZ) with eye position collected from infrared light reflected off of a dichroic mirror (part #64-472, Edmunds Optics, Barrington, NJ). The accuracy of the Arrington eye-tracking system is 0.25 dva with a precision of 0.15 dva. To minimize any potential head movements, participants performed the task using a bite bar.

Stimuli, task, and procedure

All four experiments used generally the same stimuli, task, and procedure (deviations from these defaults are described in detail below). We first describe the basic paradigm and then provide details for how other paradigms differed to address specific questions. Participants performed a cued saccade task toward peripheral motion apertures (Figure 1A). Each trial was initiated by fixation of a small dot (0.5 cd/m^2 center, 230 cd/m^2 surround) with a radius of 0.25 dva for 50 ms, presented on a gray background (115 cd/m^2). Fixation had to stay within 2.0 dva of the fixation point or the trial was aborted and followed by a 2-s time out. After a variable fixation period of 150–200 ms, four dot motion apertures (each 4 dva in diameter and 5 dva in eccentricity) appeared in the periphery. The four

apertures were presented either in a square or a diamond configuration (Figure 1B). To avoid stereotyped eye movements, we varied saccade directions across trials, including horizontal, vertical, or oblique axes. However, we also anticipated that smooth movements would be limited within the extent of the aperture and, thus, desired to use the largest aperture possible. As such, we used four apertures on any given trial, but from trial to trial, we varied between a square and diamond configuration of the apertures to sample across a total of eight locations. A movement cue (white bar, 1 dva in length) was used to indicate the target dot motion aperture for a saccade. Of particular note, *the motion itself or its direction was irrelevant to the task*. The movement cue appeared for 50 ms, simultaneously with the dot motion apertures, which remained present for 500 ms. Each aperture contained 100 dots moving at a speed of 6.75 dva/s, and each dot had an infinite lifetime in which the dots were replotted on the opposite edge of the aperture once they crossed its boundary. The motion within the aperture was 100% coherent and ran along a direction that was tangential to the line from the fixation point to the aperture. For each aperture, the motion was selected independent of the other apertures in one of the two tangential directions, either in a clockwise or counterclockwise direction relative to the screen center.

Participants were instructed to make a saccade to the peripheral aperture as quickly as possible following the movement cue. A saccadic grace period (i.e., a maximum latency) was allowed for participants to initiate the saccade as indicated by their eye position leaving the 2-dva fixation window. If the participant initiated the saccade after that latency, then the peripheral motion aperture disappeared in saccade flight (timed within the 120-Hz display refresh rate) and a feedback tone was played during the intertrial interval to indicate the saccade was too slow (150 Hz, 100 ms duration) at 500 ms after saccade landing. These trials provided a crucial condition to examine eye movements when the target motion could only be viewed peripherally as the target was removed prior to the saccade bringing the aperture to the fovea. For those saccades initiated during the grace period, the stimulus remained visible with continued motion, and a different tone was played (500 Hz, 100 ms) to indicate the saccade had occurred within the grace period.

To ensure that the motion stimulus was removed during the saccade in a subset of trials such that no foveal motion was present upon landing, we applied a staircase procedure on the saccadic grace period. Each daily session began with a grace period set at a default of 300 ms. If the subject made a saccade with a latency shorter than the grace period, then the saccade grace period was reduced by 10 ms. If the subject made a late saccade (counted as an error), then the grace period

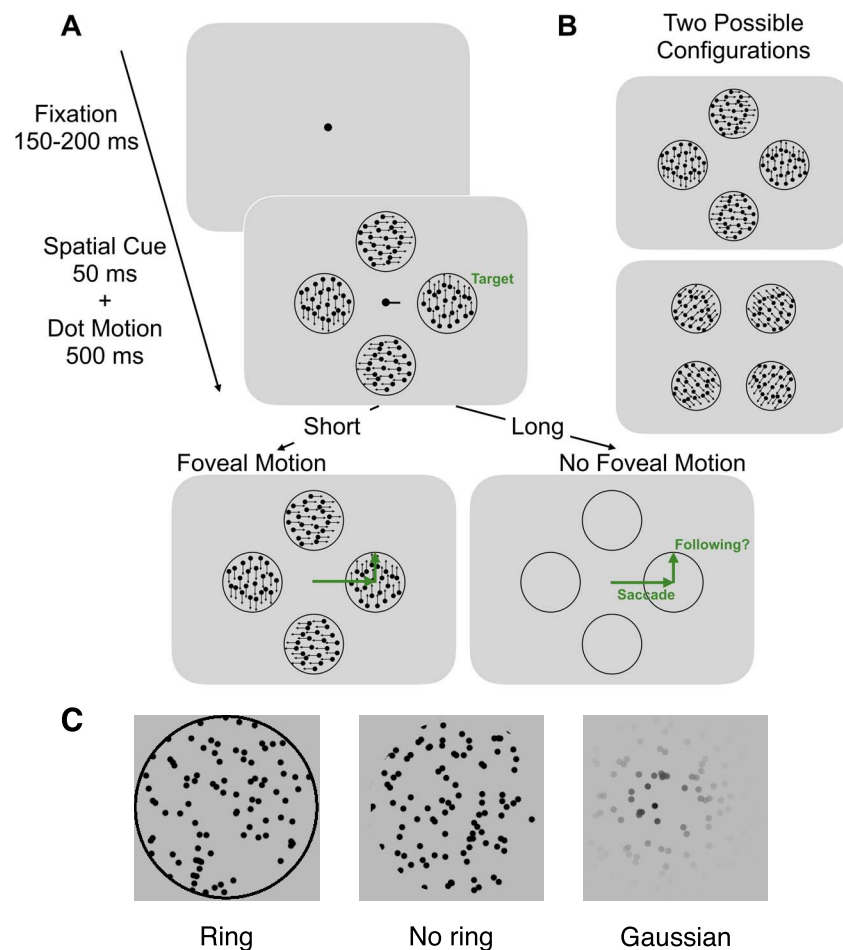


Figure 1. Experimental paradigm. (A) In each task trial after a fixation period, participants were presented with four equally eccentric motion apertures. Dot-motion apertures contained 100% coherent motion along a randomly assigned direction (clockwise or counterclockwise assigned independently for each aperture) that was tangential to the center-out saccade to the aperture. The spatial cue, which indicated the target aperture, appeared simultaneously with the apertures for 50 ms, and the participant was instructed to initiate a saccade toward it as quickly as possible. An adaptive staircase was used to adjust the grace period allowed to make the saccade. If the participant made a saccade after the grace period, stimuli disappeared during saccade flight such that no stimulus motion was ever presented foveally. (B) To sample from horizontal, vertical, and oblique saccade directions, the four motion apertures could appear with equal probability from trial to trial either in a square or in a diagonal configuration. (C) Three different bounding apertures were tested (panel C) that varied in their spatial uncertainty (dot stimuli shown as they appeared in a single video frame of the task).

was increased by 10 ms. An adaptive staircase method (three down, one up; Levitt, 1971) was applied to the saccade latency grace period, resulting in about 79.3% of the trials with stimuli present (foveal motion) upon landing and 20.7% of the trials with stimuli absent (no foveal motion) upon landing.

Each participant completed two experimental sessions (1–1.5 hr each) for each of the four experiments. The order in which the four experiments were completed was randomized across the participants such that each of the four experiments occurred with equal frequency across participants at each of the eight session numbers and such that there was a complete set of the four experiments within the first four and second four sessions for each participant.

Experiment 1: Spatial uncertainty

We first examined eye movements after saccades to motion apertures to establish if there was a PFR and to determine how visual cues manipulating the spatial certainty of the motion aperture's location influenced the magnitude of the PFR. To this end, three different types of motion dot aperture stimuli were used, which we refer to as the ring, no-ring, and Gaussian condition (Figure 1C). In the ring condition (cf. White et al., 2013), we enclosed each motion aperture with a black ring (luminance of black ring: 0.5 cd/m², ring line width: 0.065 dva, diameter: 4 dva). A previous study found that the location of an aperture is perceived as shifted along the direction of motion contained in the

aperture (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990), which is associated with localization errors along that motion direction in saccades to the aperture (Kosovicheva, Wolfe, & Whitney, 2014). The recent study (Kosovicheva et al., 2014) further compared two aperture conditions, one with a “hard aperture” that dropped stimulus contrast to zero at the boundary and the other in which contrast dropped gradually following a Gaussian aperture. They found that saccadic errors were most prominent when the aperture was Gaussian smoothed. This suggests that reducing the salience or spatial certainty of the bounding aperture increases the influence of the contained motion on eye movements. Therefore, we considered two other conditions that varied the salience of the ring bounding the motion aperture. In the no-ring condition, there was no aperture outline, yet the dot motion was contained within the defined stimulus radius (dots disappeared on one edge and reappeared at a random position on the opposite side). In the Gaussian condition, we applied a Gaussian envelope on top of the no-ring condition to create a gradient in dot contrast from the center of the aperture (Gaussian sigma: 1 dva).

Experiment 2: Duration of presaccadic motion integration

We next examined what duration of motion integration prior to the saccade was necessary to produce any measurable effects on postsaccadic following responses. The behavioral task was the same as explained for Experiment 1 and focused on the Gaussian condition. Instead of presenting coherent motion stimuli for the entire trial, the motion stimuli were shown with 0% coherence initially (each dot's motion direction was drawn randomly) and then transitioned to 100% coherent motion at one of a set of time points relative to the onset of the central movement cue (0, 100, 150, 163, 175, 188, 200, 213, 225, 238, 250, or 300 ms). We then binned the onset of motion relative to the onset of the saccade for subsequent analyses.

Experiment 3: Critical interval of presaccadic motion integration

We next examined what temporal interval of motion integration prior to the saccade produced the strongest postsaccadic following responses. Again, we focused on the Gaussian condition. The motion stimuli were shown with 0% coherence at the beginning of each trial (each dot's motion direction was drawn randomly). We then introduced a 100% coherent motion pulse (the

direction was selected at random for each aperture, either clockwise or counterclockwise relative to the screen center). During this pulse, individual dots changed the direction of motion from a randomly assigned direction to that of the pulse (no replotting of their spatial positions, only a change in dot velocity). The motion pulse began at one of a set of time points after motion onset (0, 50, 100, 150, 200, or 250 ms) and had 100 ms duration. Because the saccade onset varied, we were able to bin in what presaccadic epoch the 100-ms motion pulse completed for subsequent analysis.

Experiment 4: Dot motion velocity

Finally, we varied the velocity of stimuli in the motion aperture to determine if postsaccadic following responses tracked motion speed linearly, similar to that of pursuit movements at slower velocities (Buizza & Schmid, 1986; Tychsen & Lisberger, 1986). The stimuli and the behavioral task were the same as in the Gaussian condition of Experiment 1, but we varied the dot motion speed in the apertures randomly from trial to trial, using 2.0, 3.0, 4.5, 6.75, 10.12, or 15.18 dva/s.

Eye-movement recording

Eye-position data was collected as participants performed saccades from fixation to the peripheral target. Raw horizontal and vertical eye position signals were smoothed off-line using a median filter (± 2 samples, ± 8.8 ms) and convolved with a Gaussian kernel (5 ms half width, out to 3 SD , -15 to 15 ms) to minimize high-frequency noise. The horizontal and vertical gain of the eye tracker was calibrated by asking each participant to view a set of localized face images subtending 2° in diameter and Gaussian aperture (sigma = 0.5 dva) that were displayed on the video monitor at fixed positions and also a localized white fixation point subtending 0.3° diameter at the center of the screen to fine-tune the origin of the calibration as described previously (Mitchell, Reynolds, & Miller, 2014; Nummela et al., 2017). The behavioral task control subsampled eye position using the ViewPoint Matlab toolbox (Arrington Research) at the display refresh rate (120 Hz) to initiate gaze-contingent task events (removal of stimuli for saccades performed after the grace period, auditory tones to provide feedback). Temporal events from stimulus presentation and video frame flips were logged in the ViewPoint data file with raw eye-position data in order to validate the timing of stimuli with eye-position data.

For off-line detection of saccadic eye movements, we used an automatic procedure that detected deviations in 2-D eye-velocity space (Engbert & Mergenthaler,

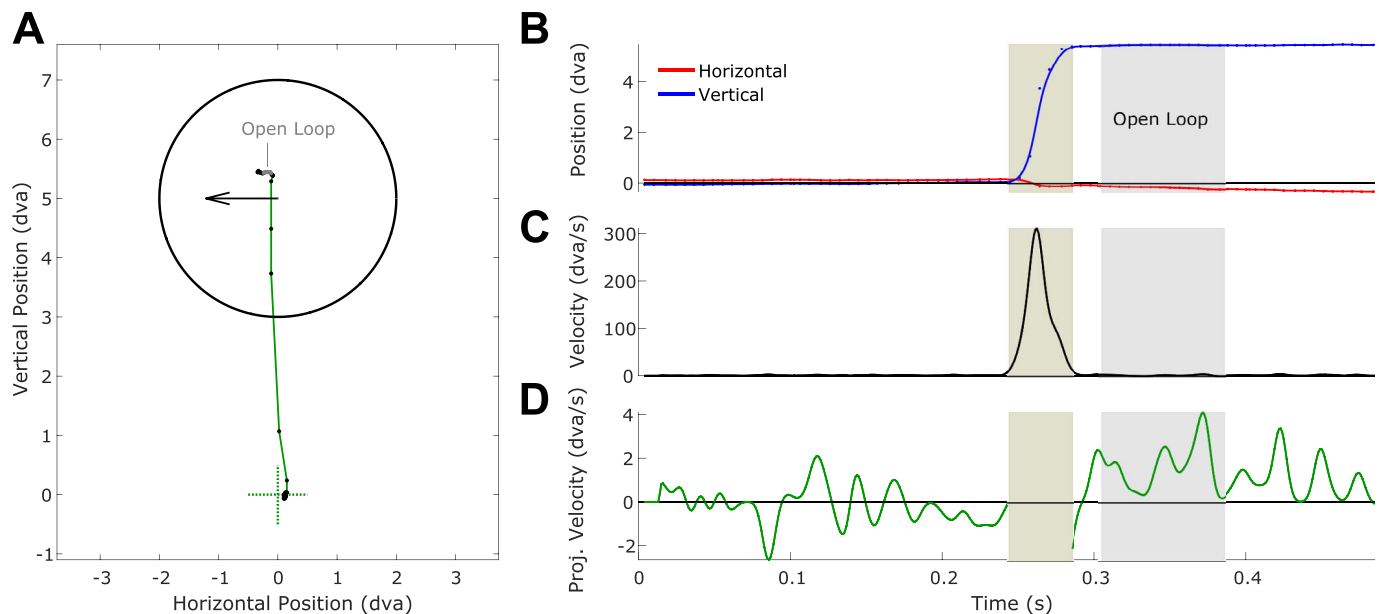


Figure 2. Eye movement traces from a single trial demonstrate a drift along the target motion. (A) The spatial trajectory for one example saccade from the fixation point to one of the four peripheral motion apertures is shown from acquisition of the fixation point up to 200 ms after saccade offset. The black dashed cross indicates fixation location, and the black circle reflects the aperture location. The black dots represent raw eye-position samples from the eye tracker. The trajectory of dots in the aperture during the 200 ms after saccade offset is represented by the amplitude and direction of the black arrow. Eye position drifts along the same direction for this trial but with reduced amplitude relative to the actual dot displacement in the same interval. The open-loop period from 20 to 100 ms after saccade offset is indicated in gray. (B) The raw horizontal and vertical eye position for this example trial (dots, red: horizontal, blue: vertical) along with the smoothed position traces (lines) are shown. (C) The 2-D eye velocity is shown for this trial with the interval flagged as a saccade indicated in light brown. (D) The eye velocity outside the saccade is shown after being projected (dot product) along the target motion direction. Positive velocities indicate that the eye is moving along the same direction as the target motion.

2006). We computed horizontal and vertical eye velocity by differencing the smoothed eye-position traces. We classified successive eye positions as saccades if they exceeded the median velocity by 20 *SD* for at least 10 ms (Engbert & Mergenthaler, 2006) and merged any two saccadic events into a single saccade if they were separated by less than 5 ms. Saccade onset and offset were determined by the first and last time the 2-D velocity crossed the median velocity threshold. We removed from our analysis any saccades that exhibited extreme curvature in which the integrated path of the saccade (from onset to offset) was larger than 20% of the length of a straight path. This constituted a median percentage of 1.4% of the total saccades detected (range of 0.15% to 10.6% across participants).

Eye movement analysis

We examined if eye velocity tracked the target motion either just prior to the saccade or immediately following saccade offset. Our analyses focused on the 200 ms prior to saccade onset and following saccade offset. Any trials that included a secondary small

saccade within 200 ms of the offset from the larger saccade into the target aperture were excluded in preliminary analyses and are considered in the end of the Results section to determine to what extent they track target motion or are directed back toward the aperture center.

First, to determine if eye velocity tracked the motion in the target aperture, we projected the 2-D eye-velocity traces onto a single velocity trace along the vector of aperture motion. In Figure 2A, the eye position in a single trial is depicted within the target aperture with target motion indicated by an arrow. The corresponding position and velocity traces are shown to the right (Figure 2B and C) along with the velocity projected along the target motion direction in the bottom right panel (Figure 2D). The motion in the target aperture was designed to be tangent to the direction of the center-out saccade in order to minimize the impact of the saccade's velocity on our estimates of the post-saccadic following response. We analyzed the velocity along this tangent direction to determine to what extent it aligned with stimulus motion (same sign) or moved in the opposite direction (different sign). If the eye velocity aligned with target motion, the projected

velocity trace would take on positive values (Figure 2D). We aligned velocity traces to saccade onset or offset and averaged these across trials for each participant to determine the average time course of velocity along the target motion. To average traces across trials (for visualization purposes only), we linearly interpolated and discretized into 1-ms time bins.

To quantify the degree of target tracking in each trial, we computed two vectors, one for the PFR and one for saccade deviation. The vector for the PFR has units of velocity (dva/s) and was computed from the raw (nonsmoothed) eye position in the interval from 20 to 100 ms following saccade offset. The vector for the PFR is the difference between postsaccadic position (x , y) at 100 ms minus the position at 20 ms, divided by the 80-ms time interval between them (dva/s). Of note, any trials in which secondary saccades were detected during the 200-ms postsaccadic interval were excluded from these analyses, and thus, the PFR is related to the mean smooth eye velocity over this interval. The interval chosen to compute the PFR excluded the first 20 ms following saccade offset to reduce any influence from saccade-related movement velocity. As with velocity traces, we projected this vector onto the vector of target motion to produce a single velocity value along the axis of stimulus motion. We term this value the “open-loop” postsaccadic following response. We also considered a later interval (100–200 ms) that we term the “closed-loop” postsaccadic following response as in this time window, postsaccadic visual signals may contribute to the oculomotor response (Lisberger & Westbrook, 1985). The deviation of saccade landing points was computed using the raw (nonsmoothed) eye position at the time of saccade offset relative to the center of the motion aperture. As with the velocity, it was projected onto the target motion axis to provide a single value in dva.

We sought to determine if the PFR could disambiguate the direction of stimulus motion on a trial-by-trial basis. We performed a receiver operating characteristic (ROC) analysis to obtain the area under the curve (AUC) for both the PFR and for the saccade deviation at landing. We sorted trials based on whether the motion aperture contained clockwise or counter-clockwise motion in the target aperture and compared the distributions of resulting postsaccadic response values and saccade landing deviations to determine how well they were separated. We also considered to what extent the PFR tracked target velocity across different conditions and experiments by quantifying its gain. To define the PFR gain, we normalized the velocity computed from the open-loop PFR by the stimulus’ velocity. A value of one would indicate a perfect match of the eye velocity to the target motion, and negative values would indicate eye velocity in the

opposite direction; values of zero would indicate no influence at all.

Results

We measured eye movements following a saccade to a motion stimulus that was bound within a spatial aperture. We analyzed eye velocity around the time of the saccade to determine how it was influenced by stimulus motion in the target aperture. Although the aperture was stationary and we instructed participants only to make a quick saccade to its location, we reasoned that presaccadic stimulus selection might still influence the resulting smooth eye movements to favor the target motion and, thus, influence either PFRs or the landing positions of saccades. In second and third experiments, we further varied the timing of coherent stimulus motion to determine first what duration of motion integration prior to the saccade was necessary to drive PFR and then by using brief pulses to determine what specific presaccadic interval most influenced PFR. In the last experiment, we measured the dependence of PFR on stimulus velocity to determine how following gain varied and to what extent it resembled OFRs or pursuit.

Participants performed the cued saccade tasks comparably well across all experimental conditions. Participants’ saccadic grace period had the mean of 272 ms ($SD \pm 10.8$ ms). The minimum and maximum saccadic grace period was 253.8 and 283.6 ms, respectively. They selected the correct aperture with high accuracy (mean $98.7\% \pm 0.8\%$ SD across participants) and with short saccade latencies (median latency of 260 ± 10 ms SD). We found no significant differences in accuracy or saccade latency as a function of spatial certainty in Experiment 1 or across experimental conditions by comparing Experiments 1–4 as factors. Therefore, we focused our analyses only on correct trials for each condition in the remaining sections of results.

Experiment 1: Varying spatial certainty

Our first experiment compared eye movements across three conditions in which we varied the spatial certainty of the motion aperture (Figure 1C). We presented moving random dot fields either windowed within a high-contrast black ring (high spatial certainty), no ring but the dots contained within a circular aperture, or with the dots’ contrast decreasing toward the edges using a Gaussian aperture (lowest spatial certainty). To isolate the influence of stimulus motion on eye movements from the larger-velocity transients

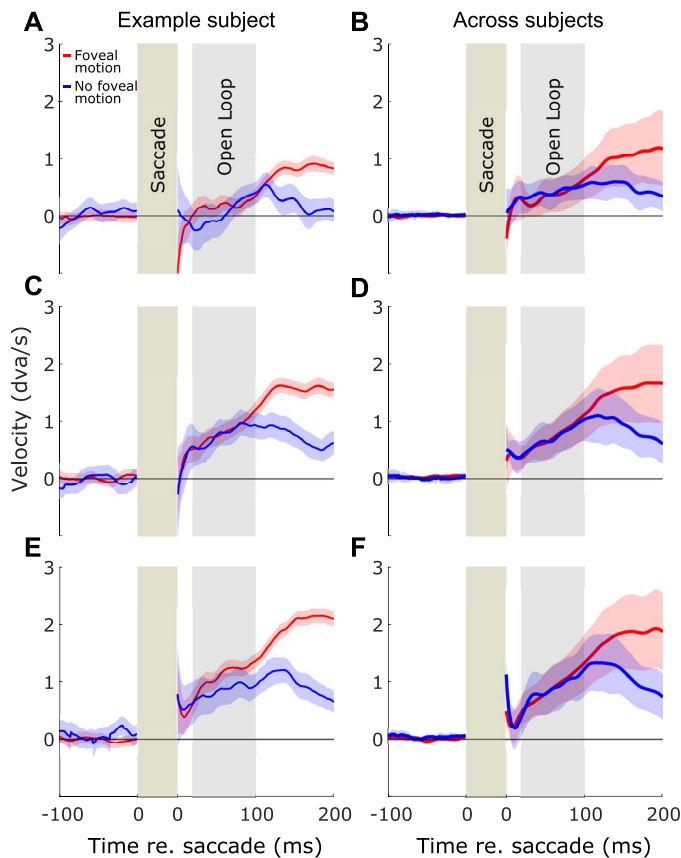


Figure 3. Mean velocity traces as a function of spatial uncertainty. Three different spatial uncertainty conditions were tested: ring (A and B), no-ring (C and D), and Gaussian (E and F), shown in the top, middle, and bottom panels, respectively. (A) For a single example subject, the mean eye velocity is shown projected onto the direction of target motion such that positive velocities indicate following. In the trials in which the participant made a saccade prior to the saccade grace period, the stimuli were still present upon landing (red; foveal motion); otherwise, stimuli were absent upon landing (blue; no foveal motion). We focused subsequent analysis on the open-loop interval from 20 to 100 ms after the saccade. Error bars represent 2 SEM. (B) Mean eye velocity traces across eight participants (same conventions as in panel A). Error bars represent 2 SEM across subjects.

induced when making saccades, we designed our study such that stimulus in the target aperture moved tangentially to the direction of the center out saccade (Figure 1A). After flagging saccades based on velocity criteria (see Methods), we could eliminate those saccadic intervals from analysis and focus on how eye velocity was modulated by target motion in the presaccadic and postsaccadic epochs (Figure 2). Here, we projected the eye velocity along the target motion such that positive values reflected motion consistent with the stimulus and negative values reflected motion opposite. This enabled us to collapse results from

saccades made to each of the eight motion apertures projecting velocity into the direction of target motion.

The eye-velocity traces for one typical participant are shown in Figure 3A; they reveal that the eyes follow the presaccadic stimulus motion upon saccade landing. As shown in the top panel, the average eye velocities are projected onto the target motion direction time locked prior to the saccade onset (−100 to 0 ms) and the saccade offset (0 to 200 ms). Velocity traces are shown for trials in which both the motion stimulus remained present on saccade landing (in red: foveal motion) and the motion disappeared in saccade flight (in blue: no foveal motion). This subset of trials in which the stimulus disappeared in saccade flight provides an important point of comparison for distinguishing what part of the eye movements are predictive because they must reflect motion integration prior to the saccade. In the ring condition (top panel), there exists a weak effect to follow target motion reflected in positive values for the eye velocity projected on target direction after the saccade. It is important to note that this effect occurs even when the stimulus is not present (in blue), and thus, there is no foveal motion to drive the following response. At the same time, the magnitude of the velocity is relatively small compared to the true stimulus speed ($6.75^\circ/\text{s}$), reflecting roughly a 5%–15% gain of the true stimulus motion. Thus, this response is not consistent with the kind of voluntary tracking found in smooth pursuit paradigms. We term this tracking of stimulus motion as a PFR to be careful not to confuse it with a voluntary pursuit.

The eye velocity within the first 100 ms after saccade offset did not differ substantially depending on whether the motion stimulus was present or absent postsaccadically (Figure 3A, red vs. blue mean traces). Due to the latency of motion processing, we anticipate that some postsaccadic interval should not be driven yet by the presence or absence of the foveal stimulus motion. We term this the open-loop (20–100 ms upon saccade offset) response period (gray box). We focus much of our analysis on this period and on the stimulus-absent trials because it reflects the influence of motion integration on eye movements prior to the saccades (i.e., the predictive component of the eye movements). The effects within first 100 ms upon saccade offset are taken as a measure of the presaccadic target motion integration. However, in the closed loop (100–200 ms upon saccade offset), the PFR in stimulus-present and -absent conditions do diverge from each other. The PFR in the foveal-motion condition continues to grow with the new foveal stimulus driving it, whereas PFR in the no-foveal-motion condition starts to decrease.

We found that the PFR increased with the uncertainty of the aperture location. This was evident in a single subject (Figure 3A, top-to-bottom panels) and also across the average velocity traces from eight

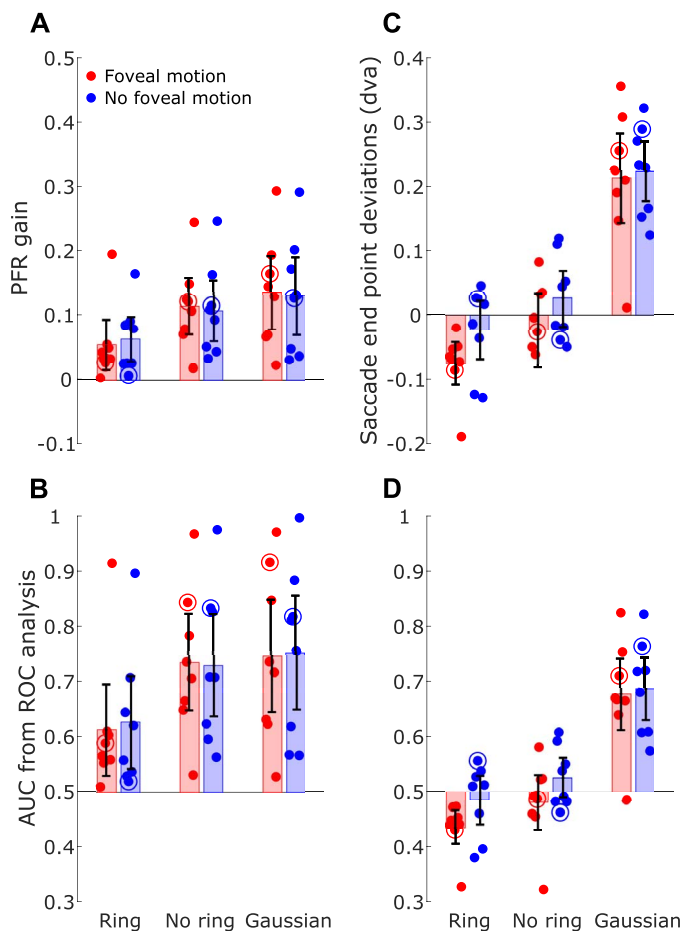


Figure 4. PFR and saccade landing points across participants during the open-loop period. (A) The PFR increased as a function of increasing spatial uncertainty, being strongest for the Gaussian condition. The PFR is shown here as the proportion of pursuit gain (one being perfect following and zero no following) with individual dots representing each participant and the example participant from Figure 3 indicated by the open circle. (B) The AUC from an ROC analysis revealed that PFR responses discriminate motion direction with up to 70% accuracy on a trial-by-trial basis. (C) Saccade landing points were deviated along the target motion direction but only in the Gaussian condition, which had the greatest spatial uncertainty. (D) AUC analysis revealed significant discrimination of target direction based on saccade deviations only in the Gaussian condition. Error bars represent 2 SEM across subjects in all plots.

subjects (Figure 3B, same format). To better quantify the effect, we computed the mean proportion of PFR gain (calculated from the PFR during the open-loop interval divided by the target motion speed) across participants (Figure 4A). For each trial, we computed a summary statistic for the PFR based on the eye position change from 20 to 100 ms after saccade offset along the target direction (see Methods). This measure is highly related to the measured eye velocity but is

estimated from the raw eye position with no filtering or smoothing as a secondary statistic. We found that, overall, there was a net positive effect across subjects (mean across all conditions per subject) consistent with PFR of the target motion in the open-loop epoch, $t(7) = 4.31$, $p = 0.0035$, that differed significantly from zero (no effect of motion on the PFR). We also sought to eliminate any potential influence of saccade landing position on the PFR measures. Thus, we analyzed the PFR for all trials in which saccade endpoint fell within $\pm 0.5^\circ$ of the aperture center and found similar results (as compared to Figure 4A) once saccade end position was restricted to this range. We ran a two-way, repeated-measures analysis of variance (rmANOVA) with spatial certainty and foveal motion condition as factors. We found a significant difference between spatial certainty conditions, $F(2, 35) = 17.73$, $p < 0.0001$, but no significant difference between the foveal-motion versus no-foveal-motion conditions, nor was there an interaction. The PFR gain was largest for the Gaussian condition, which had the highest spatial uncertainty, $t(7) = 4.26$, $p = 0.0037$, similar in the no-ring condition, $t(7) = 4.58$, $p = 0.0026$, and was smallest for the ring condition with the least spatial uncertainty, $t(7) = 3.08$, $p = 0.018$, with changes significant in all three conditions after Bonferroni–Holm correction (Holm, 1979). Thus, spatial certainty of the target aperture appeared to reduce the gain for following along target motion.

To measure how well each participant’s trial-by-trial PFR distinguished target motion direction, we computed an ROC analysis to obtain the AUC on the two distributions for trials with stimulus motion clockwise and counterclockwise (Figure 4B). As shown for the PFR gain, the AUC also increased as the spatial uncertainty was increased. In the Gaussian condition, participants yielded an average above 70% AUC. Although there was substantial interindividual variability, all participants had AUCs above chance level; thus, we can disambiguate what the participant saw, prior to the saccade, based on the PFR immediately upon saccade offset with an average of 70% accuracy.

We also found that saccade endpoints were influenced by target motion but only for the case of greatest spatial uncertainty that included the Gaussian condition (Figure 4C). We computed the saccade landing point by measuring the raw eye position at saccade offset relative to the center of the target aperture. To compute the saccade endpoint deviations, we then measured the saccade landing point along the target motion-direction axis. Therefore, the positive deviations represent landing along the target motion direction, whereas the negative deviations represent landing opposite from the target motion direction. The saccade landing points were, on average, deviated along the target motion direction, $t(7) = 3.23$, $p = 0.0145$.

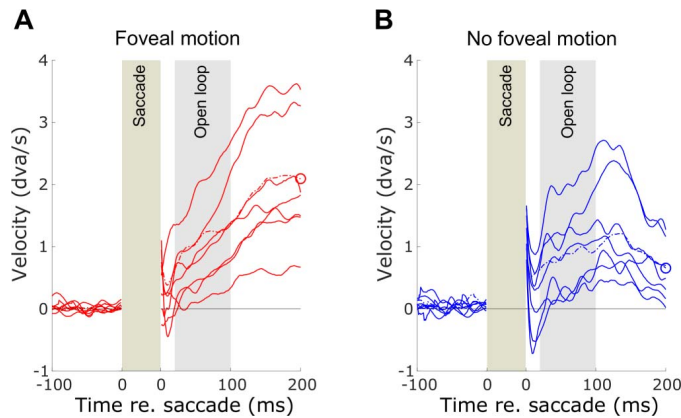


Figure 5. Mean velocity traces (PFR) for each subject in the Gaussian condition. Each colored line represents the mean velocity trace from an individual participant. The dotted line represents the example participant shown in Figure 3. The magnitude of PFR is variable across participants, but the time course was highly consistent and similar in both foveal motion (A) and no foveal motion (B) conditions.

Again, we ran an rmANOVA and confirmed that there was a significant difference in the saccade deviations based on spatial uncertainty conditions, $F(2, 35) = 64.1$, $p < 0.0001$, but no difference due to the presence of foveal motion and no interaction. The effect for saccade landing positions was significant along the direction of target motion for only the Gaussian condition, $t(7) = 7.37$, $p < 0.001$, after Bonferroni–Holm correction as shown in Figure 4C. To observe how well the deviations in saccade landing position distinguish the target motion, we computed the ROC analysis to obtain AUC for the two saccade landing distributions (clockwise and counterclockwise). Saccade landing point AUC was significant in the Gaussian condition, yielding about 70% AUC (Figure 4D).

Due to the random choice of each aperture’s motion direction, our experimental design included subsets of trials that both contained global net motion (same motion direction for each pair of apertures) across the four apertures along the target motion as well as subsets of equally balanced motion (opposite motion direction for each pair of apertures). We examined if the PFR could be influenced by the net motion in the visual field rather than be specific to the saccade target. In the subset of trials with same motion, the motion direction in the aperture opposite from the saccade target had the same direction. In the opposite condition, the motion direction in the aperture opposite from the saccade target had the opposite direction. We performed the same analysis of PFR gain for both same- and opposite-motion conditions and found no appreciable differences between them, $F(1, 82) = 3.29$, $p = 0.074$. If we excluded the same-motion condition to

focus only on the opposite-motion condition, there remained a significant mean effect across subjects for following the target motion, $t(7) = 4.04$, $p = 0.0049$, and a significant effect of spatial uncertainty, $F(2, 35) = 11.84$, $p < 0.001$. This suggests that the PFR we observed in the present experiments was specific to the spatial selection of the target aperture and its motion features, not a result from global motion processing.

The end motion vector of the postsaccadic following and saccade deviations both indicated highly consistent effects across participants but are averaged measures across specific temporal intervals. Therefore, we examined the mean eye velocity traces for all participants individually in the Gaussian condition to determine if the time course of selection was relatively consistent. Although some participants show stronger PFR than others, all of them exhibited similar time courses with positive deflections along the target motion. All subjects showed eye velocity following the target within the open-loop period (20–100 ms) regardless if a motion stimulus was foveally present (Figure 5A) or absent (Figure 5B).

Experiments 2 and 3: The impact of timing of motion integration on PFR and saccade landing deviations

Previous psychophysical studies have shown that perceptual enhancement at the saccade target is at maximum immediately prior to saccade onset (Deubel, 2008; Li et al., 2016; Ohl et al., 2017; Rolfs & Carrasco, 2012; Rolfs et al., 2011). In these experiments, we focused on the Gaussian condition exclusively and pooled across foveal-motion and no-foveal-motion conditions as we found no significant differences between them during the early open-loop epoch in Experiment 1.

We first sought to determine how much presaccadic motion coherence was necessary to drive PFR. We presented stimuli that were incoherent (0% coherence) at the start of the trial and then transitioned to 100% coherent motion at random times before the saccade. We performed the post hoc analysis to bin the onset of coherent motion relative to the saccade onset. As shown in Figure 6A, we observed that, when the motion coherence occurred 100 ms prior to saccade onset, both the PFR gain in the open-loop epoch (shown in black) and the saccade landing positions (shown in green) were deviated toward positive values, thus reflecting selection of the presaccade target motion. The change in the magnitude of effect across different time intervals was significant both for PFR, $F(5, 35) = 28.8$, $p < 0.001$, and saccade deviations, $F(5, 35) = 9.02$, $p < 0.001$. The PFR magnitude remained significant after Bonferroni–Holm correction at 100–

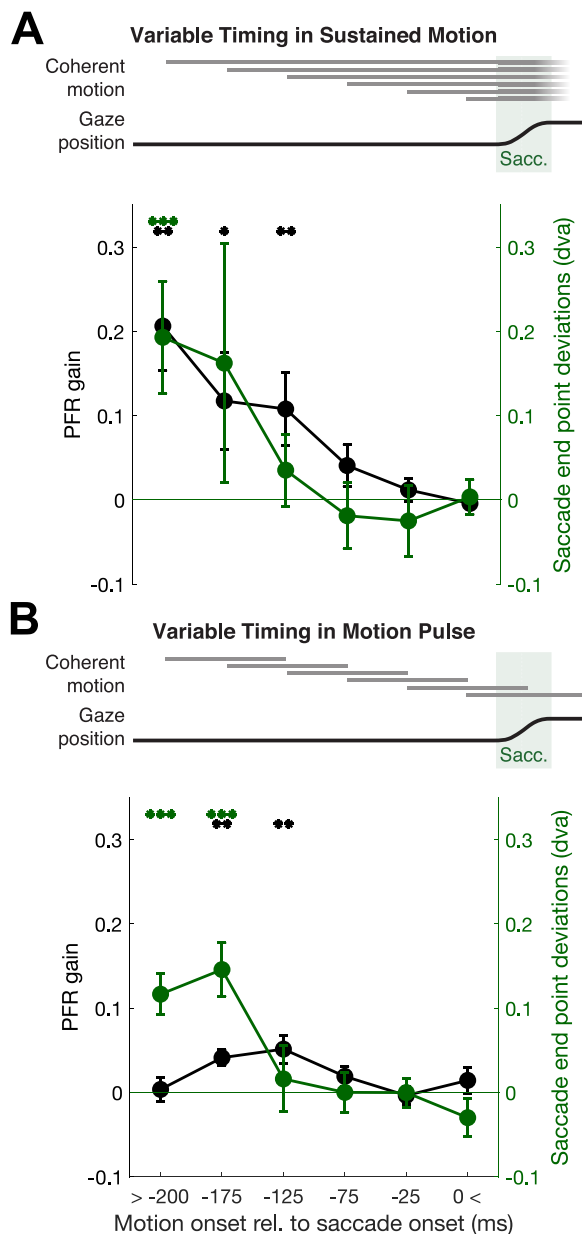


Figure 6. Presaccadic motion integration interval for PFR and saccade deviations. PFR gain and saccade endpoint deviations from Experiments 2 and 3 are illustrated as a function of motion coherence onset (sustained or pulsed motion stimulus) relative to saccade onset. The PFR and saccade landing points are shown binned in 50-ms periods before the saccade onset. (A) We varied the timing of the onset of a sustained coherent motion stimulus in all apertures relative to the saccade (see schematic above top panel). When the coherent motion stimulus occurred 100 ms or earlier before the saccade it had the greatest impact on PFR (shown in black, left y-axis) and the saccade landing points (shown in green, right y-axis). (B) We varied the timing of a brief (100-ms) pulse of coherent motion just prior to the time of the saccade (see schematic above bottom panel). Motion pulses occurring 100–150 ms prior to saccade onset had the greatest impact on the PFR (shown in

150 ms prior to the saccade, whereas the effect on saccade landing positions was nonsignificant by that time (Figure 6A).

We next sought to quantify what epochs prior to the saccade had the strongest influence on open-loop PFR and saccadic deviations. Based on the prior experiment, we estimated at least a 100-ms pulse of coherent motion was necessary to produce measurable effects both in PFR and saccade landing positions. To map out the influence of different 100 ms epochs prior to the saccade, we, thus, varied the timing of brief motion pulses of 100 ms duration, each pulse of which contained 100% coherent motion. Other than these brief motion pulses, the motion within the four apertures was incoherent. We performed the post hoc analysis to bin the trials of the motion pulse offset relative to the saccade onset. As shown in Figure 6B, we observed that, when the motion pulse occurred 200 ms prior to the saccade onset, the PFR gain (shown in black) was low, but it steadily increased for later intervals, reaching a peak between 150 and 100 ms preceding the saccade. For this range, the complete 100-ms pulse of motion would have been viewed prior to saccade onset, providing the maximum motion integration duration immediately prior to the saccade. By contrast, the influence of motion pulses on saccade landing positions (shown in green) peaked at an earlier time between 200 and 150 ms preceding the saccade. The change in the magnitude of effect across different time intervals was significant for both PFR, $F(5, 35) = 18.5$, $p < 0.001$, and saccade deviations, $F(5, 35) = 67.2$, $p < 0.001$. Again, the PFR magnitude was significantly above zero after Bonferroni–Holm correction at 100–150 ms prior to the saccade, whereas the effect on saccade landing positions was absent by that time (Figure 6B). The motion pulse placed at the optimal presaccadic interval produced PFR gains nearly half the total magnitude of that seen with the longer motion stimulus that was present from trial onset in the first experiment. On average, the peak PFR for the -150 to -100 ms pulse reached a gain of 0.0594 ± 0.008 as compared to 0.1292 ± 0.030 in the original experiment using the Gaussian condition. By the same token, the magnitude of saccade deviations at the peak prior to the saccade in the bin from -200 to -150 ms was 0.1477 ± 0.017 as compared to 0.2234 ± 0.023 in the original experiment. Thus, it appears that motion integration is specific to certain presaccadic intervals that contribute more to the net effect.

black), and the saccade landing points were relatively unaffected (shown in green), reflecting the saccade dead time of about 100 ms. Motion pulses ~ 175 ms prior to a saccade produced the strongest effect for saccade landing points (shown in green). Error bars represent 2 SEM.

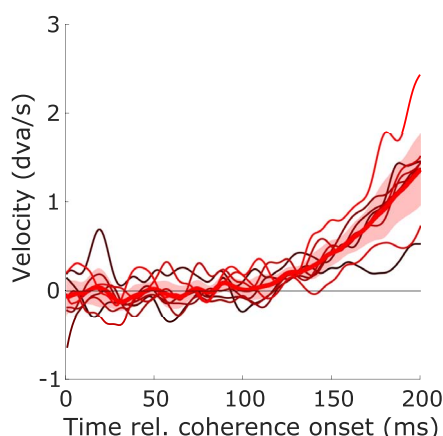


Figure 7. Ocular following response across subjects. The mean eye velocity is shown time locked to the onset from random to coherent motion of a foveally viewed dot field stimulus in the postsaccadic period of Experiment 2. Each thin line represents the mean velocity trace from an individual participant. The thick line with shaded regions represents the mean across subjects with 2 SEM.

The PFR in the open-loop interval (20–100 ms) was much shorter in latency than that expected from foveally driven OFR with our stimuli. We considered in Experiment 2 a subset of trials from which the onset of motion occurred after the saccade to the aperture when the motion stimulus was foveal, thus allowing us to measure the eye velocity time locked to motion onset across subjects and determine the latency of OFRs. As seen in Figure 7, the eye velocity across all subjects does not track motion until after 100 ms with an onset roughly at 120 ms. The PFR identified in the open-loop period can, thus, not be attributed to foveal following like OFR, but rather must reflect the integration of motion prior to the onset of the saccade itself.

Experiment 4: Velocity dependence of PFR

Smooth pursuit and OFRs both exhibit a dependence on stimulus velocity. Although pursuit typically has a linear dependence on speed that maintains close to unity gain over the range of speeds used in the current study (Tychsen & Lisberger, 1986), by contrast, OFR has much lower gain that is linearly related to the logarithm of speed (Miles et al., 1986). To determine how the PFRs vary with velocity, we repeated the Gaussian condition (Experiment 1) over a range of speeds from 2 to 15 dva/s on a log scale. As shown in Figure 8A, there was no significant difference between the foveal-motion (red) or the no-foveal-motion conditions (blue) in the open-loop interval (20–100 ms after saccade offset). As expected from the divergence in velocity traces for those conditions in Figure 3, we did obtain an influence of foveal motion during the

closed-loop interval (100–200 ms), where the foveal-motion condition showed a stronger PFR than the no-foveal-motion condition (Figure 8B). In both panels, the black line shows the unity line in log scale.

Although the PFR gain remained small relative to the unity line, there was a significant linear relationship with velocity in both the open-loop interval (foveal: slope = 0.31, $p = 0.0022$; nonfoveal: slope = 0.22, $p = 0.013$) and the closed-loop interval (foveal: slope = 0.64, $p = 0.0046$; nonfoveal, slope = 0.37, $p < 0.001$). We also considered if the dependence on velocity was better fit with a log-linear curve. Linear and log-linear models were matched in their numbers of parameters (intercept and slope). Pooling across foveal/nonfoveal and open-/closed-loop conditions, there was a net improvement in the fit using a log-linear dependence (mean $R^2 = 0.898$, 0.057 SD compared to mean $R^2 = 0.741$, 0.066 SD).

We also considered if the deviations in saccade ending position were influenced by the stimulus velocity. As shown in Figure 8C, there was no significant effect of target motion velocity on the saccade landing positions along the target motion direction. All target motion velocities showed saccade end point deviations along the target motion direction with the magnitude between 0.1 and 0.2 dva and a trend for weaker deviations at lower velocities that was not significant (slope = 0.039, $p = 0.129$). Thus, the saccade end points revealed less dependence on target velocity.

Analysis of secondary movements

We next considered to what extent the influence of target motion on PFR and saccade landing positions reflected voluntary or involuntary eye movements. Although we gave participants no instructions to follow dots in the motion aperture, it is possible that they may have adopted such a strategy. Conversely, if they had intended to target the center of the aperture as instructed, we would have expected a tendency for their eyes to drift toward the center of the aperture after saccades and for them to also make secondary corrective saccades toward the center. We examined two measures to distinguish between these possibilities. First, we analyzed how the PFR was related to the magnitude of saccade deviations. If participants sought to arrive at the center of the aperture, we would expect a larger drift back toward the center of the aperture on those trials in which saccades deviated further away from it. As such, the drift to the center of the aperture would act more strongly against the PFR gain on those trials with larger saccade deviations along target motion, and thus, we would predict a negative correlation between saccade deviations and PFR on a

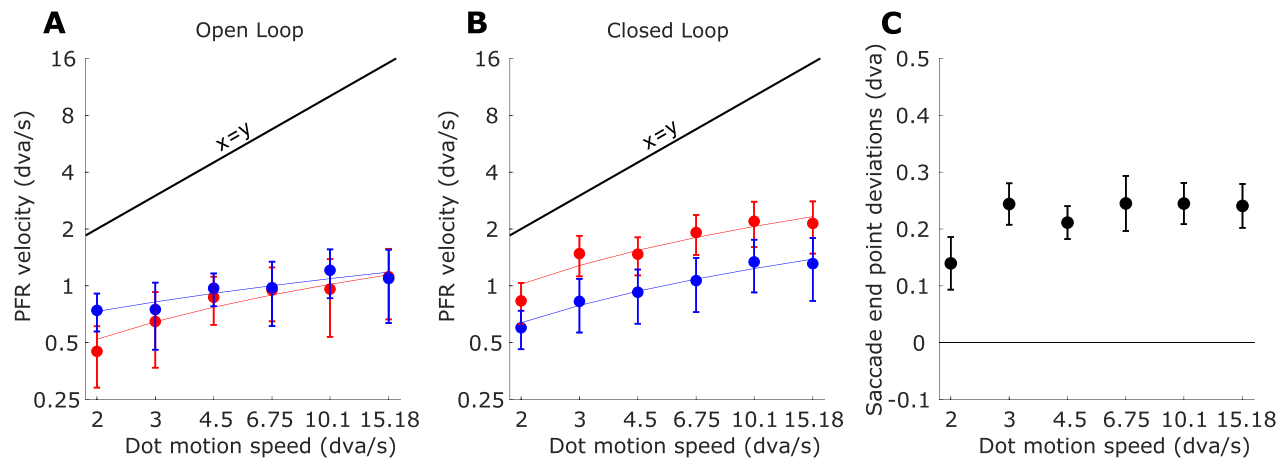


Figure 8. Mean PFR across subjects as a function of stimulus velocity. We measured the PFR velocity after saccade offset as a function of increasing stimulus velocity (2.0, 3.0, 4.5, 6.75, 10.10, and 15.18 dva/s). (A) The PFR during the open-loop interval (20–100 ms) increased with velocity for both foveal (red) and no foveal motion (blue) conditions. The PFR velocity was substantially below the line of unity (shown in black). The increase in PFR with stimulus velocity was best fit as linearly dependent on the logarithm of velocity (curve fits as solid lines). (B) The same conventions to shown PFR velocity during the closed-loop (200–400 ms) period. (C) The saccade endpoint deviations are shown as a function of stimulus velocity (foveal and no foveal motion conditions are pooled). No significant linear trend was found. Data points reflect the mean across participants at that velocity with 2 SEM error bars.

trial-by-trial basis. As shown in Figure 9A for a single participant's trial-by-trial data taken from Experiment 1 (Gaussian condition, 6.75°/s), there was a highly significant negative correlation between PFR gain and saccade deviations ($r = -0.683$, $p < 0.001$). Across participants, there was a consistent negative correlation between PFR gain and saccade end point deviation in

both the same condition of the first experiment (Figure 9B, leftmost data points) and the final experiment varying velocity (Figure 9B, right data points). The negative correlation remained around -0.6 across a range of target velocities with no significant linear trend (Figure 9B). These findings support that participants did attempt to target the center of the aperture in their

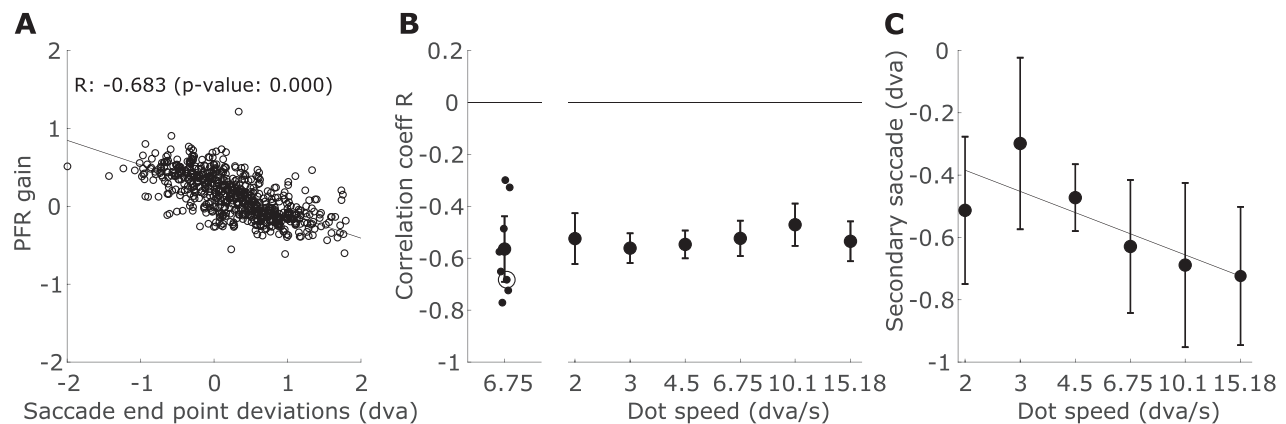


Figure 9. Secondary movements were directed against target motion toward the aperture center. (A) PFR gain showed negative correlation with saccade deviations. Data points show the PFR gain and saccade deviation across trials for an exemplar participant in Experiment 1 (Gaussian condition). Although both PFR gain and saccade endpoint deviations were positive, on average, reflecting the positive influence of target motion, the larger saccade endpoint deviations were associated with reduced or negative PFR, leading to a significant negative correlation of the two measures. (B) The correlation coefficient R between PFR gain and saccade endpoint deviations is shown on the left for Experiment 1 (individual participants as gray points, exemplar circled) and for Experiment 4 across different velocities (data points are means across participants with 2 SEM error bars, in black). (C) The deviation of secondary saccades occurring within 200 ms of the saccade into the target aperture is shown for Experiment 4 as a function of stimulus velocity. Negative deviations reflect secondary saccades in the direction opposite to target motion (data points are means across participants with 2 SEM error bars in black). There was a weak but significant trend for larger negative amplitude saccades with increasing stimulus velocity.

movements and that the slow PFR movements observed do not reflect voluntary pursuit. Instead, there appears to be a voluntary trend to redirect the eyes toward the aperture center, which is reflected in the smooth eye movements. As a secondary measure of whether or not subjects tracked target motion voluntarily or involuntarily, we analyzed corrective saccades that occurred within 200 ms of saccade landing within the target aperture. In the analyses presented thus far, any trials exhibiting such corrective saccades were excluded from analysis to prevent any corruption of velocity estimates. The corrective saccades occurred very rarely but were more frequent in the foveal-motion than in the no-foveal-motion conditions. They occurred at a median percentage of 12.3% of the total trials (range from 2.6% to 37.2%), pooling both stimulus-present (foveal motion) and stimulus-absent trials. We tested whether or not the direction of secondary saccades was negatively related to target motion as would be expected if participants resisted following the dot motion. As shown in Figure 9C, we observed that corrective saccades were, on average, made against the target motion with typical amplitudes in the range from 0.2 to 0.8 dva, $t(7) = -6.73$, $p < 0.001$, and had a significant linear trend for increasing amplitude with stimulus velocity (linear regression, slope = -0.168 , $p = 0.056$). Overall, these findings support that participants were engaged in following for target motion involuntarily and otherwise attempted to move opposite of dot motion.

Last, we also considered if the peripheral selection in the present task uniquely contributed to the PFR or if a similar selection during covert attention might also lead to involuntary eye movements. In a control study with five participants (four of the original eight participants and one of the authors; see Supplementary File S1 and Supplementary Figures S1–S3), we included a perceptual judgment of the motion direction in the cued target aperture. The motion direction was tilted from the tangent direction to perform a two-alternative, forced-choice task, and the magnitude of tilt was titrated to control difficulty. Participants were cued to one of two target apertures, either to the left or right of fixation. In a “presaccadic” block of trials, participants performed the quick saccade task with a brief motion pulse (50 ms) occurring at varying delays prior to the saccade (similar to Experiment 3) but additionally reported the direction of motion of the tilt. In the second block of “covert” trials, they maintained fixation and only reported the tilt at the cued location. In the presaccadic trials, we were able to replicate the main results showing PFR along the direction of target motion. However, in covert trials, we found no significant eye drift for the target motion after time locking to the motion onset of the pulse. But the motion pulse itself was sufficient to induce OFR when it was viewed

foveally after a saccade. Therefore, although the motion pulse was sufficient to drive OFR and also evoked a predictive PFR after saccades to the cued aperture, it had no appreciable effect on eye movements during covert attention.

Discussion

In the current study, human participants performed a saccade to one of four peripherally presented dot motion stimuli, each bounded within a spatial aperture and with motion balanced across the set of stimuli. We found that, immediately upon saccade offset, the eyes followed the presaccadic motion in the target aperture. This PFR persisted even when the motion stimulus was removed in saccade flight. The early latency of this response and its presence when foveal motion is absent, reflect that presaccadic predictions of target motion drove the responses. The landing positions of saccades were also displaced along the target motion direction. We were able to dissociate effects of landing position from smooth eye velocity and found the two responses differed in the timing with which they integrated motion in the presaccadic interval.

These findings demonstrate that PFR can be influenced predictively by target selection during presaccadic attention. Indeed, on a trial-by-trial basis, we were able to predict what stimulus had been peripherally viewed based only on the PFRs with more than 70% accuracy on average and, in a few participants, with almost perfect accuracy. Spatial selection for the area of motion integration is known to strongly influence voluntary pursuit (Heinen & Watanianuk, 1998; Orban de Xivry & Lefevre, 2007). The low-gain PFR movements we find could be useful as an oculomotor readout of the spatial selection in presaccadic attention for motion stimuli even when there are no task demands for tracking. In this regard, the paradigm may provide comparable measures to what has been termed postsaccadic enhancement: the transition from vector averaging to target selection that occurs around the time of saccades during voluntary pursuit when selecting one of two moving targets (Case & Ferrera, 2007; Gardner & Lisberger, 2001; Schoppik & Lisberger, 2006).

The magnitude of PFR and saccadic displacements along target motion depended critically on the spatial certainty of the aperture that bounded the dot-motion stimuli. The PFR gain was largest under conditions in which the spatial aperture had the highest uncertainty, for example, when it was bounded by a smooth Gaussian aperture as opposed to a high-contrast salient ring. Displacements in saccade landing position depended on the spatial uncertainty in a stronger way

with no significant effects observed except in the condition of highest uncertainty when the motion stimulus was bounded by a smoothed Gaussian. These deviations in saccade landing positions are consistent with the direction of the illusory displacement in perceived locations reported in previous studies (De Valois & De Valois, 1991; Kosovicheva et al., 2014; Kwon, Tadin, & Knill, 2015; Ramachandran & Anstis, 1990). One way to reconcile the dependence on aperture certainty is to consider the planning of the saccade in a Bayesian framework (Kersten & Yuille, 2003; Knill & Pouget, 2004). Both the spatial aperture and the motion provide cues for the future location of the target aperture and are weighted in decision making for eye movements. As the salience of the spatial aperture increases, it is weighted more heavily in saccade planning than the motion cues, thus reducing both the PFR and saccadic displacements.

The timing of motion integration in the current studies is highly consistent with that of the perceptual enhancement typically observed for presaccadic attention. Previous studies have shown that the orientation and contrast of saccade targets are enhanced in the 50–100 ms immediately before a saccade (Li et al., 2016; Ohl et al., 2017; Rolfs & Carrasco, 2012; Rolfs et al., 2011). Focusing on the condition of highest spatial uncertainty (Gaussian condition), we varied the presaccadic intervals in which coherent motion was displayed before the saccade to map out which intervals drove the response (Figure 6). Compared to oriented stimuli in previous studies in which pulses within 50 ms of saccade onset were most effective (Rolfs & Carrasco, 2012), we used motion pulses of 100 ms duration for which the peak effect occurred 100–150 ms before the saccade such that there was sufficient time for the pulse to complete. This is in agreement with the fact that motion—as compared to oriented stimuli—becomes more efficient in driving PFR when the entire integration time falls into the interval right before saccade onset. The displacements in saccade landing positions relied on motion integration from an earlier interval occurring prior to 100 ms before the saccade with a peak around 200–150 ms before the saccade. This difference in timing may reflect the saccadic dead time, which is thought to preclude integration of additional sensory information in planning saccadic movements within 80 ms before the saccade (Becker 1991; Findlay & Harris, 1984; Ludwig, Mildinhal, & Gilchrist, 2007).

The PFRs in the current study appear consistent with involuntary smooth eye movements, more similar to OFRs rather than pursuit. In our task, participants were instructed to saccade as quickly as possible to the target aperture and otherwise had no task demands requiring them to either attend to the motion in the aperture or to track its motion. Although it is possible

that participants may have adopted a strategy for tracking dots in the motion aperture, we find this contradicts several features of the observed eye movements. First and foremost, the smooth eye movements persisted even when the target motion disappeared in saccade flight, demonstrating at minimum that the movements were predictive if not involuntary. Second, there was a negative correlation between the size of the saccade displacements along target motion and the magnitude of PFR on a trial-by-trial basis. If participants had voluntarily tracked dot motion, we would expect the saccadic displacements and PFR to be positively correlated as trials with stronger effort or attention would produce larger effects in both measures. Instead, we found a consistent negative correlation between displacements and PFR (Figure 9). This trial-by-trial opposition would support a strategy in which participants attempted to reach the center of the aperture after the saccade as opposed to tracking stimulus motion. Thus, for trials with larger excursions in saccades landing away from the center of the aperture, there was a corresponding push in eye drift back to the center. On average, this contributes to the PFR acting in opposition (negatively correlated) to the saccade deviations. A second finding that supports that participants sought to land at the center of the aperture is that secondary saccades made after landing within the aperture did not track the direction of target motion, but rather were directed, on average, back toward the center of the aperture. Together, we take these findings to support that participants did indeed adopt the strategy to saccade to the center of the aperture but, despite this, were influenced by the target motion in presaccadic planning.

The gain and velocity dependence of the PFRs also support that these responses are more similar to involuntary OFR than pursuit. Whereas pursuit movements often track targets with close to unity gain for speeds up to 45 dva/s (Buizza & Schmid, 1986; Tychsen & Lisberger, 1986), the gains in the current study were considerably smaller, ranging from 5% to 15%. The responses across different subjects, although consistent in their alignment with motion, also varied considerably in gain. Previous studies of OFR find a wide variation in the gain across individuals in a similar range of low gain (Miles et al., 1986). The dependence as a function of speed was also better fit as a linear dependence on the logarithm of speed (Figure 8), which mirrors that observed for OFR (Gellman et al., 1990; Miles et al., 1986). There are, however, several interesting caveats to our findings in comparison to previous literature on OFR. First, we show that a spatially specific presaccadic mechanism is able to select the motion that drives the PFR. Although previous studies have established that following can be driven by smaller stimuli, particularly when they are near the

fovea, our study may be the first to demonstrate that the spatial selection involved in saccade planning can modulate PFR.

Investigation of the neural mechanisms supporting pursuit and OFR suggests that, although they may have different implementations at the level of the brainstem, both appear to rely on motion processing from similar sensory cortical areas, including medial temporal (MT) and medial superior temporal (MST) areas (Bakst, Fleuriot, & Mustari, 2017; Mustari, Ono, & Das, 2009; Nuding, Ono, Mustari, Buttner, & Glasauer, 2008). It is well established that sensory processing within areas MT and MST can be strongly influenced by attention (Martinez-Trujillo & Treue, 2002; Treue & Martinez-Trujillo, 1999; Treue & Maunsell, 1996) and by the target selection preceding eye movements (Ferrera & Lisberger, 1997; Recanzone & Wurtz, 2000). The preferential weighting of pre-saccadic motion information in the current study could reflect underlying changes in neuronal gain at the level of areas MT or MST consistent with that predicted during covert spatial attention tasks. In that context, brainstem areas planning PFR might pool widely across sensory representations in MT/MST but with the selective weighting applied to favor the presaccadic target, thus showing preferential PFR to it.

Two alternative neural pathways could be involved in the PFR observed in the current studies. PFR might rely on pathways that mediate OFR, which pass from areas MT/MST to the dorsolateral pontine nuclei floccular complex in the cerebellum. If so, a sensory selection of peripheral motion for the target would be present well before the saccade and already exert a sensory drive into the OFR pathway, but the resulting smooth eye movements would be suppressed until the constraint for fixation was terminated by the saccade itself. Given that we observed OFR to have a latency of roughly 120 ms with our stimuli (Figure 7) and that the peak PFR was evoked for motion pulses that onset between 150 and 100 ms prior to the saccade (Figure 6B), the timing of the PFR would be consistent with this possibility. If so, it would indicate that presaccadic attention can modulate OFR. A second alternative is that some additional circuitry may be involved in mediating PFR through pathways in the frontal lobe. In that case, motion information might be stored in memory prior to the saccade and then released upon saccade landing. That circuitry may overlap with those areas thought to be involved in target selection of motion during pursuit movements, such as the frontal eye fields (FEF) or frontal pursuit area (Case & Ferrera, 2007; Schoppik & Lisberger, 2006). Without visual information processing, information from FEF can move the eyes with latency around 26 ms (Tanaka & Lisberger, 2002). Therefore, it could drive smooth movements at the short postsaccadic latencies we

observe for PFR. Further, the FEF can impact motion integration at the saccade target location as it may mediate visual attention through reciprocal connections with MST (see Stanton, Bruce, & Goldberg, 1995; Stanton, Friedman, Dias, & Bruce, 2005). And it is also established that portions of FEF that are involved in pursuit (FEFsem) can interact with the reflexive pathway involved in OFR (Bakst et al., 2017). Thus, modulations of FEF neurons could not only directly drive eye velocity, but they might also act to influence following responses (both OFR and PFR) through their interactions in sensory processing at the level of MT/MST. Future studies could investigate whether predictive PFR activity is present in MT/MST, FEF, or both. Irrespective of the underlying mechanisms, the current findings support that presaccadic planning selects peripheral motion information for the saccade target, which predictively influences subsequent PFR.

Keywords: presaccadic attention, random dot kinetogram, smooth pursuit, ocular following, prediction

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Corresponding author: Jude F. Mitchell.

Email: jmitch27@ur.rochester.edu.

Address: Brain and Cognitive Sciences, University of Rochester, NY, USA.

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