# Micropursuit and the control of attention and eye movements in dynamic environments

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**It is more challenging to plan eye movements during perceptual tasks performed in dynamic displays than in static displays. Decisions about the timing of saccades become more critical, and decisions must also involve smooth eye movements, as well as saccades. The present study examined eye movements when judging which of two moving discs would arrive first, or collide, at a common meeting point. Perceptual discrimination after training was precise (Weber fractions < 6%). Strategies reflected a combined contribution of saccades and smooth eye movements. The preferred strategy was to look near the meeting point when strategies were freely chosen. When strategies were assigned, looking near the meeting point produced better performance than switching between the discs. Smooth eye movements were engaged in two ways: (a) low-velocity smooth eye movements correlated with the motion of each disc (micropursuit) were found while the line of sight remained between the discs; and (b) spontaneous smooth pursuit of the pair of discs occurred after the perceptual report, when the discs moved as a pair along a common path. The results show clear preferences and advantages for those eye movement strategies during dynamic perceptual tasks that require minimal management or effort. In addition, smooth eye movements, whose involvement during perceptual tasks within dynamic displays may have previously escaped notice, provide useful indictors of the strategies used to select information and distribute attention during the performance of dynamic perceptual tasks.**

## Introduction

Visual tasks depend on eye movements to explore the environment and to gather the information needed to accomplish task goals (Hayhoe, 2017; Viviani, 1990). Most studies of the role of eye movements have focused on the saccadic eye movements used to bring the line of sight to a succession of selected regions of the visual array. These studies have shown that decisions about where to look depend on many different factors, such as the visibility of eccentric details, the value of the information obtained from each fixation, or the cognitive effort required to develop or to carry out the saccadic plans (e.g., Ballard, Hayhoe, & Pelz, 1995; Castelhano, Mack, & Henderson, 2009; Crespi, Rabino, Silva, & de'Sperati, 2012; Eckstein, 2011; Epelboim & Suppes, 2001; Epelboim et al., 1995; Gerstenberg, Peterson, Goodman, Lagnado, & Tenenbaum, 2017; Gottlieb, Hayhoe, Hikosaka, & Rangel, 2014; Hoppe & Rothkopf, 2016; Johansson, Westling, Backstrom, & Flanagan, 2001; Kandil, Rotter, & Lappe, 2009; Kandil, Rotter, & Lappe, 2010; Knöll, Pillow, & Huk, 2018; Koehler & Eckstein, 2017; Land & Lee, 1994; Matthis, Yates, & Hayhoe, 2018; Melcher & Kowler, 2001; Najemnik & Geisler, 2005; Rubinstein & Kowler, 2018; Semizer & Michel, 2017; Sullivan, Johnson, Rothkopf, Ballard, & Hayhoe, 2012).

Eye movement strategies during dynamic tasks present special challenges because decisions about where to look must take into account the constantly changing locations of key objects. In addition, smooth eye movements may be involved. Relatively few of the prior studies of eye movement strategies during dynamic visual tasks considered the role of smooth eye movements. This is surprising, because smooth eye movements, like saccades, play important roles in vision (Intoy & Rucci, 2020; Kowler, Rubinstein, Santos, & Wang, 2019; Krauzlis, 2004; Kuang, Poletti Victor, & Rucci, 2012; Murphy, 1978; Palidis, Wyder-Hodge, Fooken, & Spering, 2017; Schütz, Braun, Kerzel, & Gegenfurtner, 2008), and, like saccades, may provide overt indicators of underlying cognitive events, including those involving either attention or prediction (Barnes, 2008; Fiehler, Brenner, & Spering, 2019; Kowler, 2011; Kowler et al., 2019). Nevertheless, most of the previous studies using dynamic displays did not report characteristics of smooth eye movements. In those that did discuss smooth eye movements, there was disagreement about their occurrence or their value for the task. The present study attempted to

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gain greater insights about eye movement strategies in tasks involving moving objects and fill in some of the gaps in our knowledge regarding the role of smooth eye movements. These goals were addressed by investigating both eye positions and smooth eye movement velocities in a visual task that required judgments about the relative motion of a pair of moving targets.

## Smooth eye movements during visual tasks

Smooth eye movements are used to maintain the line of sight on either stationary targets (Steinman & Collewijn, 1980; Steinman et al., 1973) or moving targets (Kowler et al., 2019; Krauzlis, 2004; Lisberger, 2010), producing the retinal conditions that support clear vision (Intoy & Rucci, 2020; Murphy, 1978; Palidis et al., 2017; Schütz et al., 2008). Smooth eye movements during fixation, like smooth pursuit of moving targets, depend on retinal velocity signals, and as such have been likened to smooth pursuit of a stationary target (Epelboim & Kowler, 1993; Nachmias, 1959; Nachmias, 1961; Steinman et al., 1973).

Relatively few studies have focused on the occurrence or value of smooth eye movements during active, dynamic perceptual or visuomotor tasks involving moving objects. Smooth pursuit has been reported to occur while watching videos (Corrigan, Gulli, Doucet, & Martinez-Trujillo, 2017; Dorr, Martinetz, Gegenfurtner, & Barth, 2010; Goettker, Agtzidis, Braun, Dorr, & Gegenfurtner, 2020; Ross & Kowler, 2013) or driving (Lappi, Pekkanen, & Itkonen, 2013); however, in these studies, the pursuit was not explicitly related to performance of a task. One example in which smooth pursuit was related to visual performance is Spering, Schütz, Braun, and Gegenfurtner (2011), who studied the role of smooth pursuit when judging whether a moving target on one side of a display would hit a stationary target on the other side. Perceptual performance was better in a condition that required pursuit of the moving target than in a condition that required fixation of the stationary target, suggesting that the accuracy of perceiving the motion path benefited either from the effect of pursuit on retinal image motion or from the information gained about the path of motion from extraretinal factors, such as monitoring of the pursuit commands.

Some studies reported spontaneous smooth pursuit during visual tasks and linked the spontaneous pursuit to a presumed useful role in the task. Brenner and Smeets (2011) observed spontaneous smooth pursuit during interception of a moving target. The tasks were either (a) to hit a small moving target so that it landed inside a large gap, or (b) to move a cursor so that it intercepted a large target moving behind a small gap. The preferred strategy was to keep the line of sight near the smaller of the two features (i.e., pursue the small moving target in the first task or fixate the small gap in the second), suggesting that the spontaneous pursuit was motivated by the visual demands of the task. Smooth pursuit was also discussed by Land and McLeod (2000), who found that highly skilled cricket batters spontaneously pursued the moving ball after the bounce. Diaz, Cooper, Rothkopf, and Hayhoe (2013) suggested that such pursuit might generate extraretinal signals that help predict the future location of the ball. Other studies inferred a useful role for both retinal and extraretinal aspects of pursuit of the target or cursor in tasks that required manual interception of a moving object (Camara, Lopez-Moliner, Brenner, & de la Malla, 2020; Cesqui, Mezzetti, Lacquaniti, & d'Avella, 2015; Danion & Flanagan, 2018; Fooken, Yeo, Pai & Spering, 2016).

Given these demonstrated preferences for using pursuit, it seems surprising to find that several studies that used tasks involving moving targets reported no spontaneous pursuit and instead found an exclusive reliance on saccades. Spontaneous pursuit was not reported when threading a virtual needle (Ko, Poletti, & Rucci, 2010), grasping a physical bar and moving it to a designated position (Johansson et al., 2001), or navigating a cursor through a virtual maze in overhead view (Kowler, Aitkin, Ross, Santos, & Zhao, 2014). It is possible that spontaneous pursuit might have been present during the intervals between saccades but escaped notice either because the velocities were too low to be noticeably different from slow eye movement velocities during fixation pauses (Ko et al., 2010) or because the analyses reported were not sufficient to reveal correlations between the continually changing trajectories of the moving objects and the movements of the eye (Johansson et al., 2001; Kowler et al., 2014). The inability to fully explain why smooth pursuit would occur spontaneously in some tasks and not in others shows that the factors that promote use of smooth pursuit during visual tasks are not well understood.

## Eye movements and attention

One reason to analyze eye movements, including smooth eye movements, during dynamic tasks is to draw inferences about the distribution of perceptual attention. Attention during visual tasks with moving objects was discussed by Fehd and Seiffert (2008, 2010), who found that the preferred, and better, strategy during a multiple object tracking task was to maintain fixation near the centroid of the set of moving objects, rather than to constantly use saccades to switch fixation from one object to another. They concluded that central fixation was likely to have resulted from the division of attention among the targets and that central fixation would be preferable to frequent saccades because any momentary benefit of fixating or pursuing one target might be offset by the time and effort involved in planning and carrying out the saccade to another. Interestingly, performance was better when central fixation occurred spontaneously rather than as a result of instructions (Fehd & Seiffert, 2010). Fehd and Seiffert (2008, 2010) did not analyze smooth eye movements, but did report occasional instances of pursuit (Fehd & Seiffert, 2008, figure 1B).

Smooth eye movements may also provide indicators of attention. Links between smooth eye movements and attention go back to early reports that pursuit of large moving patterns could be suppressed by voluntary fixation of a superimposed stationary target (Dodge & Fox, 1928; Murphy, Kowler, & Steinman, 1975). Comparable selective abilities have been found for a variety of different stimulus patterns, with the effectiveness of the selection depending on aspects of the stimuli or tasks (Collewijn & Tamminga, 1984; Collewijn & Tamminga, 1986; Kowler, van der Steen, Tamminga, & Collewijn, 1984; Masson, Proteau, & Mestre, 1995; Spering & Gegenfurtner, 2007). Subsequent studies confirmed and extended the link between smooth eye movements and attention by showing that perceptual judgments are better for the target of smooth eye movements than for non-targets (taking effects of retinal velocity into account) (Chen, Valsecchi, & Gegenfurtner, 2017; Jin, Reeves, Watamaniuk, & Heinen, 2013; Heinen, Jin & Watamaniuk, 2011; Khan, Lefèvre, Heinen, & Blohm, 2010; Khurana & Kowler, 1987; Lovejoy, Fowler, & Krauzlis, 2009; Souto & Kerzel, 2011), and that smooth pursuit and saccades can jointly target the same moving object, a result consistent with a common selective mechanism for both (Erkelens, 2006; Gardner & Lisberger, 2001; Gardner & Lisberger, 2002; Krauzlis & Dill, 2002; Liston & Krauzlis, 2003; Liston & Krauzlis, 2005).

A role of attention in smooth pursuit has also been invoked to explain characteristics of pursuit in response to multiple moving targets. Soon after the onset of motion of a target pair, for example, pursuit follows a weighted vector average of the two motions (Lisberger & Ferrera, 1997; Recanzone & Wurtz, 1999), with the weights sensitive to cues that bias attention to one or the other (Ferrera, 2000). Weighted pooling of local motion signals is also reflected in characteristics of pursuit of random dot kinematograms (Heinen & Watamaniuk, 1998; Mukherjee, Liu, Simoncini, & Osborne, 2017). Spering, Gegenfurter, and Kerzel (2006), using a somewhat different paradigm than the previous studies of vector averaging, found that a suddenly appearing distractor repelled the path of pursuit away from the distractor (i.e., opposite to averaging). They also found that, although the influence of the distractor was not affected by voluntary shifts of attention, it could be reduced or eliminated by making the stimulus motion more predictable. Spering et al. (2006) suggested that involuntary attention to a stimulus transient could be the basis of the influence of the distractor on pursuit in their experiments.

The studies summarized above show that both smooth eye movements and saccades reflect aspects of the distribution of attention during the performance of dynamic visual tasks. Smooth eye movements can be influenced by motion signals generated by more than one object, and the influences of multiple motion signals combine in ways that depend on stimulus characteristics as well as high-level factors such as selective attention.

## Present study

The brief review above shows that the choice of eye movement strategies during perceptual tasks in which critical objects are in motion may depend on the temporal and spatial aspects of the display and may involve both saccadic and smooth eye movements. By studying eye movements during visual tasks involving moving objects we can get a better understanding of decision-making and attentional strategies in changing visual environments and of the role of different patterns of eye movements, including smooth eye movements. To address both goals, we studied a fairly simple task and analyzed choices about fixated locations, as well as the use and possible value of smooth eye movements. The task required judging which of two moving objects would arrive first at a common, centrally located meeting point.

Two experiments were done. In Experiment 1, observers were free to choose their eye movement strategy. In Experiment 2, eye movement strategies were specified by instructions to adopt either of the two main strategies found in Experiment 1—namely, central fixation or sequential fixations of the targets (i.e., switching). Results were analyzed to determine the preferred strategies (Experiment 1) and whether fixating or switching, when assigned, were associated with better perceptual performance (Experiment 2). Additional analyses focused on the relationship between smooth eye movements and the motion of the targets. As a preview, there were four main outcomes. First, when strategies were freely chosen, three of the four subjects preferred to maintain eye position approximately midway between the moving targets, and one preferred to switch. Second, when instructed to adopt either central fixation or switching, central fixation led to better perceptual performance. Third, spontaneous smooth pursuit at velocities close to that of the pair of targets was found after the perceptual decision was reported, when the pair of targets moved along a common path. Although this pursuit occurred after the decision, there was evidence that it served a useful purpose. Finally, low-velocity smooth eye movements, correlated with the velocity of each target, were found while the line of sight was located between the two targets, a phenomenon we refer to as micropursuit (similar to Parisot, Zozor, Guérin-Dugué, Phlypo, & Chauvin, 2021). The results show that there are advantages attached to using eye movement strategies that serve the requirements of vision and attention without undue management or executive control and that smooth eye movements, as well as the selection of fixation locations, can provide useful indicators of the decisions and strategies employed. A portion of the results presented here was first described in Wang (2019a) and Wang (2019b).

# Methods

## Eye movement recording

Eye movements were recorded using the EyeLink 1000 (SR Research, Ottawa, ON, Canada), the tower-mounted version with sampling at 1000 Hz. A chin rest was used to stabilize the head. Viewing was binocular, and eye movements were recorded from the right eye.

## Subjects

Subjects were four undergraduate students (paid volunteers) at Rutgers University denoted as SS, EM, JJ, and MM. All had normal vision and were naïve as to the purpose of the experiments. All experimental procedures were approved by the Rutgers University Institutional Review Board and adhered to the tenets of the Declaration of Helsinki.

## Stimuli

Stimuli were displayed on a Dell U241 liquid-crystal display monitor (Round Rock, TX), with 1280 × 1024-pixel resolution (28.2° × 22.5° at a viewing distance of 60 cm), with a refresh rate of 60 Hz. Stimuli were viewed in a fully lighted room, and the boundaries of the display were visible.

Displays consisted of a white outline drawing of a diamond-shaped "traffic circle" (referred to as the "traffic diamond"), with runways on the left and right sides, displayed on a black background (Figure 1). Two discs (standard, red with luminance of 55 cd/m$^2$; comparison, green with luminance of 144 cd/m$^2$) moved toward the traffic diamond starting from the endpoint of either the short (standard disc) or the long (comparison disc) runway. The velocity of the standard was 5.28°/s. The velocity of the comparison was chosen at random from one of 11 equally spaced values (spacing 0.12°/s) ranging from 4.62°/s to 5.94°/s. The discs moved toward the intersection of the long runway and the traffic diamond (0.35° relative to the center). This intersection, which is the location where the standard disc and the comparison disc met

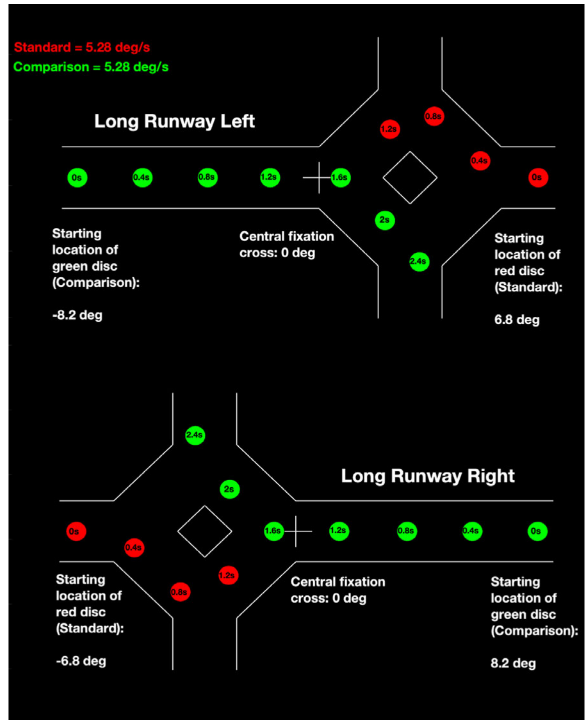


Figure 1. Stimulus displays drawn to size. The stationary outline of the traffic diamond showing the positions of the central fixation cross and a depiction of positions of the standard (red, diameter 1.2°) and comparison (green, diameter 1.2°) discs at different points in time when the long runway was on the left (top) or right (bottom). In the actual experiment, the fixation cross appeared alone at the center (0°) and 0.5 seconds after a button press was replaced by the outline of the traffic diamond and the two stationary discs at their starting locations shown in the figure at the end of the short runway (standard) or long runway (comparison). Motion started 1 second later. The standard moved on the path shown at a constant velocity (5.28°/s). The comparison moved on the path shown at a velocity randomly chosen from one of 11 values (range, 4.62°/s–5.94°/s). The figure depicts the path for the central velocity (5.28°/s). After 1.6 seconds of motion the discs arrived at the meeting point, 0.35° relative to the center, and exited the traffic diamond together (the diagram shows only the green disc). Negative position values indicate positions to the left of center. In the experiment, the only features visible during the trial were the stationary outline of the display, the standard disc, and the comparison disc. The numbers inside each disc show the times the disc arrived at the depicted positions.

when moving at the same velocity, is referred to as the "meeting point." The dimensions of the stimulus, the starting locations and paths of the discs, the locations of a central fixation cross (which was removed shortly after the onset of trials), and the meeting point are shown in Figure 1. The meeting point was shown by a total overlap of the two discs (Figure 1). The total path length traveled between each disc and the meeting point was 8.55°. The horizontal distances relative to the meeting point were 6.45° (for the standard) and 8.55° (for the comparison).

## Procedure

Subjects fixated a central cross located at the center of the display and started each trial when ready by means of a button press. The fixation cross disappeared after a delay of 500 ms and was replaced by the traffic diamond, with the standard and comparison discs at their respective start locations. After a delay of 1 second, both discs began moving toward the meeting point.

Two different perceptual tasks were used. In the *which-first* task (two-alternative forced choice [2AFC]), subjects were asked to press one of two buttons to indicate which disc (standard [red] or comparison [green]) would arrive at the meeting point first. A second task (three-alternative forced choice [3AFC]), referred to as the *collision* task, was also tested. This second task was included because it seemed to more closely resemble the types of judgments often made involving targets moving toward one another (when entering a real traffic circle, the decision to speed up or slow down is often made on the basis of the estimated probability of a collision) and because it added a level of difficulty to the decision-making (three alternatives rather than two) that might influence eye movement strategies. In the *collision* task, subjects were asked to press one of three buttons to indicate whether (a) the discs would collide, (b) the red disc would arrive first, or (c) the green disc would arrive first. A collision was defined as any overlap in the disc positions when they arrived at the meeting point. At the velocities tested, a collision occurred for the central five velocity values of the comparison disc so that the probability of collision was 0.45. In both the *which-first* and *collision* tasks, responses had to be made before either disc reached the meeting point; otherwise, the trial was not included. Discs continued along the paths after the response, with both discs traveling toward the exit of the traffic diamond (Figure 1). Feedback was displayed on the screen at the end of the trial to inform subjects which disc arrived at the meeting point first, whether a collision occurred, and their response time. A zero was displayed for trials in which responses were given too late.

### *Experiment 1: Free viewing*

In the free-viewing condition of Experiment 1, subjects were given no instructions about where to look or whether to pursue either moving disc.

Experimental sessions consisted of a block of 40 trials. The location of the runway (left or right) and the task (*which-first* or *collision*) were the same throughout a session. Two subjects (SS and JJ) were tested in three consecutive sessions with the same task and six consecutive sessions with the same runway location. The other two (MM and EM) were tested in two consecutive sessions with the same task and four consecutive sessions with the same runway location. Subject SS was tested in 60 sessions over 10 days, JJ in 78 sessions over 12 days, MM in 100 sessions over 10 days, and EM in 94 sessions over 12 days.

### *Experiment 2: Fixate versus switch*

In the fixate versus switch conditions of Experiment 2, two instructions were tested: (a) fixate the meeting point, or (b) switch between fixating the discs. Subjects were told that instructions applied only to the period prior to making the report. For the switch instruction, subjects were told to try to spend about the same amount of time fixating each disc but were not told when to make the switches or how often to switch. The same instruction was tested in two consecutive blocks of 40 trials.

The displays and tasks (*which-first* or *collision*) were the same as in Experiment 1. Two different eye movement instructions were tested in separate sessions, with all subjects running in two consecutive sessions with the same instruction and task and eight consecutive sessions with the same runway location. Subjects SS and JJ completed all sessions of the *which-first* task before starting the *collision* task. The task assignment was changed every two to four sessions for subjects MM and EM. SS was tested in a total of 38 sessions over 10 days, JJ in 42 sessions over 10 days, MM in 36 sessions over 7 days, and EM in 40 sessions over 8 days.

## Analysis

### *Perceptual data*

*Which-first task*. The perceptual performance of each subject in the *which-first* task was represented by psychometric functions showing the proportion of comparison-first reports as a function of the comparison velocity. Data from both runway locations (left or right) were pooled. Each psychometric function was fitted by the Weibull function using the algorithm (MATLAB; MathWorks, Natick, MA) in Lu and Dosher (2014,pp. 321–322). Difference thresholds were calculated from the fitted Weibull functions as half the difference between the velocities corresponding to the 75% and at 25% performance levels. Weber fractions were obtained from dividing the standard velocity by the calculated difference thresholds. Standard deviations of the calculated difference thresholds were determined by a bootstrapping method[1] (Lu & Dosher, 2014, p. 324). Biases to report standard or comparison first were determined from the 50% level of the fitted Weibull.

*Collision task*. In order to compare thresholds in the *collision* task with those of the *which-first* task, responses were collapsed into two categories in two different ways: (a) comparison disc first versus collision + comparison second; (b) collision + comparison first versus comparison second. This produced two psychometric functions for each condition, which were analyzed in the same way as the data from the *which-first* task.

*Improvements over sessions in Experiment 1*. Analysis of the performance on a session by session basis for Experiment 1 showed improvement over the initial sessions and days. The improvement was expected given the novelty of the task and the subjects' need to establish decision criteria. The results described for Experiment 1 consist of performance in the final 18 sessions for each task when performance had reached near asymptotic levels.

*Number of trials.* The final 18 sessions contained 720 trials for each subject and each task. Trials in which responses was made after the discs reached the meeting point were eliminated from the reports of perceptual performance (2% for subjects SS, JJ, and EM; 8% for MM). These few trials were not eliminated when analyzing eye positions and velocities.

### Eye movement data

Analyses were performed using custom-developed MATLAB software. The onsets and offsets of saccades were determined offline by computing eye velocity during consecutive 13-ms samples, with onsets separated by 1 ms. Saccade onsets and offsets were detected using a velocity criterion that was determined and subsequently confirmed for each subject by examining a large sample of recordings of eye positions. The criteria were 11°/s for JJ and MM and 18°/s for SS and EM.

Horizontal and vertical eye velocities were computed for 100-ms intervals with onsets of successive samples separated by 1 ms. Samples containing saccades, blinks, or portions of saccades or blinks were removed. Velocities were then averaged over time, from 500 ms before the onset of motion until the end of the trial. Horizontal and vertical eye positions for the same 100-ms saccade-free and blink-free intervals were also determined. To pool eye movement data over the left and right runway locations, data from the runway on the left trials were first rotated 180°.

# Results

## Experiment 1: Free viewing

### Perceptual discrimination and responses times

Perceptual discrimination was precise for both the *which-first* and the *collision* tasks (Figure 2). The average Weber fraction was 3.75% ($SD = 0.29$) for the *which-first* task, 4.66% ($SD = 0.38$) for the *collision* task when responses were grouped as comparison disc first versus collision + comparison second, and 4.28% ($SD = 0.32$) for when the responses were grouped as comparison first + collision versus comparison second. A two-way (task × subject) analysis of variance (ANOVA) showed no main effect of either the task (*which-first* vs. *collision*), $F(1, 8) = 3.64$ , $p = 0.09$, or the subject, $F(3, 8) = 1.57$, $p = 0.27$. Bias, the difference between performance at the 50% point of the fitted psychometric function and the true 50% point, was small (<2.5%) except for subject MM (9.2%) in the collision task, who often reported "collision" when the comparison disc arrived first.

Responses were made about 300 to 500 ms before the discs reached the meeting point, after about 1.1 to 1.3 seconds of viewing, when the discs were still separated by 4° to 6°. Figure 3 shows the mean time (±*SD*) between the deadline and the response as a function of the comparison velocity, where "deadline" refers to the time when the first disc reached the meeting point. The decisions took longer for the 3AFC collision task. A three-way (2 tasks × 11 comparison velocities × 4 subjects) ANOVA confirmed the main effect of task on decision time, $F(1, 30) = 214.26$, $p = 10^{-15}$). In addition, subjects SS and MM tended to respond later (less time remaining) for the faster comparison velocities, resulting in a significant interaction between subject and comparison velocity, $F(30, 30) = 3.38$, $p = 10^{-04}$).

### Eye movement strategies

What types of eye movement strategies accompanied the successful perceptual performance described above? Eye movement strategies were freely chosen in Experiment 1; thus, a variety of strategies seemed possible. These included keeping the line of sight at or near the meeting point of the two moving discs, switching between fixation of each disc, fixating one disc for the entire trial, or some mixture of these. Strategies involved not only the choice of where to look

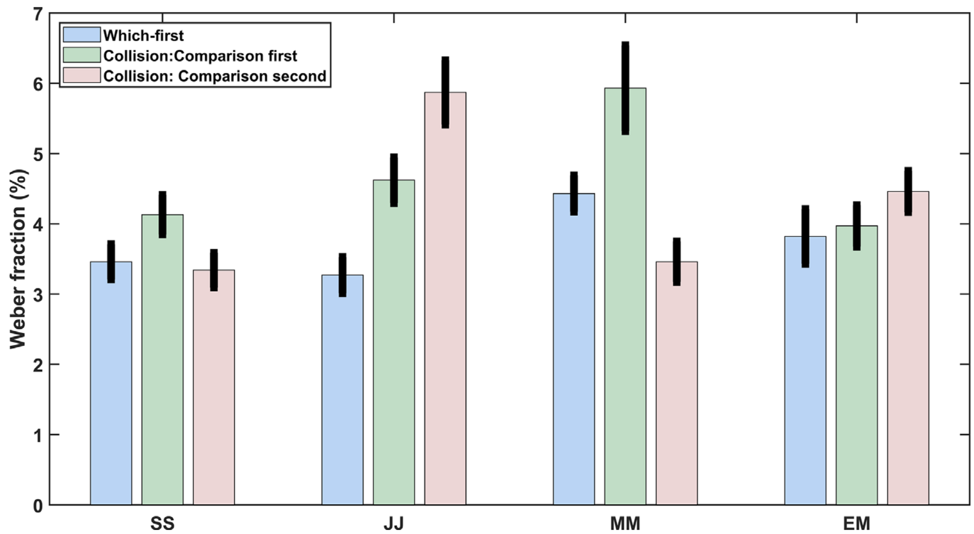


Figure 2. Perceptual discrimination in Experiment 1. Weber fractions (±*SD*) for each subject (SS, JJ, MM, EM) for the *which-first* and *collision* tasks. Weber fractions from the *collision* task were obtained by grouping the responses as comparison first versus collision + comparison second (green bars) or as comparison first + collision versus comparison second (pink bars). Each Weber fraction is based on 713 to 717 trials for SS, 711 to 717 trials for JJ, 665 to 714 trials for MM, and 706 to 716 trials for EM.

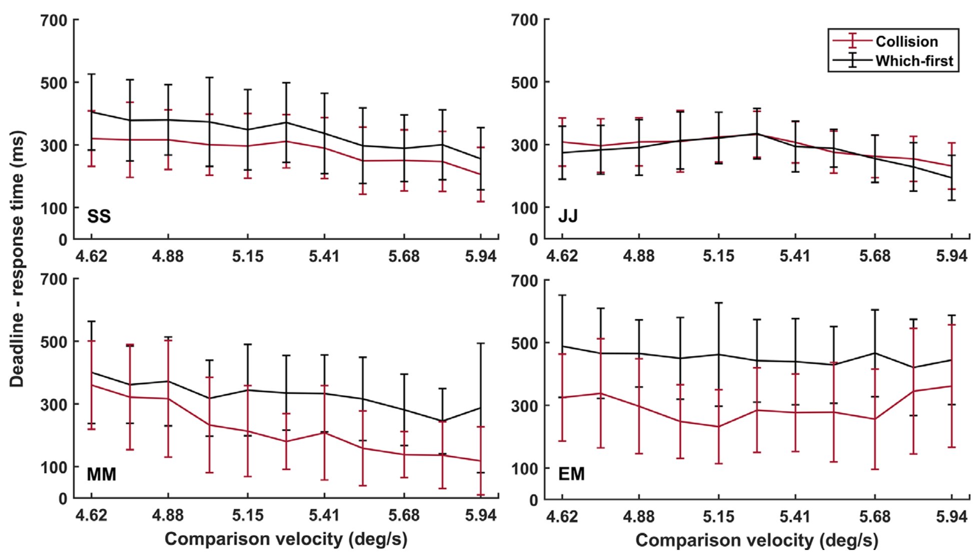


Figure 3. Mean (±*SD*) difference between deadline and response time as a function of the comparison disc velocity in Experiment 1 for the two tasks. Deadline is the time when the first of the two discs reached the meeting point (1.4–1.6 seconds relative to the start of the motion), and response time is the recorded time of the button press responses. Larger means indicate earlier responses. Each mean is based on 54 to 79 trials for SS, 52 to 89 trials for JJ, 47 to 81 trials for MM, and 50 to 79 trials for EM.

but also decisions about how or when to use smooth eye movements.

Here, we present eye movement results for each subject in sequence, starting with the subject whose strategy was the simplest. The presentation of the results for each subject begins with a movie that shows horizontal and vertical eye positions over time followed by (a) summaries of saccade frequency and horizontal saccade sizes; (b) heat maps of horizontal eye position versus horizontal eye velocity (we are focusing on horizontal eye movements because the main motion of the discs was horizontal); and (c) mean eye velocities (both horizontal and vertical) over time. Following the presentation of the eye movement strategies of all four subjects, we then take a closer look at the fine-grained properties of eye velocities that were not apparent from this initial analyses.

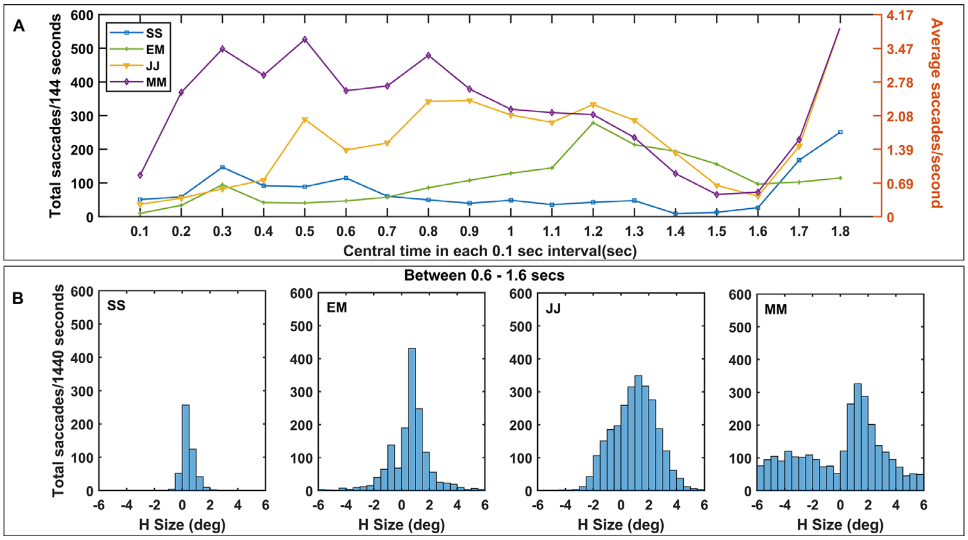


Figure 4. Saccades in Experiment 1. (A) Number of saccades during successive 100-ms time windows plotted as a function of the center of each time window. Results are shown as number of saccades over the 1440 trials (left *y*-axis) or as saccade frequency (right *y*-axis). (B) Distributions of the sizes of the horizontal components of saccades for each subject during the 1-second interval before the discs reached the meeting point.

*Subject SS*: SS maintained the line of sight near the meeting point as the two discs moved toward each other. Once the two discs reached the meeting point, and thus well after the report was given (see Figure 3), SS tracked the disc pair as it exited the traffic diamond. This strategy can be seen in Supplementary Movie S1, which shows distributions of eye positions and disc positions over time from all trials from both tasks (*which-first* and *collision*). (Inspection of the movies from the two tasks separately showed no major differences.) The movie was constructed by compiling horizontal and vertical eye positions during successive 100 ms samples whose onsets were separated by 100 ms. Samples containing saccades or portions of saccades were not included. The rate of presentation was slower in the movie (samples within each 100-ms window were shown for 1 second) than it was during the actual experiment to aid viewing. Each 100-ms window was denoted according to its central time stamp. The color code denotes the number of samples in a given position (the color bar is shown in the movie). The intersection of the white lines shows the meeting point. The two small dots (in real size) show the positions of the standard disc (red) and average positions of the comparison disc (green). Please watch the movie before going on to the rest of this section.

As shown in the movie, SS kept the line of sight near the meeting point as the discs moved toward one another, with the cluster of eye positions displaced slightly below and to the left of the meeting point. When the discs reached the meeting point, and well after the report was given, the eye tracked the pair of discs as they moved up and to the left to exit the traffic circle. Although the tracking of the discs occurred after the report was given (Figure 3), subsequent analyses, including those in Experiment 2, suggest that this post-decision tracking may have served a useful purpose.

Further analyses confirmed the strategy described above:

1. SS made relatively few saccades (less than one per second) (Figure 4A). Directions were mainly rightward, toward the comparison disc, with sizes less than 2° (Figure 4B).
2. Heat maps of horizontal eye positions (*x*-axis) versus horizontal eye velocity (*y*-axis) (Figure 5) confirmed that SS used smooth pursuit to track the pair of discs as they moved to exit the traffic diamond. The heat maps in Figure 5 show results from seven 100-ms intervals (intervals with saccades not included) labeled according to the midpoint of the interval. The vertical white line in each panel shows the horizontal position of the meeting point, and the horizontal line marks zero horizontal velocity. The red and green bars represent the standard and comparison discs, respectively, with size drawn to scale to represent the horizontal size of the discs. It can be seen that SS's eye position remained near the meeting point with little change in eye velocity as the two discs moved toward each other. Eye velocities to the left can be seen at about 1.4 seconds, with velocity increasing over time. The leftward eye velocities confirm that the tracking movements seen in the movie as the discs exited the traffic diamond were smooth pursuit.

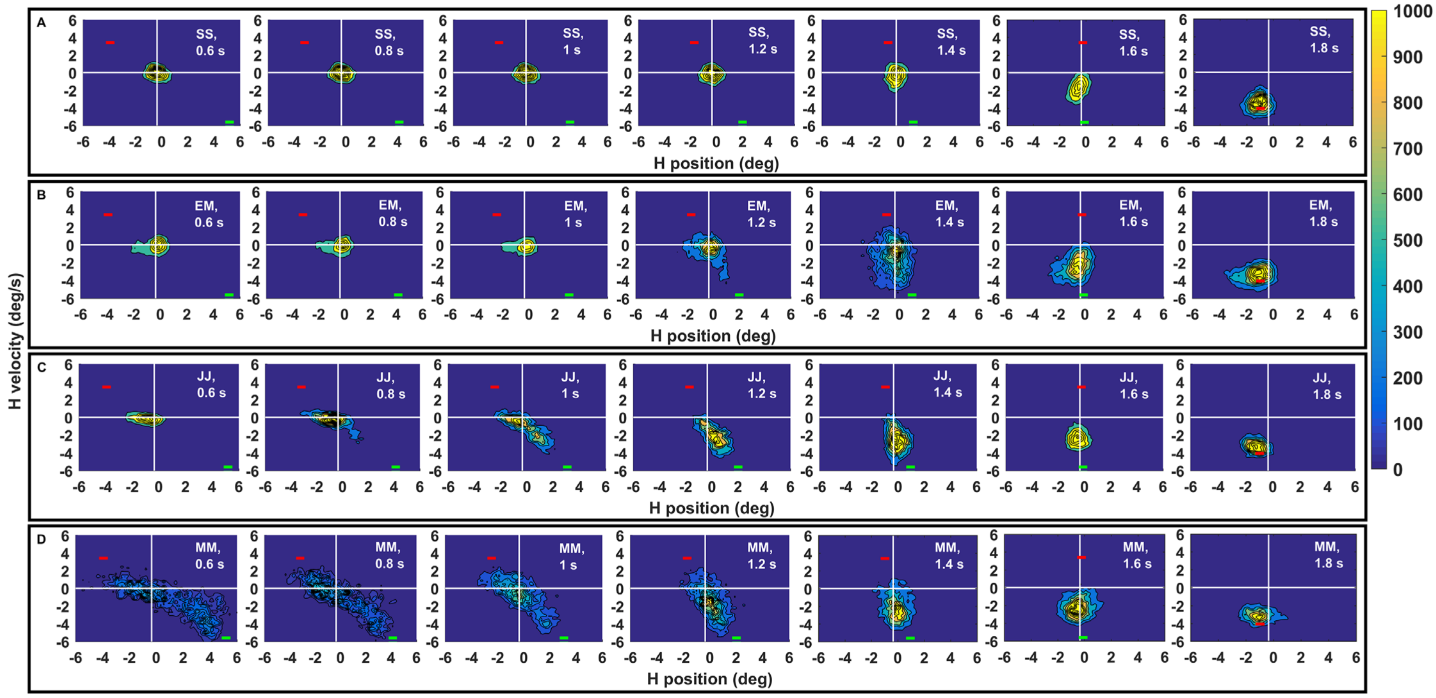


Figure 5. Three-dimensional distributions (heat maps, top view) representing horizontal eye position (*x*-axis) and velocity (*y*-axis) for successive (0.1-second) time samples in Experiment 1. Eye samples were pooled across the two tasks (*which-first* and *collision)* and the two long runway locations (right and left) and are shown as representing the long runway on the right. Each panel is labeled according to the center of the time interval. Red and green bars represent the standard and comparison discs, respectively, with size drawn to scale to represent the horizontal size of the discs. The colored legend bar represents the number of accumulated eye samples. Note that 0 on the *x*-axis marks the center of the display, and negative values along the axis indicate the left of center (short runway); 0 on the *y*-axis marks zero horizontal velocity, and negative values along the axis indicate the eye velocity to the left (same as the motion direction of the comparison disc). The vertical white line in each panel shows the horizontal position of the meeting point (–0.35°), and the horizontal line marks zero horizontal velocity. Samples containing saccades or portions of saccades were not included.

3. The smooth pursuit occurring after the discs reached the meeting point can be seen in Figure 6, which shows mean horizontal and mean vertical eye velocities ($\pm SD$) over time. These graphs took into account the trial-by-trial variation in the velocity of the comparison stimulus. This was done by first shifting both eye and stimulus velocities in time so that the results were aligned according to the time the comparison reached the meeting point, which was 1.6 seconds relative to the start of motion for the central velocity of the comparison disc. Eye and stimulus velocities were then scaled to compensate for the differences in the comparison velocities. The scaling was done by multiplying each original eye velocity $v$ for each time interval $t$ of each trial $n$ ($E_{v,n,t}$) by $V_c/V_n$, where $V_c$ is the central comparison velocity (5.28°/s), and $V_n$ is the velocity of the comparison on trial $n$. Figure 6 shows that mean eye velocities (horizontal and vertical) remained near but not necessarily equal to zero until about 1.2 seconds after the start of motion (400 ms before the discs reached the meeting point), after which the eye began to move smoothly up and to the left. One-sample $t$-tests done for both horizontal and vertical eye velocities confirmed that both were significantly different from zero at 1.2 seconds after the start of motion (horizontal: $t = –2.79$, $p = 0.005$; vertical: $t = 19.20$, $p = 10^{-73}$). Figure 6 also shows that, although horizontal eye velocities were close to an average of the horizontal eye velocities of both discs as the discs moved in opposite directions toward the meeting point, average vertical eye velocities were much closer to the velocity of the comparison disc. This difference across the meridians rules out simple vector averaging of both disc motions. The heat maps of Figure 5 verify that the mean horizontal velocities in Figure 6 were representative of performance and not the results of averages of movements in opposite directions. Inspection of distributions of vertical eye velocities showed that they were unimodal. Eye velocities before the discs reached the meeting point are discussed further below.

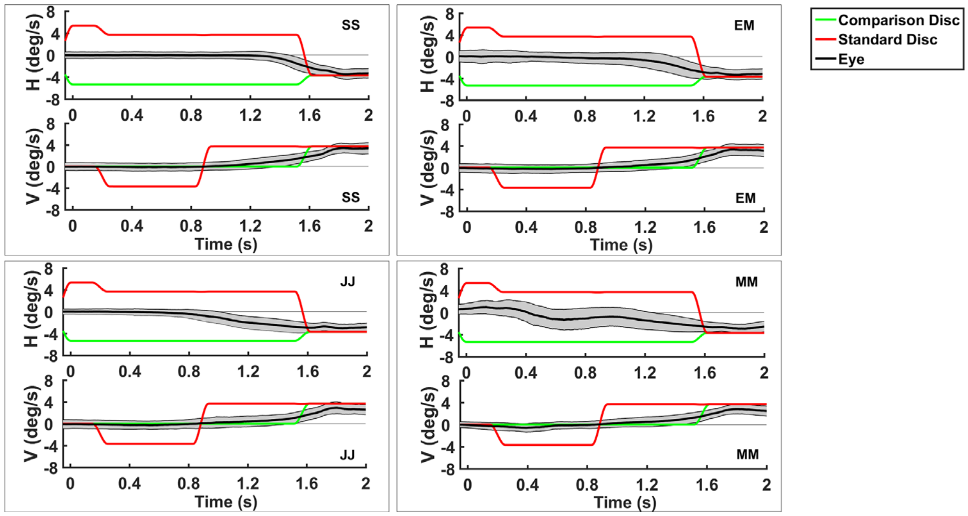


Figure 6. Mean velocities over time for Experiment 1. Horizontal (H) and vertical (V) velocities are shown for the standard disc (red), comparison disc (green), and eye (black), with gray shading representing ±*SD* for the *which-first* and *collision* tasks. Each trace shows mean velocities during successive 100-ms time periods whose onsets were advanced by 1 ms. Time 0 on the *x*-axis is the onset of motion of the discs. Stimulus and eye velocities for trials in which the long runway was on the left or the right were averaged together, with velocities for trials with the runway on the left rotated. Stimulus and eye velocities were shifted in time and then scaled to compensate for the differences in the comparison velocities before averaging (see text). The negative values indicate velocities to the left or down. Each mean is based on 706 to 1407 trials for SS, 793 to 1347 trials for JJ, 559 to 1209 trials for MM, and 729 to 1408 trials for EM.

*Subject EM*: EM's strategy was similar to that of SS in that EM maintained the line of sight near the meeting point and pursued the disc pair as it exited from the traffic diamond (see Supplementary Movie S2). The movie and the heat maps (Figure 5) show that EM's eye positions were distributed over a larger area than those of SS. The greater scatter of eye positions was due in part to more frequent (Figure 4A) and larger (Figure 4B) saccades. EM's saccades, like those of SS, were usually to the right, toward the comparison disc, with eye positions usually falling short of the comparison disc, as can be seen in the heat maps (Figure 5). The heat maps (Figure 5) and mean eye velocities (Figure 6) show eye velocities up and to the left by 1.2 seconds after the start of motion (eye velocities at 1.2 seconds were significantly different from zero; horizontal: $t = -15.17$, $p = 10^{-47}$; vertical: $t = 16.81$, $p = 10^{-56}$). The heat maps (Figure 5) and the mean eye velocities (Figure 6) confirmed the smooth pursuit of the pair of discs when the disc pair entered the last leg of the traffic diamond.

*Subject JJ*: Like SS and EM, JJ also maintained the line of sight near the meeting point and pursued the disc pair as it left the traffic diamond (see Supplementary Movie S3). However, there were some obvious differences. The heat maps show that beginning at about 0.8 to 1 second after the start of motion, when the discs were separated by more than 6°, JJ used saccades to look toward the comparison disc (note the increase in saccade frequency beginning at 0.8 seconds and predominance of directions to the right) (Figure 4). The increase in saccade frequency was accompanied by an increase in eye velocity in the direction of the comparison (Figure 5). JJ, like the other subjects, showed pursuit of the disc pair as it exited the traffic diamond with eye velocities significantly different from zero at 1.2 seconds after the start of motion (horizontal: $t = -56.38$, $p = 10^{-308}$; vertical: $t = 13.83$, $p = 10^{-40}$) (Figure 6). In summary, JJ's strategy was like those of SS and EM, except that at about 0.8 to 1 second after the start of motion and 0.6 to 0.8 seconds before the discs reached the meeting point JJ began to look toward the comparison disc and move smoothly in its direction, with eye positions and eye velocities falling short of the comparison disc (Figure 5).

*Subject MM*: MM's strategy differed from those of the other three subjects in that switching fixation between the discs was apparent as soon as the motion started, as can be seen in Supplementary Movie S4. MM typically began by looking at the standard disc, then the comparison, and then back toward the standard. MM made more frequent (Figure 4A) and larger saccades (Figure 4B) than the other subjects, and the saccades occurred in both horizontal directions, consistent with switching. Switching is also evident in the heat maps (Figure 5), which show that MM's eye velocities tended to be in the same direction as the disc currently being fixated (i.e., to the right when looking near the standard and to the left when looking near comparison). As was

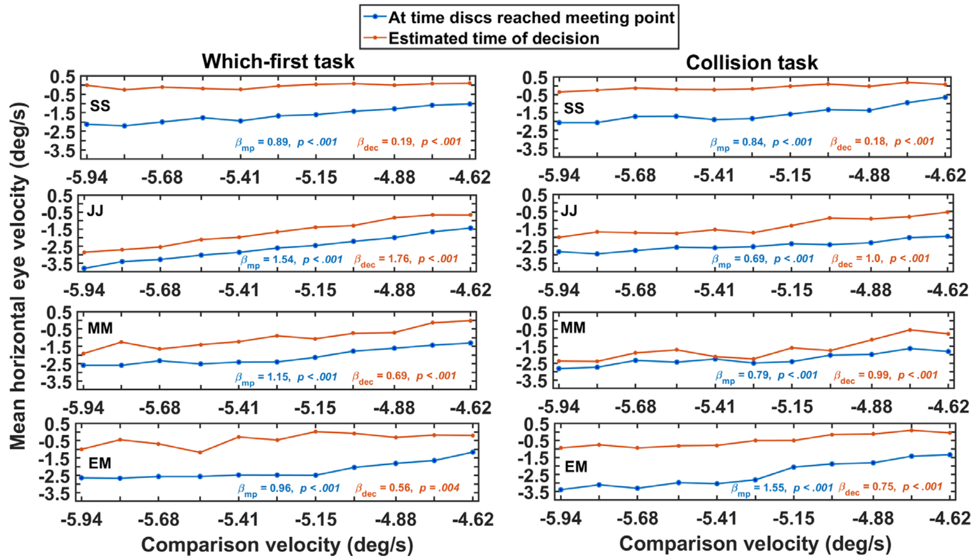


Figure 7. Mean horizontal eye velocity as a function of the comparison disc velocity at two time intervals in Experiment 1. Mean horizontal eye velocities at estimated time of decision (200 ms before button press; blue) and at the time the discs reached the meeting point (red) as a function of the comparison disc velocity for each subject and each task (left column, *which-first*; right column, *collision*). $\beta_{mp}$ is the slope of the best fitting line to the eye velocities when the first disc reached the meeting point. $\beta_{dec}$ is the slope of the line at the estimated time of decision. Each mean is based on 49 to 80 trials for SS, 32 to 79 trials for JJ, 22 to 79 trials for MM, and 43 to 71 trials for EM.

the case for the other three subjects, mean eye velocities different from zero were evident by 1.2 seconds (horizontal: $t = -27.90$, $p = 10^{-127}$; vertical: $t = 17.88$, $p = 10^{-62}$), with pursuit of the disc pair occurring as the discs exited the traffic diamond (Figures 5 and 6). In summary, MM preferred to switch between the standard and the comparison until the discs reached the meeting point when MM pursued the disc pair as it left the traffic diamond.

### *Micropursuit*

The results described in the prior section indicated that three subjects favored a strategy of maintaining eye position between the discs as they moved toward one another and one preferred to switch between the discs. The three who chose to look between the discs made small saccades (usually $<2°$ horizontally) (Figure 4) toward the comparison disc, a strategy most prominent in subject JJ. The heat maps (Figure 5) also show changes in horizontal eye velocities in all subjects as the discs moved toward one another. The most prominent changes seen thus far are the horizontal eye velocities in the direction of the comparison disc when eye positions shifted toward the comparison (JJ and MM) or when the comparison disc reached the meeting point (SS and EM). This section takes a closer look at the low-velocity smooth eye movements made while the discs approached one another.

To examine the effect of the motion of each disc on smooth eye velocity, we first took advantage of the fact that the horizontal velocity of the comparison disc on each trial was chosen from one of 11 closely spaced values. (The horizontal velocity of the standard disc remained the same on each trial.) Figure 7 illustrates mean horizontal eye velocity as a function of the horizontal velocity of the comparison disc during two different time intervals, 200 ms before the button press on each trial (thus, while the decision was being made) and the time that the first disc (standard or comparison) reached the meeting point. Figure 7 shows that the average horizontal eye velocity increased as a function of the velocity of the comparison disc during both time intervals. Slopes of the best fitting lines were significantly greater than zero in all cases (see Figure 7 for slope $\beta$ and $p$ values). Eye velocities were much slower than the comparison disc velocity as the discs moved toward one another (well under 50%). We refer to these low-velocity smooth eye movements that are correlated with the motion of the target disc as "micropursuit."

Micropursuit was found early in the trial. Figure 8 shows how the slopes of the functions relating horizontal eye velocity to comparison disc velocity changed over time. Slopes increased over time, reaching values significantly greater than zero as early as 0.5 seconds after the start of motion for three subjects (EM, JJ, and MM) and 1 second for the fourth (SS), well before the decision was made and while the two discs

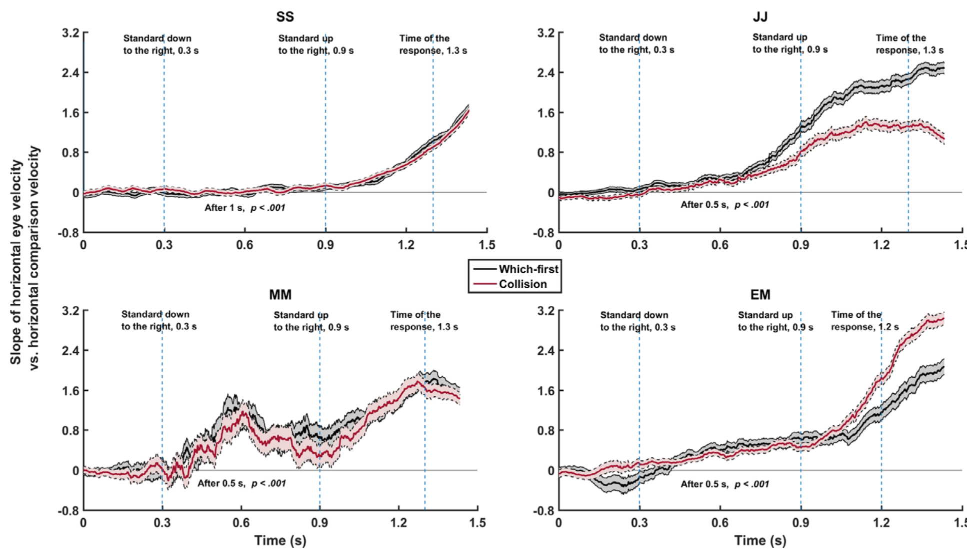


Figure 8. Slope (±*SE*) of eye velocity versus comparison disc velocity over time in Experiment 1. Slopes of best fitting lines (horizontal eye velocity vs. comparison disc velocity) during successive 100-ms time periods whose onsets were advanced by 1 ms. Time 0 marks the start of motion. Each trace ends 1.4 seconds relative to the start of the motion, marking the time when the comparison disc at its fastest velocity (5.94°/s) reached the meeting point. The time when the standard disc entered each oblique path in the traffic diamond before the meeting point and the average time of the button press between the *which-first* and *collision* tasks are marked by the vertical blue dashed lines.

were separated by 6° to 10° (see Figure 5). MM, the sole subject who favored a switching strategy, showed greater fluctuation in the horizontal slopes over time (Figure 8), with steeper slopes at about 0.6 seconds, when MM was looking closer to the comparison disc (Figure 5).

The smooth eye movement response to the disc motion shown in Figure 8 was not due to a few instances of high-gain pursuit of the comparison disc. This can be seen in the heat maps (Figure 5), which show that the distributions of eye velocities remained centered on low eye velocities during the time intervals when significant relationships between eye velocity and comparison disc velocity were observed (beginning at 0.5 seconds for JJ and EM and at 1 second for SS) (Figure 8). The fastest eye velocities were less than half of the comparison disc velocity until at least 1 second (JJ), 1.2 seconds (EM), or 1.6 seconds (SS) after the start of motion. The eye velocities of MM, the subject who switched between the discs, were different in that there were instances of eye velocities close to the velocity of the comparison that can be seen when eye position shifted toward the comparison.

To determine whether the standard disc also influenced eye velocity we turn to the vertical meridian. This is because the vertical component of motion of the standard varied during the trial, whereas the comparison disc did not move along the vertical meridian (until it reached the meeting point) (Figure 1). Note that, by analyzing the effect of the comparison disc on horizontal eye velocity (Figures 7 and 8) and the effect of the standard disc on vertical eye velocity (see below), we are not suggesting that each disc affected a different meridian of smooth eye movements. Rather, we are taking advantage of the fact that the comparison velocity varied along the horizontal meridian and the standard varied along the vertical in order to investigate the effect of each disc on smooth eye movements.

Figure 9 shows average vertical eye velocities during three episodes—namely, when the standard disc had no vertical motion, when it moved down, and when it moved up. In each case, the figure shows mean vertical eye velocity during the 100-ms interval at the center of each of these episodes (0.1 seconds, standard not moving vertically: 0.6 seconds, standard moving down; 1.3 seconds, standard moving up). Figure 9 shows that mean vertical eye velocities varied as a function of the vertical component of the velocity of the standard. Slopes of the functions shown in Figure 9 were significantly greater than zero: *which-first* (SS: $\beta = 0.09$, $p = 10^{-48}$; EM: $\beta = 0.11$, $p = 10^{-54}$; MM: $\beta = 0.12$, $p = 10^{-62}$; JJ: $\beta = 0.09$, $p = 10^{-41}$) and *collision* (SS: $\beta = 0.11$, $p = 10^{-64}$; EM: $\beta = 0.11$, $p = 10^{-58}$; MM: $\beta = 0.11$, $p = 10^{-62}$; JJ: $\beta = 0.10$, $p = 10^{-35}$). ANOVA (task × subject × velocity) confirmed that the effects of the velocity of the standard disc were reliable, $F(2, 6) = 356.63$, $p = 10^{-07}$ (vertical eye distributions were unimodal). Figure 9 also shows that vertical eye velocity was considerably slower than the velocity of the standard (less than 20%); thus, as was the case for the comparison disc, the smooth movements were too slow to be characterized as conventional smooth pursuit.

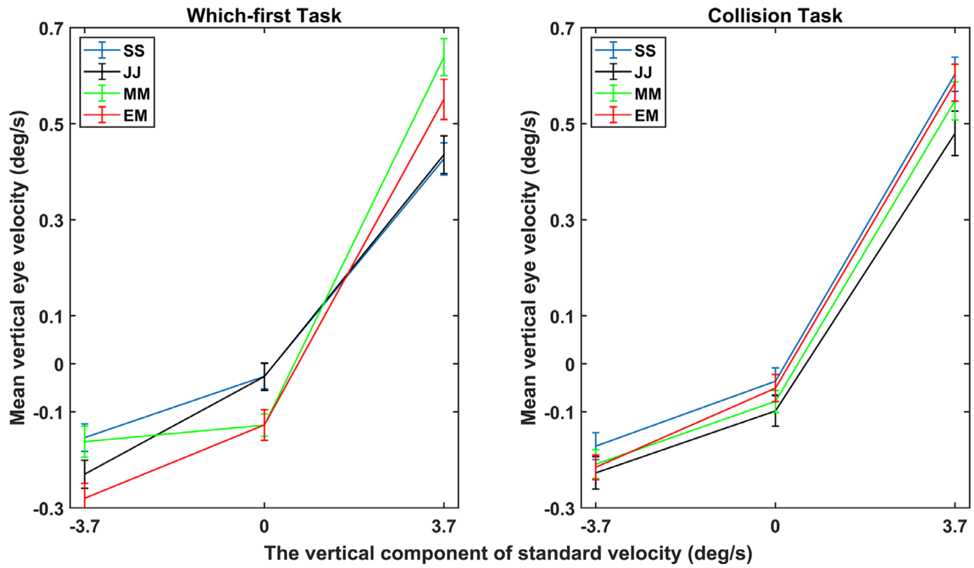


Figure 9. Mean vertical eye velocity (±*SD*) as a function of the three vertical components of the standard disc velocity in Experiment 1. Means across trials for each subject and each task were computed by averaging vertical eye velocities during 0.1-second windows centered at (a) 0.1 seconds, when the disc reached the midpoint of the short runway and the standard motion had no vertical component (0°/s); (b) 0.6 seconds, when the standard reached the midpoint of the first oblique branch and was moving down (−3.7°/s); and (c) 1.3 seconds, when the standard reached the midpoint of the second oblique branch and was moving up (3.7°/s). Each mean is based on 648 to 701 trials for SS, 472 to 685 trials for JJ, 364 to 567 trials for MM, and 537 to 714 trials for EM.

### *Summary of Experiment 1*

When asked to decide which of two discs would reach a meeting point first (2AFC) or whether a collision would occur (3AFC), perceptual performance was accurate and precise. The preferred eye movement strategy (3/4 subjects) can be characterized as looking near the meeting point while dividing attention between the discs. The fourth subject chose to switch between the discs. Two types of spontaneous smooth eye movements were observed: (a) low-velocity smooth eye movements (micropursuit) that correlated with the motion of both discs as they moved toward one another, and (b) spontaneous smooth pursuit of the pair of discs along the final leg of the traffic diamond, well after the response was made.

## Experiment 2: Fixate versus switch

Experiment 2 compared performance under two assigned strategies—namely, fixate a location near the meeting point, and switch fixation between the two discs. These strategies represent two extremes along a continuum of possible eye movement strategies that might be adopted during the task. These two strategies also capture the main aspects of the strategies found in Experiment 1, in which three subjects looked near the meeting point and one switched between the discs. Experiment 2 also provided an opportunity to determine whether the spontaneous smooth eye movements observed in Experiment 1 would occur when strategies were not freely chosen.

### *Methods*

The methods were the same as in Experiment 1 except for the instructions. In the fixate instruction, subjects were asked to fixate the meeting point. In the switch instruction, subjects were asked to switch fixation between two discs at least once after the discs started moving. Subjects were told that the instructions only applied to the time between the onset of motion until the button press. Instruction (fixate or switch) and task (*which-first* or *collision*) were changed every two to four sessions. Perceptual performance and eye movement results from the final 18 sessions (720 trials for each type of instruction and each task, the same as for Experiment 1) were analyzed and are reported below.

### *Perceptual performance*

Perceptual discrimination was precise for both tasks (Figure 10) and both eye strategies (fixate and switch), with Weber fractions ranging from 2% to 5%. Thresholds were lower under the fixate instruction for three subjects (SS, EM, and MM) and lower under the switch instruction for one subject (JJ). These differences were statistically reliable in each subject.

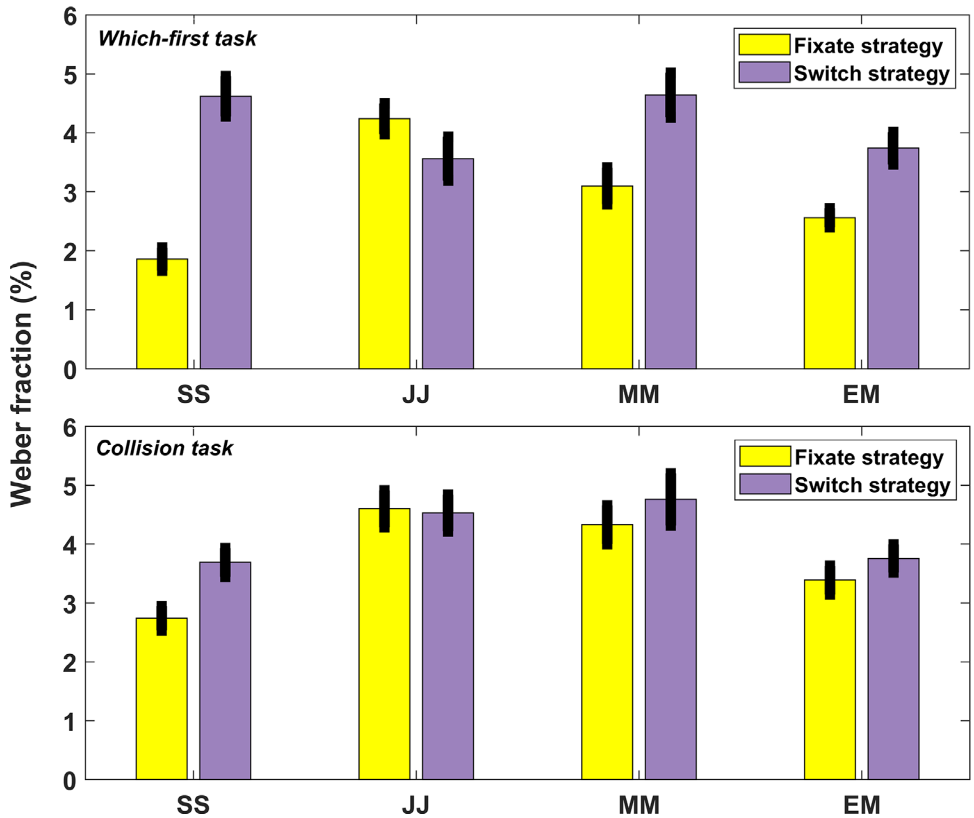


Figure 10. Perceptual discrimination in Experiment 2 under fixate and switch instructions. Weber fractions ($\pm SD$) for each subject (SS, JJ, MM, EM) are shown for the *which-first* and *collision* tasks. Weber fractions from the *collision* task reported in the bottom panel were obtained by grouping the responses as comparison first versus collision + comparison second. Weber fractions for the *which-first* task (top panel) are based on 706 to 718 trials for SS, 710 to 714 trials for JJ, 717 to 720 trials for MM, and 713 to 717 trials for EM. Weber fractions for the *collision* task (bottom panel) are based on 718 trials for SS, 714 to 716 trials for JJ, 714 to 720 trials for MM, and 686 to 708 trials for EM.

To compare performance across the two strategies statistically, we compared two models: unconstrained and constrained (Lu & Dosher, 2014, pp. 329–330; Zhao, Gersch, Schnitzer, Dosher, & Kowler, 2012). In the unconstrained model, parameters of the Weibull (slope and threshold) were estimated independently for each psychometric function. In the constrained model, parameters were constrained to be the same for the fixate and switch strategies within a given subject and condition. A likelihood ratio test was conducted to compare the goodness of fit between the constrained and unconstrained models. A significantly better fit under the unconstrained model would show that the performance was significantly different across the two strategies. The chi-square values showed that over all subjects the unconstrained model gave a significantly better fit to the data for both the *which-first* ($\chi^2 = 112.26$, $p = 10^{-23}$) and *collision* ($\chi^2 = 6.03$, $p = 0.003$) tasks. Results were similar when the data from the *collision* task were grouped as collision + comparison first versus comparison second ($\chi^2 = 57.74$, $p = 10^{-12}$). Tests on individual subjects including data from both the *which-first* and *collision* tasks showed that the unconstrained model provided a significantly better fit to the data for every subject (SS: $\chi^2 = 72.75$, $p = 10^{-15}$; JJ: $\chi^2 = 14.85$, $p = 0.005$; MM: $\chi^2 = 17.69$, $p = 0.001$; EM: $\chi^2 = 22.99$, $p = 10^{-04}$).

The overall superiority of perceptual discrimination under the fixate strategy extended to finding earlier response times (Figure 11). A four-way ANOVA (2 eye strategies × 2 tasks × 11 comparison velocities × 4 subjects) showed a main effect of eye strategy, $F(1, 103) = 358.89$, $p = 10^{-35}$.

Weber fractions under the fixate instruction in Experiment 2 were not statistically different from those in Experiment 1, where strategies were freely chosen. Two-way ANOVAs (subject × experiment) showed no main effect of subject or experiment for either the *which-first* task, subject: $F(3, 3) = 0.79$, $p = 0.58$; experiment: $F(1, 3) = 1.82$, $p = 0.27$, or the *collision* task, subject: $F(3, 3) = 1.45$, $p = 0.38$; experiment: $F(1, 3) = 2.27$, $p = 0.23$. Results were similar when comparing Weber fractions under the switch instruction in Experiment 2 with those in Experiment 1. Two-way

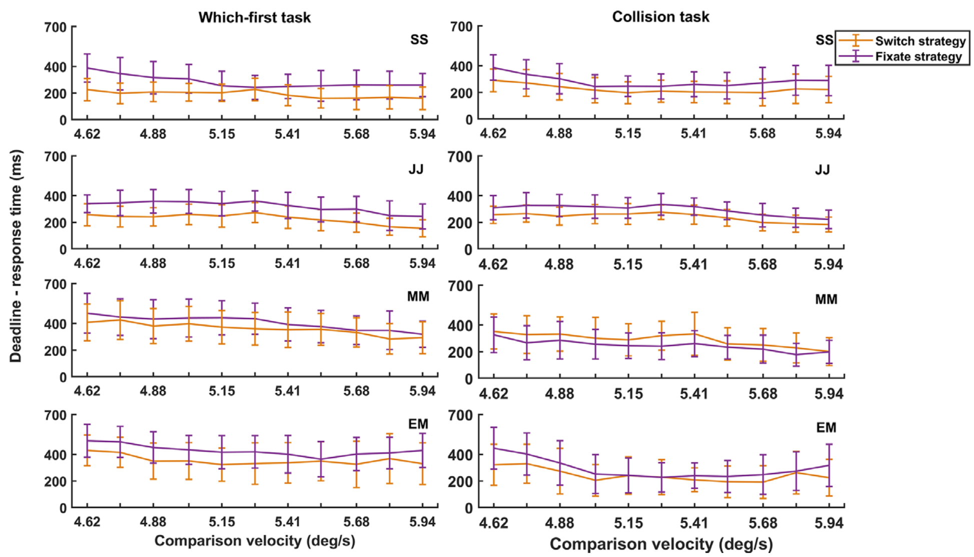


Figure 11. Mean (±*SD*) difference between deadline and response time as a function of the comparison disc velocity in Experiment 2 for the two tasks and the fixate and switch instructions. Deadline is the time when the first of the two discs reached the meeting point (1.4–1.6 seconds relative to the start of the motion), and response time is the recorded time of the button press responses. Larger means indicate earlier responses. Each mean is based on 45 to 81 trials for SS, 50 to 89 trials for JJ, 39 to 80 trials for MM, and 45 to 81 trials for EM.

ANOVAs (subject × experiment) showed no main effect of subject or experiment for either the *which-first* task, subject: $F(3, 3) = 3.11$, $p = 0.18$; experiment: $F(1, 3) = 2.19$, $p = 0.24$, or the *collision* task, subject: $F(3, 3) = 3.17$, $p = 0.18$; experiment: $F(1, 3) = 1.67$, $p = 0.29$.

These analyses show that a strategy of fixating near the meeting point, which was closer to the preferred strategies found in Experiment 1 in three of the four subjects, led to better perceptual discrimination than a strategy of deliberately switching between the discs in three of the four subjects. One subject, JJ, performed better under the switch strategy, a result that was likely to be due to a stricter interpretation of "fixate," as is shown in the following sections.

### Eye movements

Movies showing eye and disc positions over time from all trials from both tasks (*which-first* and *collision*) confirmed that all four subjects fixated near the meeting point under the fixate instructions (see Supplementary Movies S5, S6, S7, and S8) and looked at each disc, with some pursuit of each while fixated, under the switch instruction (see Supplementary Movies S9, S10, S11, and S12). MM, who preferred switching over central fixation in Experiment 1, executed the switch strategy similarly in the two experiments except for one characteristic. In Experiment 1, MM always started by looking near the standard disc, then switching to the comparison disc (Supplementary Movie S4). In Experiment 2, MM started by looking at either disc, and showed more pursuit of each while fixated (Supplementary Movie S12).

One notable characteristic of performance under the fixate instruction was that three subjects (SS, EM, and MM) spontaneously tracked the disc pair as it was exiting the traffic diamond (as they did in Experiment 1), whereas one (JJ) remained fixated near the meeting point for the entire trial. The absence of tracking of the disc pair at the end of the trial may be a sign that JJ took the instruction to fixate more seriously than the other three subjects. This strategy, which might have also affected the distribution of attention, may have been responsible for JJ's higher perceptual thresholds under the fixate instruction than the switch instruction.

We limited further analyses of the eye movements of Experiment 2 to the fixate instruction because of its greater similarity to the more popular strategy of Experiment 1. A detailed analysis of eye movements under the switch instruction is beyond the scope of this paper.

The fixate instruction in Experiment 2 led to stricter adherence to looking near the meeting point than was found in the freely chosen strategies of Experiment 1. Saccades were less frequent (Figure 12A) and smaller (Figure 12B) than in Experiment 1 (Figure 4). Saccade directions were once again mainly rightward, toward the comparison disc. The heat maps (Figure 13) show that eye positions remained near the meeting point and horizontal smooth eye movements remained close to 0°/s as the discs approached one another, with increases in horizontal eye velocity becoming apparent by about 1.4 seconds after the start of motion in all except JJ,

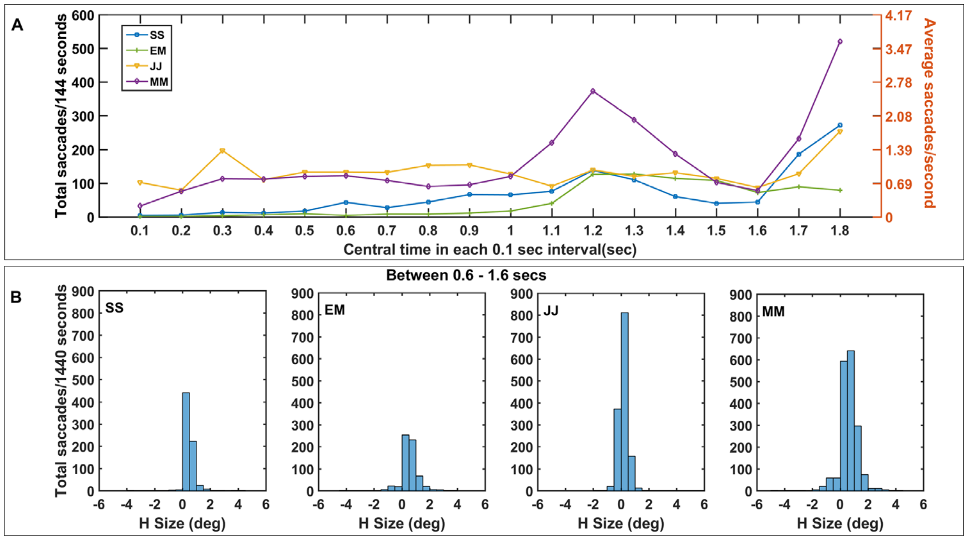


Figure 12. Saccades under the fixate instruction in Experiment 2. (A) Number of saccades over successive 100-ms time windows. Results are shown as the number of saccades over the 1440 trials (left *y*-axis) or as saccade frequency (right *y*-axis). (B) Distributions of the sizes of the horizontal components of saccades for each subject during the 1-second interval before the discs reached the meeting point.

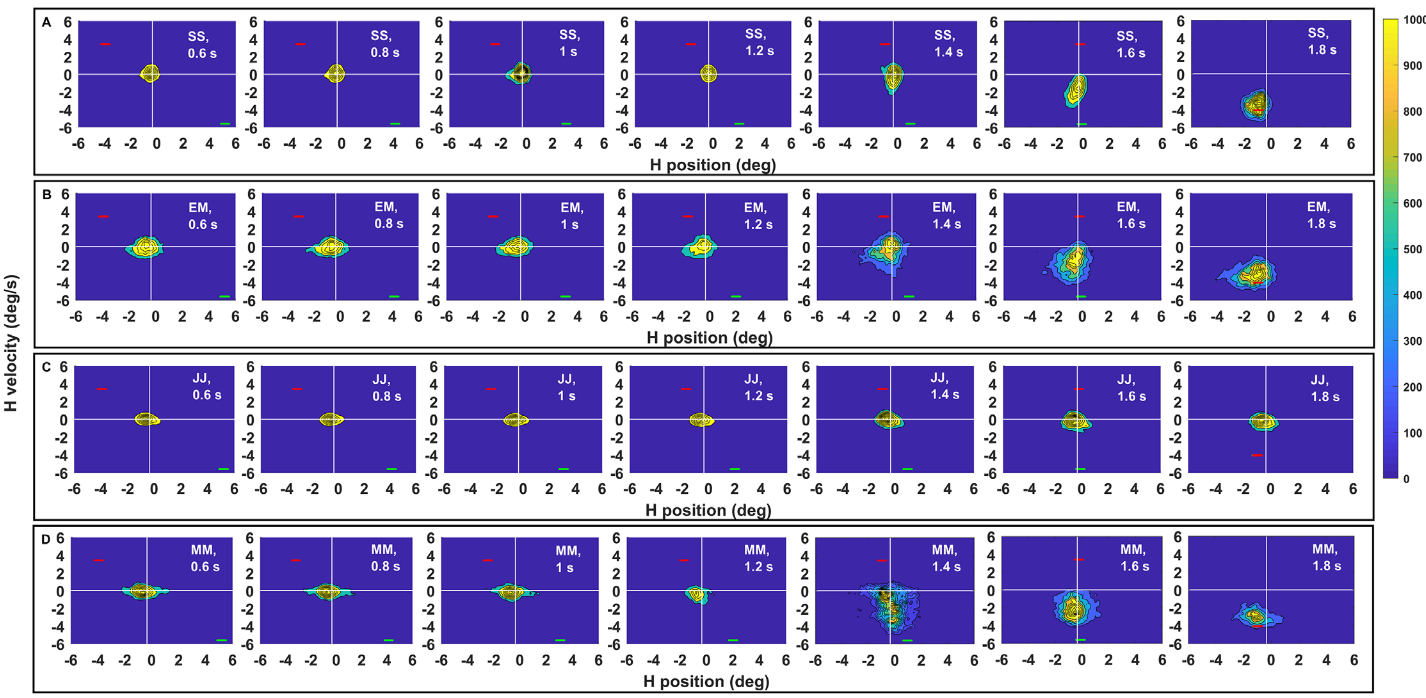


Figure 13. Three-dimensional distributions (heat maps, top view) representing horizontal eye position (*x*-axis) and velocity (*y*-axis) for successive (0.1-second) time samples in Experiment 2, fixate instruction. Eye samples were pooled across the two tasks (*which-first* and *collision*) and the two long runway locations (right and left) and are shown as representing the long runway on the right. Each panel is labeled according to the center of the time interval. Red and green bars represent the standard and comparison discs, respectively, with size drawn to scale to represent the horizontal size of the discs. The colored legend bar represents the number of accumulated eye samples. Note that 0 on the *x*-axis marks the center of the display, and negative values along the axis indicate the left of center (short runway); 0 on the *y*-axis marks zero horizontal velocity, and negative values along the axis indicate the eye velocity to the left (same as the motion direction of the comparison disc). The vertical white line in each panel shows the horizontal position of the meeting point (–0.35°), and the horizontal line marks zero horizontal velocity. Samples containing saccades or portions of saccades were not included.

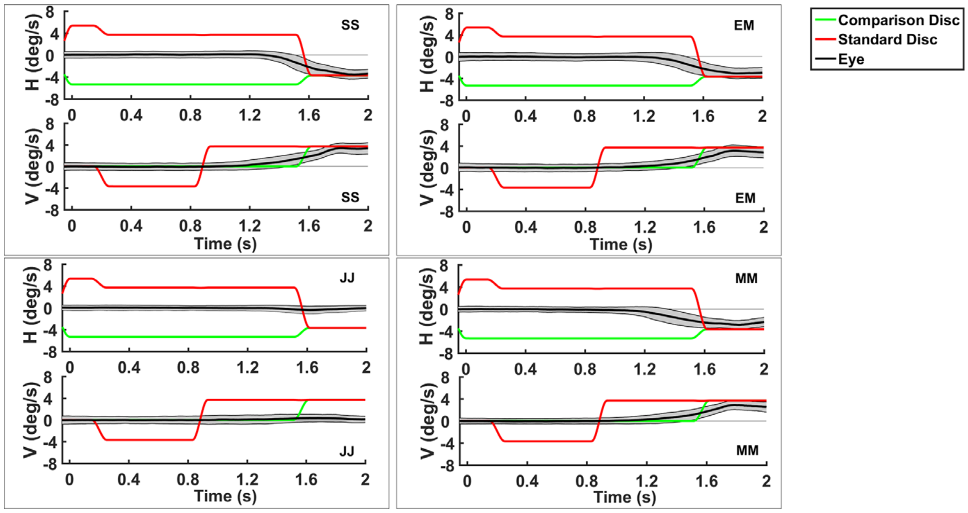


Figure 14. Mean velocities over time for Experiment 2, fixate instruction. Horizontal (H) and vertical (V) velocities are shown for the standard disc (red), comparison disc (green), and eye (black) with gray shading representing ±*SD* for the *which-first* and *collision* tasks. Each trace shows mean velocities during successive 100-ms time periods whose onsets were advanced by 1 ms. Time 0 on the *x*-axis is the onset of motion of the discs. Stimulus and eye velocities for trials in which the long runway was on the left or the right were averaged together, with velocities for trials with the runway on the left rotated. Stimulus and eye velocities were shifted in time and then scaled to compensate for the differences in the comparison velocities before averaging (see text). The negative values indicate velocities to the left or down. Each mean is based on 855 to 1437 trials for SS, 1077 to 1303 trials for JJ, 723 to 1370 trials for MM, and 843 to 1437 trials for EM.

who remained near the center with little change in horizontal eye velocities throughout. The absence of the spontaneous pursuit for JJ was confirmed by the mean eye velocities shown in Figure 14.

### *Micropursuit*

Micropursuit was evident in Experiment 2 under the fixate instruction, although diminished relative to what was found in Experiment 1. Figure 15 shows the

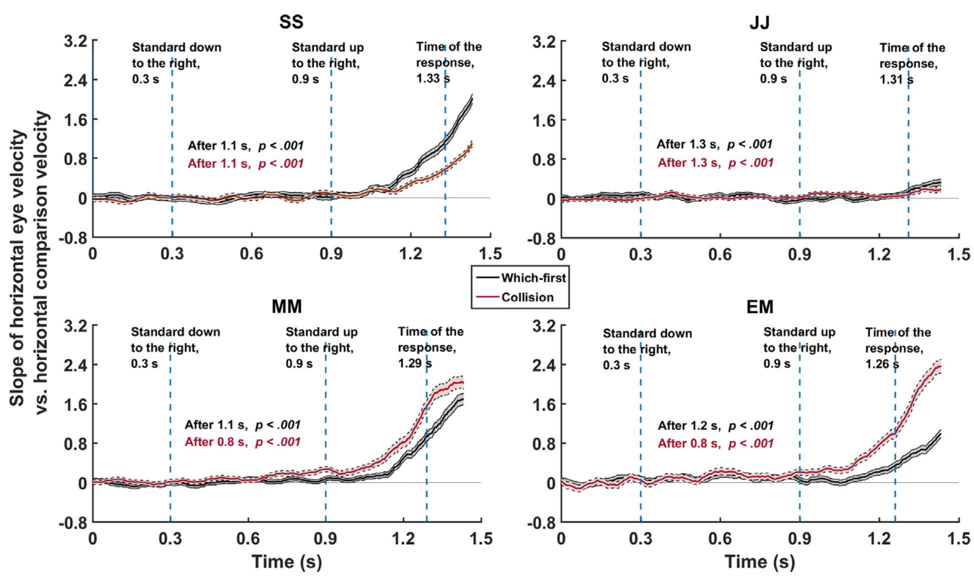


Figure 15. Slope (±*SE*) of eye velocity versus comparison disc velocity over time in Experiment 2, fixate instruction. Slopes of best fitting lines (horizontal eye velocity vs. comparison disc velocity) during successive 100-ms time periods whose onsets were advanced by 1 ms. Time 0 marks the start of motion. Each trace ends 1.4 seconds relative to the start of the motion, marking the time when the comparison disc at its fastest velocity (5.94°/s) reached the meeting point. The time when the standard disc entered each oblique path in the traffic diamond before the meeting point and the average time of the button press between the *which-first* and *collision* tasks are marked by the vertical blue dashed lines.

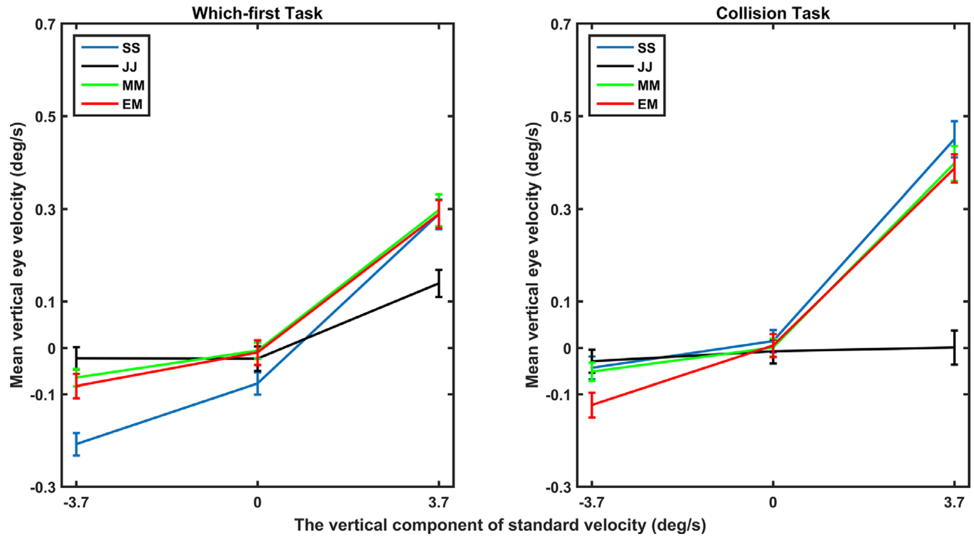


Figure 16. Mean vertical eye velocity (±*SD*) as a function of the three vertical components of the standard disc velocity in Experiment 2, fixate instruction. Means across trials for each subject and each task were computed by averaging vertical eye velocities during 0.1-second windows centered at (a) 0.1 seconds, when the disc reached the midpoint of the short runway and the standard motion had no vertical component (0°/s); (b) 0.6 seconds, when the standard reached the midpoint of the first oblique branch and was moving down (–3.7°/s); and (c) 1.3 seconds, when the standard reached the midpoint of the second oblique branch and was moving up (3.7°/s). Each mean is based on 622 to 719 trials for SS, 618 to 677 trials for JJ, 499 to 694 trials for MM, and 578 to 720 trials for EM.

slopes of the functions relating mean horizontal eye velocity to the horizontal velocity of the comparison disc over time. Slopes did not exceed zero until about 0.8 to 1.3 seconds after the start of motion (Figure 15), about 0.5 seconds later than the slopes exceeded zero in Experiment 1 (Figure 8). Note that JJ's slopes were shallower than those of the other subjects, consistent with JJ's lack of overt smooth pursuit at the end of the trial.

Mean vertical eye velocities were again significantly affected by the vertical component of the standard velocity, as in Experiment 1. Figure 16 shows mean vertical velocity as a function of the vertical component of motion of the standard. Analysis of variance (task × subject × velocity) confirmed that the effects were reliable, $F(2, 6) = 112.68$, $p = 10^{-05}$ (vertical eye distributions were unimodal). Slopes were shallower in Experiment 2 under the fixate instruction than in Experiment 1 (Figure 9) when the eye strategy was freely chosen. Slopes were significantly greater than zero except for JJ in the *collision* task: *which-first* (SS: $\beta = 0.067$, $p = 10^{-36}$; EM: $\beta = 0.05$, $p = 10^{-20}$; MM: $\beta = 0.061$, $p = 10^{-37}$; JJ: $\beta = 0.016$, $p = 0.002$; *collision* (SS: $\beta = 0.065$, $p = 10^{-29}$; EM: $\beta = 0.0568$, $p = 10^{-35}$; MM: $\beta = 0.059$, $p = 10^{-31}$; JJ: $\beta = 0.004$, $p = 0.48$). Figure 16 also shows that JJ's slopes were closer to zero than those of the other subjects, once again consistent with JJ's lack of overt pursuit at the end of the trial.

### *Summary of Experiment 2*

Perceptual performance was better under the fixate instruction than the switch instruction in three of the four subjects. JJ, the subject who showed better performance under the switch instruction, did not pursue the pair of discs at the end of the trial under the fixate instruction (Figure 14). We suspect that JJ fixated more carefully than the other three, presumably allocating less attention to the pair of the discs and more to maintaining fixation or to the stationary outline of the display.

The micropursuit observed in Experiment 1 was also found in Experiment 2 but with lower velocity. This suggests that micropursuit was not determined solely by low-level sensory factors associated with the motion of the discs (which were the same in both experiments), but rather involved higher level decisions, such as decisions about the allocation of attention. Another example of the role of decisions was that the saccades were smaller and occurred less frequently under the fixate instruction of Experiment 2 than found with the freely chosen strategies of Experiment 1.

## Discussion

Dynamic perceptual tasks, in which critical objects are in motion, present different challenges for eye movement planning than found in tasks employing static visual arrays. Eye movement plans need to take into account the changing locations of key objects and may involve smooth eye movements, as well as saccades. Most previous studies of dynamic tasks have focused on using sequences of eye positions to infer which locations are judged to contain useful information at different stages of task performance (Brenner & Smeets, 2011; Corrigan et al., 2017; Crespi et al., 2012; Diaz et al., 2013; Dorr et al., 2010; Johansson et al., 2001; Kandil et al., 2009; Kandil, Rotter, & Lappe, 2010; Knöll et al., 2018; Ko et al., 2010; Land & Lee, 1994; Land & McLeod, 2000; Lappi et al., 2013; Matthis et al., 2018; Ross & Kowler, 2013; Sullivan et al., 2012). Smooth eye movements have received less attention. Some previous studies have reported a useful role for smooth pursuit during perceptual or visuomotor tasks (Cesqui et al., 2015; Danion & Flanagan, 2018; Spering et al., 2011), others have reported the occurrence of spontaneous smooth pursuit (Brenner & Smeets, 2011; Corrigan et al., 2017; Dorr et al., 2010; Goettker et al., 2020; Land & McLeod, 2000; Lappi et al., 2013; Ross & Kowler, 2013), and still others have not reported changes in smooth eye movements, despite the fact that key objects were continually in motion (Johansson et al., 2001; Ko et al., 2010; Kowler et al., 2014). The present study sought to better understand eye movement strategies during dynamic perceptual tasks, with an emphasis on the involvement of smooth eye movements, including their role as indicators of the distribution of attention over time.

We studied eye movement patterns during a relatively simple perceptual task, judging which of two moving discs would arrive first at a common meeting point. When strategies were freely chosen (Experiment 1), we found a preference (in three of four subjects) to maintain the line of sight between the discs as they headed toward the meeting point. When strategies were assigned (Experiment 2), we found that keeping the line of sight near a central location between the moving discs, similar (but not identical) to the preferred strategy in Experiment 1, led to better perceptual performance than switching between the discs. We also found two unexpected properties of smooth eye movements: (a) spontaneous smooth pursuit of the pair of discs after they reached the meeting point and moved together along a common path, after the perceptual report was given, and (b) micropursuit, low-velocity smooth eye movements that were correlated with the motion of each disc and that occurred while the line of sight remained between the moving discs. We consider below these three major findings—better performance and preferences for central fixation over switching, spontaneous smooth pursuit, and micropursuit—and their implications for understanding both the eye movement strategies and the distribution of attention during the performance of dynamic visual tasks.

## Central fixation versus switching

A strategy of looking between the moving discs was preferred by three of the four subjects when strategies were freely chosen in Experiment 1 and produced better perceptual performance than switching between the discs when the strategies were assigned in Experiment 2. These results extend the observations made by Fehd and Seiffert (2008, 2010), who studied multiple-object tracking and found that the preferred and better strategy was to look near the center of the set of moving objects rather than to constantly switch fixation among them.

In considering why central fixation might be a better strategy than switching, it is helpful to note several potential disadvantages associated with switching when key objects are in motion. Switching may be problematical because of the tradeoff: Any momentary benefit to the visual resolution or motion discrimination for the fixated object due to reduced retinal eccentricity (McKee & Nakayama, 1984; McKee & Welch, 1989) or to presaccadic shifts of attention (Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995; Li, Barbot, & Carrasco, 2016; Zhao et al., 2012) might occur at the cost of losing irrecoverable perceptual information about the changing properties of non-fixated objects. Another potential disadvantage of switching is that the saccades themselves may impair visual resolution (Burr, Morgan, & Morrone, 1999). Finally, planning and carrying out the switches place demands on executive processes and thus may interfere with other ongoing cognitive decisions. In support of the importance of demands on executive processes, Rubinstein and Kowler (2018) showed that saccades made to switch between a graph and accompanying text are avoided when the effort level associated with planning the saccades is increased by using a gaze-contingent paradigm. Maintaining eye position at or near a chosen central location, the preferred and the better strategy in the current task, is less demanding and may provide adequate visual resolution of all critical objects (Najemnik & Geisler, 2005), as well as providing a central vantage point from which to evaluate the relative motion of the objects.

Despite the disadvantages that made switching less popular in Experiment 1 and less effective in Experiment 2, we note that there were no significant differences between perceptual performance across the two experiments. Comparing across the experiments is difficult because performance or strategies of using attention may have changed over time. Further work will be needed to better understand differences between freely chosen and instructed strategies, taking into account the eye movements themselves (for example, certain strategies, such as total suppression of the micropursuit, may have been detrimental to perceptual performance), as well as the higher level processes needed to manage and execute the eye movements and control the distribution of attention.

Another key question for future investigation is how strong the demands for visual precision must be in order for observers to decide spontaneously that the visual benefits of fixation or pursuit of a critical object outweigh any costs of switching, where costs include the extra cognitive load required to plan the saccades, the possible decrements in visual resolution for some critical moving objects within the display, and the need to coordinate the timing of the saccades with the changes in positions of the relevant objects.

Eye movements when keeping the line of sight between the discs in Experiment 1 were categorically similar to the eye movements in response to the fixate instruction in Experiment 2, but the line of sight was more stable in Experiment 2. Saccades were smaller and occurred less frequently (compare Figure 4 and Figure 12) and smooth eye movements were slower. The differences between the eye movements observed in the two experiments were most striking for subject JJ. JJ adhered more closely to the instruction to fixate than the other subjects, showing slower eye velocities as the discs moved toward one another and abandoning the otherwise ubiquitous spontaneous smooth pursuit at the end of trials, after the decision was recorded. These smooth eye movement characteristics are discussed below.

## Spontaneous smooth pursuit

Studies of eye movements during visual tasks typically assume that the spontaneous eye movements are not frivolous but rather are made for a useful purpose relating to the immediate needs of the task—for example, producing retinal eccentricities that are optimal for task performance in the case of saccades or reducing the retinal image speed of attended targets in the case of smooth pursuit. The assumption that eye movements are made for a useful purpose forms the basis of attempts to infer aspects of task strategies from observations of eye movements. The assumption that eye movements serve useful purposes related to the immediate needs of the task does not appear to apply to the spontaneous smooth pursuit that we found at the end of the trials because the pursuit occurred after the decision was reported, when the discs moved as a pair to exit the traffic diamond (see Supplementary Movies and Figures 6 and 14). In a study that was designed in part to investigate possible useful roles for smooth pursuit, we were surprised to find that the most prominent pursuit occurred when it had no obvious effect on the immediate decision.

It is tempting to dismiss the spontaneous post-decision smooth pursuit as irrelevant (not helping, but not hurting either), except for one result—namely, that the one case that lacked any spontaneous pursuit (JJ's eye movements under the fixate instruction in Experiment 2) was associated with a significant reduction in perceptual performance. Could this result point to a useful role for the spontaneous pursuit? Perhaps. One possibility is that the spontaneous pursuit of the disc pair contributed to some type of online feedback process in which the decision was compared to the perceived motion of the discs as they were tracked. An alternative, which we believe requires fewer assumptions and is more likely, involves attention. If the perceptual judgments required attending to the moving discs, the spontaneous pursuit may have simply followed as a consequence of the continued attention to the discs. Disengaging attention from the discs after the judgments would have imposed an extra processing step that was not required and potentially would have added to the task load by introducing another decision, or incur the risk of disengaging attention too early (for discussions of preferences to minimize cognitive load, see Shenhav, Musslick, Lieder, Kool, Griffiths, Cohen, & Botvinick, 2017; for how this preference affects the planning of saccadic eye movements, see Rubinstein & Kowler, 2018). The absence of spontaneous pursuit for JJ in Experiment 2 under the fixate instruction could have been due to an effort to disengage attention from the discs or, alternatively, to a decision to fixate more carefully by increasing attention to the stationary outline of the display at the expense of attention to the discs during the earlier and task-critical intervals. These considerations lead us to draw two conclusions from the spontaneous smooth pursuit eye movements. First, spontaneous pursuit that is unrelated to the immediate demands of the task may, nevertheless, provide a useful indicator of how attention is distributed over time. Second, managing changes in the distribution of attention may itself be costly, leading to a preference to keep attention where it is (divided between the discs, in this case) as long there are no deleterious consequences. Spontaneous pursuit provides another example of preferences to avoid adding cognitive steps that increase demands on executive function (Rubinstein & Kowler, 2018; Shenhav et al., 2017).

## Micropursuit

A novel finding of this study was the observation of low-velocity smooth eye movements, which we termed micropursuit, during the portion of the trial when the discs moved toward one another and the perceptual judgment was being made. This finding is novel in the context of the prior literature on eye movements during dynamic tasks, which either did not report properties of smooth eye movements or reported that smooth eye movements were not affected by the motion of objects in the displays. Micropursuit velocity was low (<50% of the velocities of the discs, thus far slower than conventional smooth pursuit) and depended on the velocity of both the comparison disc (Figures 7, 8, and 15) and the standard disc (Figures 9 and 16). Micropursuit began as early as 0.5 seconds after the onset of motion, about 1 second before the discs reached the meeting point; thus, it occurred while the decision was being made and while the discs remained separated by several degrees. Differences between the relative contributions of the motion of the standard and comparison discs along the two meridians rules out a simple weighted vector average of the motion of the discs. We use the term "micropursuit" to highlight the fact that the smooth eye movements were correlated with the motion of the targets (like conventional pursuit) but, unlike conventional pursuit, were not made as part of an overt effort to track the targets but rather reflected a higher-level strategy. What strategy or strategies could have been used? Possibilities include distributing attention between the discs using weights that differed for the horizontal and vertical meridians, allocating some attention to the stationary outline of the display, or trying to suppress pursuit or reduce its gain (Steinman, Skavenski, & Sansbury, 1969). Any or all of the three could have occurred. Future work that examines subtle aspects of smooth eye movements coupled with different perceptual tasks and perceptual measures and specific incentives to control attention, image motion, and eye position can shed more light on the options people have to choose strategies that may optimize performance of a task. Smooth eye movements, even slow and subtle effects such as shown by the micropursuit, may be important and useful indicators of the strategies employed.

Micropursuit has not been reported in prior studies involving perceptual judgments of moving targets (Johansson et al., 2001; Ko et al., 2010; Kowler et al., 2014). It is possible that micropursuit was not noticed either because stimulus velocities were low enough to fall within the range of slow eye velocities during fixation, a possibility noted by Ko et al. (2010), or because the analyses were not sufficient to disclose any small moment-by-moment correlations between stimulus and eye (Johansson et al., 2001; Kowler et al., 2014). Micropursuit might have been present in the study of multiple-object tracking by Fehd and Seiffert (2008), who reported smooth eye movements during multiple-object tracking but did not report a quantitative analysis.

The suggestion that the micropursuit was due at least in part to the distribution of attention across the display is consistent with prior findings showing that attention is allocated to the selected motion during smooth pursuit (Chen et al., 2017; Heinen et al., 2011; Jin et al., 2013; Khan et al., 2010; Khurana & Kowler, 1987; Lovejoy et al., 2009; Souto & Kerzel, 2011; Watamaniuk & Heinen, 2015). Another finding supporting a role for attention or other high-level factors is that micropursuit was diminished under the fixate instruction of Experiment 2. Had the micropursuit been due solely to an automatic influence of low-level sensory or motion cues, it should have been the same in both experiments. We also note that the reduction in micropursuit in Experiment 2 was associated with a reduction in the sizes and frequencies of saccades. The reduction in both micropursuit velocity and saccade frequency and size in Experiment 2 may be the result of both pursuit and saccades reacting independently to efforts to fixate more strictly. Alternatively, it is possible that there was some interaction between the saccades and micropursuit at the level of either oculomotor programming or a shared selective mechanism, similar to what has been proposed for pursuit/saccade interactions in other tasks (Erkelens, 2006; Gardner & Lisberger, 2001; Liston & Krauzlis, 2003).

Although micropursuit was diminished (but not abolished) in Experiment 2, perceptual judgments did not suffer as a result. This result is not necessarily surprising because withdrawing some attention from the moving discs in Experiment 2 may have been sufficient to reduce the micropursuit velocity but might not have been sufficient to impact the perceptual judgments. (Withdrawing more attention might have been detrimental.) It is well known that the relationship between the strength of attention and the resulting performance differs according to the task (Sperling & Dosher, 1986). Khurana and Kowler (1987), for example, found that diverting some attention away from the pursuit target to the non-target improved perceptual performance for the non-target without having much effect on perceptual performance for the target.

A phenomenon termed micropursuit was recently reported by Parisot et al. (2021). In their study, micropursuit was detected in a task in which the instruction was to fixate a central target while monitoring for changes in a non-target moving stimulus. The authors suggested that the micropursuit they observed was similar to the low eye velocities observed when fixating a stationary target in the presence of moving non-targets (e.g., Collewijn & Tamminga, 1984; Collewijn & Tamminga, 1986; Kowler et al., 1984; Masson et al., 1995; Murphy et al., 1975; Spering & Gegenfurtner, 2007). Parisot et al. (2021) argued that micropursuit should be considered a separate "class" of eye movements.

Although the factors that generated micropursuit in the study by Parisot et al. (2021) and in the present study may be similar, we do not believe that the evidence calls for a separate eye movement class or subsystem. Rather, we believe that the significance of micropursuit is functional: Micropursuit reflects the contribution of the decisions that are invoked in order to meet the requirements of a dynamic perceptual task that requires monitoring objects moving along different trajectories. These decisions might include the distribution of attention to the available targets, as well as overt efforts to control the gain of the response (Steinman et al., 1969). Many factors might dictate these decisions, including the assessed benefits of different distributions of attention, the cost of disengaging attention from different targets, or the need to maintain eye position near some optimal location for some period of time. Control of micropursuit velocity may also reflect the need to maintain retinal image velocities at some optimal values for visibility (Epelboim, 1998; Intoy & Rucci, 2020). Because of the low eye velocities involved and the difficulties of parsing out the influence of multiple moving targets, the small eye movements found in micropursuit are easily ignored or dismissed. Nevertheless, micropursuit may provide a useful way to infer attentional and other high-level strategies used to perform dynamic tasks.

## Conclusions

Most studies on the role of eye movements in visual tasks focus on the choice of which locations to fixate within displays. The locations chosen are typically those that are needed to overcome the limits of retinal heterogeneity and thus provide sufficiently high-quality spatial resolution to identify, recognize, locate or memorize key components of the display (e.g., Ballard et al., 1995; Eckstein, 2011; Koehler & Eckstein, 2017; Najemnik & Geisler, 2005; Semizer & Michel, 2017).

Dynamic environments provide extra challenges, particularly when tasks require monitoring the locations of more than one object. The present results found an overall preference for looking at an intermediate location that facilitated concurrent monitoring of the moving objects and avoided resource-intensive switching. We found that when strategies were dictated by instruction, fixating a central location produced better perceptual performance than deliberately switching between the two moving objects.

The present results also show how smooth eye movements, all too often neglected in studies of dynamic tasks, can provide indicators of the distribution of attention during perceptual tasks. There were two main indications of the role of attention: (a) the occurrence of micropursuit, low-velocity smooth eye movements that varied as a function of the velocities of the moving discs; and (b) the spontaneous smooth pursuit of the disc pair near the end of the trial when the discs moved along a common path. One of the main conclusions of this work is that smooth eye movements can provide a useful, and typically untapped, source of information about task strategies, including the role of attention.

We also found that different eye movement strategies led to about the same level of perceptual performance and that performance may have suffered only at the extremes in Experiment 2 where strategies were specified by instruction: either the highly stable fixation shown by JJ in Experiment 2 or the periodic, deliberate switching by the other three subjects. These strategies each required a relatively high level of management. As a result, attention and executive processes may have shifted from the primary task of judging the moving objects to other aspects needed to plan the eye movements. Thus, for the present task, as may be the case for many non-laboratory, real-world tasks, several different eye movement patterns may produce equally good performance as long as the eye movements flow from higher level decisions made about the task, rather than from explicit, effortful eye movement planning. The spontaneous smooth pursuit and the micropursuit are both examples of spontaneous eye movements that result from high-level decisions about the task.

*Keywords: eye movements, smooth pursuit, micropursuit, attention, eye movement strategies, fixation, motion perception, active vision*

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## Footnote

[1]Bootstrapping was based on the assumption that the responses for one choice (i.e., comparison first), $P_i^{observed}$, for each level of the comparison were drawn from a binomial distribution. The original number of responses, $P_i^{observed}$, was replaced by the number of responses, $P_i^{resampled}$, sampled from the same binomial. Sampling was repeated 2000 times, with each of the 2000 resulting psychometric function fit by a Weibull using a maximum likelihood method. The standard deviation of the difference thresholds reported was based on the SD of the distribution of parameters estimated from the 2000 psychometric functions.

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## Supplementary Material

Supplementary Movie S1. Experiment 1, subject SS. Distributions of eye positions and disc positions over time from all trials from both tasks (*which-first* and *collision*). The movie was constructed by compiling horizontal and vertical eye positions during successive 100-ms samples whose onsets were separated by 100 ms. Samples containing saccades or portions of saccades were not included. The rate of presentation was slower in the movie (samples within each 100-ms window are shown for 1 second) than it was during the actual experiment to aid viewing. Each 100-ms window was denoted according to its central time stamp. The color code denotes the number of samples in a given position (the color bar is shown in the movie). The intersection of the white lines shows the meeting point. The two small dots (in real size) show the positions of the standard disc (red) and average positions of the comparison disc (green).

Supplementary Movie S2. Experiment 1, subject EM. See caption for Supplementary Movie S1 for details.

Supplementary Movie S3. Experiment 1, subject JJ. See caption for Supplementary Movie S1 for details.

Supplementary Movie S4. Experiment 1, subject MM. See caption for Supplementary Movie S1 for details.

Supplementary Movie S5. Experiment 2, fixate instruction, subject SS. See caption for Supplementary Movie S1 for details.

Supplementary Movie S6. Experiment 2, fixate instruction, subject EM. See caption for Supplementary Movie S1 for details.

Supplementary Movie S7. Experiment 2, fixate instruction, subject JJ. See caption for Supplementary Movie S1 for details.

Supplementary Movie S8. Experiment 2, fixate instruction, subject MM. See caption for Supplementary Movie S1 for details.

Supplementary Movie S9. Experiment 2, switch instruction, subject SS. See caption for Supplementary Movie S1 for details.

Supplementary Movie S10. Experiment 2, switch instruction, subject EM. See caption for Supplementary Movie S1 for details.

Supplementary Movie S11. Experiment 2, switch instruction, subject JJ. See caption for Supplementary Movie S1 for details.

Supplementary Movie S12. Experiment 2, switch instruction, subject MM. See caption for Supplementary Movie S1 for details.