

# Shared attention for smooth pursuit and saccades

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**Identification of brief luminance decrements on parafoveal stimuli presented during smooth pursuit improves when a spot pursuit target is surrounded by a larger random dot cinematogram (RDC) that moves with it (Heinen, Jin, & Watamaniuk, 2011). This was hypothesized to occur because the RDC provided an alternative, less attention-demanding pursuit drive, and therefore released attentional resources for visual perception tasks that are shared with those used to pursue the spot. Here, we used the RDC as a tool to probe whether spot pursuit also shares attentional resources with the saccadic system. To this end, we set out to determine if the RDC could release attention from pursuit of the spot to perform a saccade task. Observers made a saccade to one of four parafoveal targets that moved with the spot pursuit stimulus. The targets either moved alone or were surrounded by an RDC (100% coherence). Saccade latency decreased with the RDC, suggesting that the RDC released attention needed to pursue the spot, which was then used for the saccade task. Additional evidence that attention was released by the RDC was obtained in an experiment in which attention was anchored to the fovea by requiring observers to detect a brief color change applied 130 ms before the saccade target appeared. This manipulation eliminated the RDC advantage. The results imply that attentional resources used by the pursuit and saccadic eye movement control systems are shared.**

## Introduction

It is commonly thought that smooth pursuit eye movements are used to foveate moving objects. Accordingly, most smooth pursuit research employs a small, foveal target. However, observers can accurately pursue stimuli containing only peripheral motion (Steinbach, 1976). Moreover, pursuit of random-dot cinematograms (RDCs) that extend into the periphery is better than that of foveal targets (Heinen & Watamaniuk, 1998). In fact, larger stimuli more closely approximate natural pursuit objects, such as a proximal moving person, and since they are pursued voluntarily, they are in a different class from full-field optokinetic stimuli that reflexively stabilize the world. Moreover, since pursuing larger objects (unlike smaller objects) does not necessitate foveation, the mechanism of pursuit might differ for small and large objects.

Attention also contributes to driving smooth pursuit. Studies employing a secondary task during pursuit have shown that either pursuit (Souto & Kerzel, 2008), or performance on the task is compromised (Acker & Toone, 1978; Brezinova & Kendell, 1977). These results suggest that the attentional resources subserving pursuit and the secondary tasks are shared, finite, and inadequate to fully support both tasks. A second line of research employing attention experiments using secondary tasks instead investigated how attention remaining from that used to drive pursuit was spatially allocated. A common finding is that spatial attention is displaced ahead of the pursuit target (Kanai, van der

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Geest, & Frens, 2003; Khan, Lefèvre, Heinen, & Blohm, 2010; Seya & Mori, 2012; Smeets & Bekkering, 2000; Tanaka, Yoshida, & Fukushima, 1998; van Donkelaar, 1999; van Donkelaar & Drew, 2002).

In stark contrast to these studies, other work has found attention to be restricted to a narrow region centered on the fovea (Lovejoy, Fowler, & Krauzlis, 2009). One potential reason for this discrepancy regarding how attention is allocated is the nature of the stimuli used in the different studies. The studies reporting an asymmetric distribution of attention during pursuit measured saccadic or button press reaction time (RT) to targets that abruptly appeared or changed. The stimulus used by Lovejoy et al. (2009) was a horizontal array initially composed of uniform characters. At a random time, the target changed to an “E” or a “3” while the distractors changed to a different set of characters for 200 ms, then returned to the uniform state. Lovejoy et al. argued that the transient change of the target in the RT studies evoked shifts of attention, and did not assess attention allocation per se, whereas their approach controlled for transients since both targets and distractors changed simultaneously. Furthermore, in the RT studies, the target remained visible until the observer responded, whereas in the Lovejoy et al. study, the target presentation was brief. This brief presentation, coupled with the lack of confounding transients, could have forced observers to allocate their attention more narrowly and evenly in the Lovejoy et al. study, limiting its scope. Another possible alternative explanation for the discrepant results is that the close spacing between adjacent characters in the Lovejoy et al. (2009) stimulus may have induced a crowding effect (e.g., Chung, Levi, & Legge, 2001; Pelli, Palomares, & Majaj, 2004), limiting good performance to just a small region surrounding the pursuit target, an explanation discussed, though not embraced, by the authors.

We think there is another reason that Lovejoy et al. found a narrow range of attention centered at the fovea. It is possible that the character identification task required more attention than responding to a flashed target, and therefore sufficient attention to perform the task could not be allocated much beyond the pursuit target in the central fovea, which was likely usurping attention for pursuit. However, recent work that also used a non-RT measure and brief target presentation showed that when attention used to drive pursuit is released, the attentional pool is not spatially restricted, and can be flexibly allocated if attention is released from the pursuit target (Heinen et al., 2011). In this study, observers performed a secondary task during pursuit of a foveal stimulus in conditions where a random-dot cinematogram (RDC) that moved with the stimulus was either present or not. Observers identified which one of five spots (four parafoveal, left,

right, up, and down, and one foveal) dimmed briefly (167 ms) during pursuit. Higher identification rates were found when the RDC was present than when it was not, despite that the parafoveal targets were  $\pm 3^\circ$  eccentric, considerably further out than the approximately  $\pm 1.2^\circ$  region of uniformly high performance found by Lovejoy et al. (2009). This wider attention span was thought to occur because the moving RDC motion helped drive pursuit, and consequently released attention consumed by foveal pursuit for use in the identification task. This result implies that attention used to drive pursuit is shared with attention needed to perform the identification task.

There is also generally a tight coupling between attention and saccades. Previous work has shown that during saccade preparation, a visual stimulus is better identified when it is spatially coincident with the saccadic target than when it is at a different location (Castet, Jeanjean, Montagnini, Laugier, & Masson, 2006; Deubel, 2008; Deubel & Schneider, 1996; Kowler, Anderson, Doshier, & Blaser, 1995; Montagnini & Castet, 2007; Wilder, Kowler, Schnitzer, Gersch, & Doshier, 2009). However, there is evidence that saccades do not utilize all attentional resources, leaving residual attention for other tasks (Kowler et al., 1995; Montagnini & Castet, 2007; Wilder et al., 2009), and that attention can be shifted several degrees from one side of the fovea to the other without a saccade (Reeves & Sperling, 1986). Neurophysiological studies also show a close link between saccades and attention. Areas that generate eye movements are functionally connected to attention areas (Moore & Armstrong, 2003; Moore, Armstrong, & Fallah, 2003). Additionally, spatial attention shifts and saccade planning typically occur in the same brain structures (Bisley & Goldberg, 2010; Gottlieb & Goldberg, 1999; Lovejoy & Krauzlis, 2010; Schall & Hanes, 1993). This likely facilitates the coupling of these functions when both functions are task-relevant, but it does not compel them to be coupled otherwise (as pre-motor theory suggests), leaving the possibility of residual attention open.

Here we asked whether attention that is used for foveal pursuit is shared with the saccadic system. It might not be surprising that if pursuit and perception share attentional resources, those same attentional resources are shared with the saccadic system, as posited by the premotor theory, which claims that a covert shift of attention is neurologically identical to the preparation of an eye movement to that location (Rizzolatti, Riggio, Dascola, & Umiltà, 1987). In fact, it might be reasonable to assume that attentional resources are shared between any motor systems that are used to perform a task on visual targets. If so, one would expect reaction time to be correlated across eye movements and finger presses. However it has been shown that manual reaction time and saccade reaction

time are not correlated on a trial-by-trial fashion when a fixation point disappears briefly before a target appears (gap paradigm) (Jin & Reeves, 2009). Indeed, in a major review of premotor studies, Smith and Shenk (2012) concluded that covert orienting is autonomous from motor activation, while motor preparation is sufficient but not necessary for covert orienting. Furthermore, attention resources appear not even to be shared between pursuit of large and small targets (Heinen et al., 2011).

To answer whether attention used for foveal pursuit is shared with the saccadic system, we used an RDC (100% coherence) to supplement the pursuit drive afforded by the spot, and tested performance on a secondary saccade task. Four perifoveal saccade targets surrounded the pursuit target, and the array moved with or without a moving RDC. Observers made a saccade to one of the four targets, which was brightened and enlarged at random. When the RDC was present, saccade latency was reduced. Moreover, the latency reduction was abolished when attention was forced to the foveal pursuit target, supporting shared attention by the pursuit and saccadic systems.

## Methods

### Subjects

Five healthy observers, two males (YJ & KS) and three females (AK, ZL, & JR) participated in the experiments. YJ and KS were completely naïve, and received at least one block of training on basic pursuit. AK had performed pursuit and saccade experiments before, but was completely naïve to the purpose of the current study. JR had done pursuit experiments previously, and was naïve to the purpose of the second experiment, but not to the first. ZL had experience in pursuit and saccade studies and is an author on this manuscript. All observers had normal or corrected to normal vision and ranged in age from 24–31 years. Four of the five observers participated in both experiments.

### Apparatus and stimuli

Visual stimuli were generated in MATLAB using the PsychToolbox (Pelli, 1997) on a Macintosh computer and presented on a 17-inch high resolution Nanao color monitor (1.76 min arc/pixel) at a rate of 60 Hz. The display resolution was  $1024 \times 768$ , and the display subtended  $37.7^\circ \times 27.5^\circ$ . Both horizontal and vertical eye position were recorded by an EyeLink 1000 eye tracker (SR Research Ltd., Kanata, Canada) at a rate

of 1000 Hz. The eye tracker has an overall system noise of less than  $0.01^\circ$  (RMS eye position with an artificial eye) and a tracking range of  $\sim 30^\circ$  horizontally and  $\sim 20^\circ$  vertically. The tracker was calibrated and validated by having the observer fixate nine locations distributed across the display using a standard software routine provided with the EyeLink system. A chin and forehead rest stabilized the head and maintained observers at a constant viewing distance of 48 cm from the display.

Task stimuli were composed of a small central square ( $0.26^\circ$  per side,  $40.0 \text{ cd/m}^2$  luminance) and four spots ( $0.2^\circ$  in diameter,  $3.7^\circ$  eccentricity,  $20.0 \text{ cd/m}^2$  luminance) arranged in an “X” configuration. The saccade target was one of the four eccentric spots that was enlarged ( $0.26^\circ$  in diameter) and brightened ( $40.0 \text{ cd/m}^2$ ) at random. We made the target changes suprathreshold so that saccade latency would not be artificially affected by visibility issues, only by the presence or absence of the RDC. The task stimulus was presented either on a homogeneous dark screen (“RDC-off” condition), or superimposed on a  $22.6^\circ \times 37.7^\circ$  field of random dots ( $0.2^\circ$  diameter,  $2.6 \text{ cd/m}^2$  luminance, 1 dot/deg<sup>2</sup> density) that moved with the task stimulus (“RDC-on” condition). The room lights were turned off. The RDC was restricted from overlapping the stimulus so that the pursuit and potential saccade targets would remain clearly visible (see Figure 1).

### Procedure

In Experiment 1, each trial began with the task stimulus at the display center. After a random fixation period (1000–1500 ms), the stimulus moved smoothly from the center, in a direction randomly chosen as either left or right. The stimulus moved for 1.4 s at a constant velocity of  $12^\circ/\text{s}$ . In 80% of trials, a saccade target was specified at a random time, 50–650 ms after motion onset, and in the remaining 20% of the trials no saccade target was presented. In each trial, the RDC either appeared (RDC-on) or not (RDC-off) (see Figure 1). RDC-off and RDC-on trials were equally likely and randomized within a block of trials. Observers were instructed to maintain gaze on the central square, and, as soon as a saccade target was specified, to saccade to it and pursue it for the remainder of the trial. If no saccade target was specified, they were required to pursue the square until the end of the trial. Within each block of 200 trials, a tone was sounded every 40 trials to signal the observer to take a break. They remained seated with their head supported in the chin rest during the break, and the experiment continued after a key press. Each observer completed two blocks of trials for a total of 400 trials.

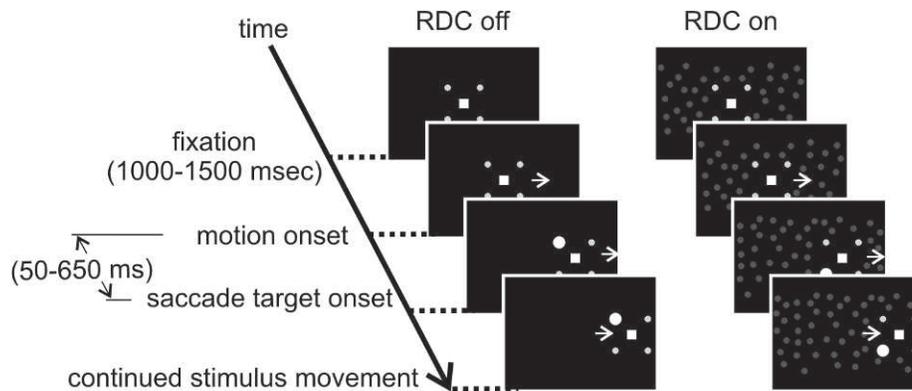


Figure 1. Schematic representation of an RDC-off and RDC-on trial sequence for Experiment 1. Stimuli appeared at the center and remained stationary for 1000–1500 ms. Observers fixated the central square, and then pursued it as the stimulus moved either left or the right at  $12^\circ/s$  for 1400 ms. The saccade target was specified by enlarging and brightening one of the four eccentric dots 50–650 ms after motion onset. The dot array was either presented alone, or accompanied by an RDC (100% coherence) that moved with it. Observers were instructed to make a saccade to the identified target and pursue it until the end of trial.

Experiment 2 was similar to Experiment 1, but a secondary task was added in which observers had to identify a color change of the central square pursuit target (Figure 2). Here, the duration of stimulus motion was increased to accommodate the extra time required to specify the saccade target after the color change. To accomplish this increased duration without the stimuli

colliding with the edge of the display, the stimuli appeared at a random position ( $3.5^\circ$ – $14.5^\circ$ ) to the left or right and moved back toward the display center after a random (1000–1500 ms) fixation period. Between 250–870 ms after motion onset, the central square changed its color from gray ( $10.2 \text{ cd/m}^2$ ) to either yellow ( $36.0 \text{ cd/m}^2$ ) or blue ( $3.3 \text{ cd/m}^2$ ) for 50 ms and

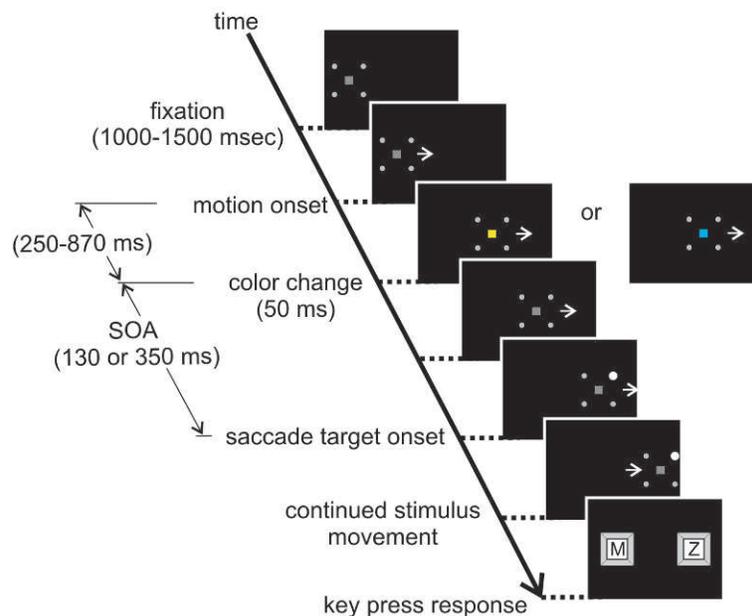


Figure 2. Schematic representation of an RDC-off trial sequence for Experiment 2. Stimuli appeared at a random position ( $3.5^\circ$ – $14.5^\circ$ ) either left or right of center and remained stationary for 1000–1500 ms. The observers fixated the central square, and then pursued it as the stimulus moved toward the center at  $12^\circ/s$  for 1400 ms. Between 250–870 ms after motion onset, the central square changed color to yellow or blue for 50 ms and then changed back to gray. A saccade target was specified 130 or 350 ms from the onset of the color change. The saccade target was specified by enlarging and brightening one of the four eccentric targets. The dots and square were either presented alone, or accompanied by an RDC that moved with it. Observers were instructed to perform the saccade task and identify the color change at the end of the trial by pressing the “M” or “Z” keys.

then returned to gray. A saccade target was specified during steady-state pursuit (600–1000 ms after motion onset) either 130 ms (short SOA) or 350 ms (long SOA) after the central square's initial color change. To minimize the possibility that the color-change would cue saccade target onset, a saccade target was specified in only 50% of the trials. However, despite this manipulation one naïve observer (AK) was able to consistently produce short latency saccades for both SOA conditions. Therefore, for AK we randomized SOAs between 50–350 ms throughout each block of trials. For the analyses, we compared AK's data for SOAs between 117–150 ms with the 130 ms SOA data from the other observers, and her 317–350 ms SOA data with the other observers' 350 ms SOA data.

As in Experiment 1, pursuit and saccade stimuli were shown either on a homogeneous dark screen (RDC-off) or with an RDC that moved with them (RDC-on). Observers were instructed to follow the central square until a saccade target was specified, and then saccade to it and pursue it for the remainder of the trial. In addition, they were asked to identify the color change of the square by pressing the “z” key for yellow and the “m” key for blue at the end of the trial. The next trial began after the color identification keypress.

## Behavioral data analysis

Horizontal and vertical eye velocity were calculated offline from the recorded position signals by differentiating and filtering (2-pole Butterworth noncausal filter, cutoff = 50 Hz). Saccade detection was also done offline by determining when eye velocity crossed an empirically-chosen threshold of 50°/s. The difference between saccade target onset time and the time the saccade was detected defined saccade latency.

During smooth pursuit of a spot stimulus, “catch-up” saccades are usually made to minimize the error between the eye and target (e.g., de Brouwer, Missal, Barnes, & Lefèvre, 2002). In our experiments, catch-up saccades might have delayed the initiation of saccades to the saccade targets either because the observer could not initiate a new saccade while making a catch-up saccade, or because detection of the saccade target was slowed by saccadic suppression during an on-going catch-up saccade. Therefore, trials in which a saccade occurred either between when the target appeared and when the targeting saccade was made, or 100 ms before the target appeared, were excluded from the analysis. This resulted in the rejection of 12.1% of trials (13.7% RDC on; 10.6% RDC off). In addition, another 2.3% of the trials were discarded because the direction of the first saccade made after the saccade target was specified was incorrect.

For the pursuit data analysis, the open-loop period was considered to have a duration of 130 ms, and an onset of 130 ms after stimulus motion onset (Heinen & Watamaniuk, 1998). Open-loop gain was calculated by dividing mean eye velocity computed over a 20 ms bin centered 260 ms after motion onset (the end of open-loop period), by stimulus velocity (Heinen & Watamaniuk, 1998). Steady-state gain was calculated by dividing mean eye velocity by stimulus velocity, and was computed 500–700 ms after motion onset.

## Results

We measured latency to the saccade targets as the index of saccade performance. Figure 3 shows representative traces of vertical eye position for one observer from one block of trials. It can be seen here that saccade latency was reduced by the presence of an RDC moving in the same direction and speed as the pursuit target. A two-way repeated-measures ANOVA with RDC presence (off or on) and saccade direction (forward or backward of pursuit direction) as independent variables, showed a significant effect of the presence of the RDC,  $F(1, 4) = 14.6$ ,  $p = 0.019$ . Saccade latency was shorter in the RDC-on (258 ms) than in the RDC-off condition (283 ms). However, neither saccade direction nor the interaction between the two factors was significant ( $p > 0.05$ ). Two observers were also tested on a stationary version of the task as a control for potential visual factors. The paradigm, stimulus configuration, and timing in the control experiment were identical to those used in the main experiment, except that instead of moving, the entire stimulus remained stationary in the center of the screen. Neither observer showed a difference in saccade latency between the RDC on and off conditions (EP:  $t(3) = -0.61$ ,  $p = 0.59$ ; SG:  $t(2) = 2.13$ ,  $p = 0.17$ ).

Previously we showed that perceptual identification of a brief luminance change improved when peripheral motion consistent with that of the task stimulus was added (Heinen et al., 2011). We hypothesized that the peripheral motion provided an alternative drive for pursuit to the foveal spot, and as a result it released attention that was used to follow the spot for use in the secondary identification task. Analogous to the putative attention release for perceptual identification, the peripheral motion could reduce saccade latency by releasing attention from the central square, thereby allowing more attention to be allocated to the candidate targets. This explanation seems reasonable given that saccade latency can be reduced when attention at the fixation location is disengaged prior to the appearance of a saccade target (Fischer & Weber, 1993; Jin & Reeves, 2009; Mackeben & Nakayama,

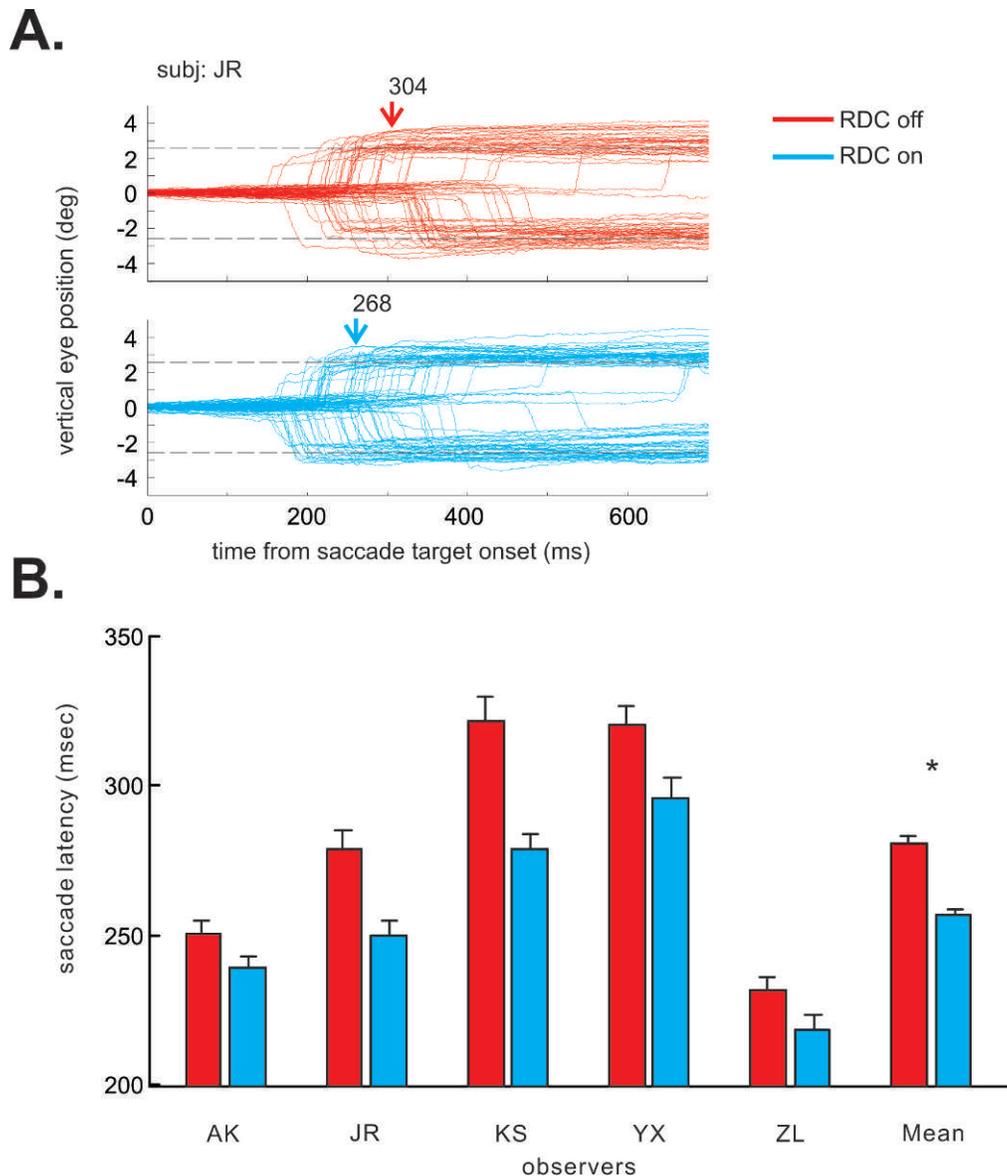


Figure 3. Saccade latency with and without an RDC. (A) Representative vertical eye position traces from one block of trials for one observer for RDC-off (top, red traces) and RDC-on conditions (bottom, blue traces). Traces are aligned on the position of the central square (pursuit target). Dotted lines show vertical positions of the saccade targets. Arrows and accompanying numbers identify mean saccade latencies in the two conditions. (B) Mean saccade latency for individual observers from Experiment 1. Red bars, RDC-off condition; blue bars, RDC-on condition. Error bars represent  $\pm 1$  standard error of the mean. Asterisks indicate significance at  $p < 0.05$ .

1993; Posner, Walker, Friedrich, & Rafal, 1984; Pratt, Lojonchere, & Abrams, 2006) or when more attention is allocated to the saccade target position (Kowler et al., 1995). Alternatively, saccades may have been initiated earlier with the peripheral motion present simply because the RDC improved pursuit performance, thereby better stabilizing the stimulus and allowing it to be more clearly viewed. To check this possibility, we analyzed smooth pursuit eye velocity with and without the RDC.

As can be seen in Figure 4a, horizontal eye velocity in RDC-on and RDC-off conditions differed in the

early period of pursuit (open-loop period), but not in steady state, consistent with earlier work showing enhancement of open-loop gain during pursuit of large RDCs moving in isolation (Heinen & Watamaniuk, 1998). *T* tests comparing RDC-on and RDC-off conditions were performed on the open-loop and steady-state gains respectively. The analysis showed a significant effect of peripheral motion on open-loop gain,  $t(4) = -4.4$ ,  $p = 0.012$ , which was higher in the RDC-on (1.073) than in the RDC-off condition (0.966), consistent with previous literature (Heinen & Watamaniuk, 1998) and consistent with either explanation

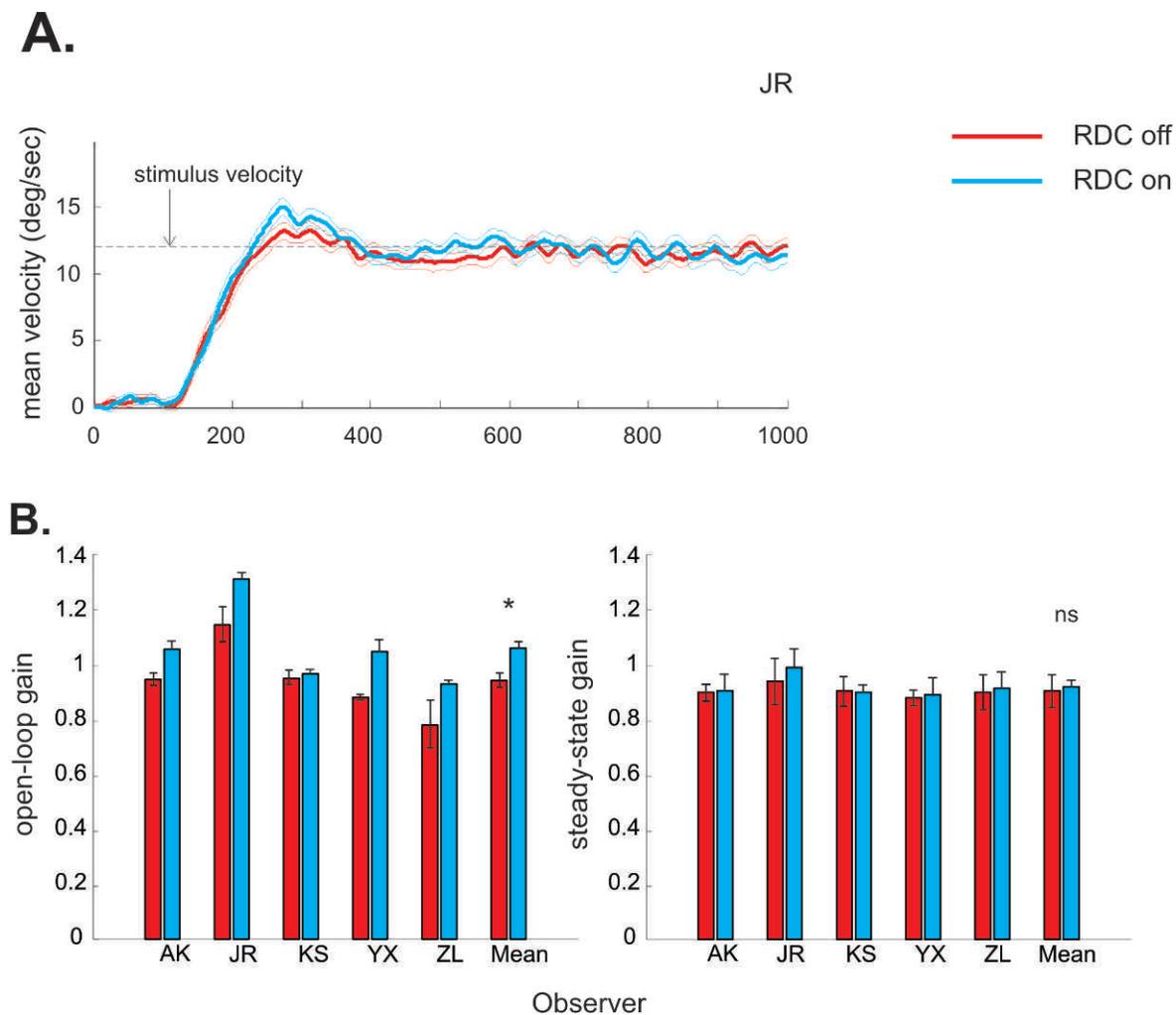


Figure 4. (A) Mean horizontal eye velocity traces for observer JR for RDC-on and RDC-off conditions in one block of trials. Thin lines accompanying the traces indicate 95% confidence intervals. (B) Pursuit gain for open-loop (left) and steady-state pursuit (right) for each observer. Error bars represent standard error of the mean. Asterisks indicate significance at  $p < 0.05$ .

(the RDC either releases attention or improves pursuit). However, no difference was found in steady-state gain between the two conditions,  $t(4) = -1.9$ ,  $p = 0.124$ . Since steady-state gain was unaffected by the RDC, we sought to determine if the secondary saccade task benefited from the peripheral motion during this epoch, potential evidence against better eye movements accounting for the improvement.

To investigate whether the saccade task was facilitated by the RDC during steady-state pursuit, we identified a subset of trials where the saccade target was specified during this period (500–700 ms after motion onset). A  $t$  test showed that saccade latencies during this epoch in the RDC-on condition (237 ms) were still significantly shorter than those in the RDC-off condition (258 ms),  $t(4) = 4.0$ ,  $p = 0.017$ . This result suggests that shorter saccade latency in the RDC-on condition is not simply due to better open-loop pursuit performance. Nevertheless, there could be some char-

acteristic of the pursuit eye movements that improved saccade performance which our analysis failed to detect. To rule out this explanation, we tested directly whether the RDC released attention from the pursuit target for the task by increasing the attentional load at the fovea. If saccade latency decreased because attention was released from the pursuit target, increasing the attentional load at the fovea should prohibit that release, and saccade latency should be unaffected by the RDC.

To increase attention at the fovea, we transiently changed the color of the central target 130 ms before the saccade target was specified, and required observers to identify the changed color (see Methods). In other trials, as a control, the color change occurred 350 ms before the saccade target was identified. The logic for choosing stimulus onset asynchronies (SOAs) of 130 and 350 ms is that attention drawn by a brief presentation of a stimulus peaks around 70–150 ms

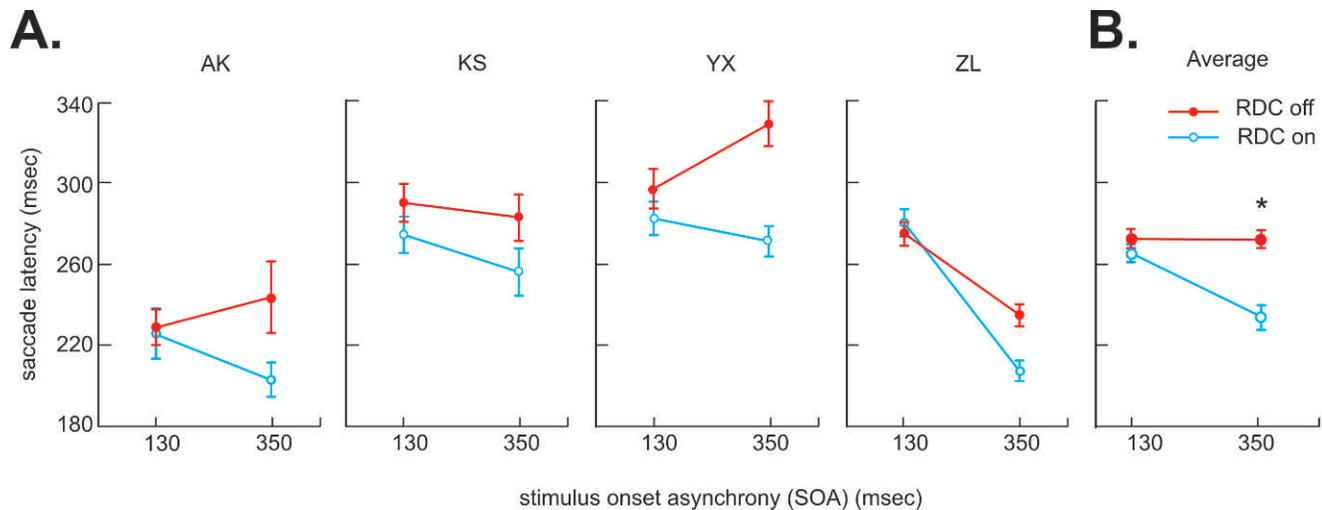


Figure 5. Saccade latency as a function of SOA between the central square color change and saccade target onset. (A) Individual observer data. Saccade latencies were shorter in the RDC-on condition, but only when the color changed 350 ms before saccade target onset. Error bars represent standard error of the mean. (B) Data averaged over all observers. Asterisks indicate significance at  $p < 0.05$ .

after stimulus onset, after which it drops dramatically and stabilizes at around 300 ms (Nakayama & Mackeben, 1989). Therefore, when the SOA was 130 ms, the color change was expected to draw attention to the fovea and prevent the RDC from releasing it for the saccade task. However, when the SOA was 350 ms, attention should have moved away from the fovea after the color change, allowing the RDC to exert its effect. (A similar time course for an attention shift was found using a probe-dot paradigm when subjects prepared a saccade: Jin & Reeves, 2009).

When the color change preceded the saccade target by 130 ms, the benefit of the RDC in reducing saccade latency was eliminated (Figure 5). A two-way repeated-measure ANOVA (RDC presence and SOA as variables) showed a significant main effect of RDC presence,  $F(1, 3) = 19.2$ ,  $p = 0.022$ , but no main effect of SOA ( $p > 0.05$ ). However, there was a significant interaction between RDC presence and SOA,  $F(1, 3) = 19.5$ ,  $p = 0.022$ . The RDC produced a significant reduction in saccade latency when the color change preceded saccade target onset by 350 ms (234 ms RDC-on vs. 272 ms RDC-off),  $t(4) = 5.6$ ,  $p = 0.011$ , but not when the color change occurred 130 ms before the target (265 ms RDC-on vs. 273 ms RDC-off condition),  $t(4) = 1.8$ ,  $p = 0.176$ . Therefore, our data support the hypothesis that peripheral motion reduces saccade latency by releasing attention from the pursuit target.

## General discussion

In the first experiment, observers performed a secondary task during smooth pursuit in which they

made a saccade to one element in an array of eccentric targets. The task was performed with and without consistent peripheral motion provided by an RDC. Saccade latency decreased when the RDC accompanied the task stimulus. Since steady-state pursuit was no better with the RDC present, it followed that the peripheral motion released attention from the foveal pursuit target to perform the attention-demanding saccade task. In a second experiment, observers again performed the saccade task, but in addition identified a color change on the foveal pursuit stimulus that occurred 130 ms before the saccade target was specified. This manipulation eliminated the benefit of the RDC, and saccade latencies increased again, direct evidence that saccade latency was reduced because the RDC released attention from the pursuit target.

An analogous experiment tested the effect of an RDC pursuit stimulus on performance in a secondary identification task (Heinen et al., 2011). The task stimulus was an array of targets similar to the one used here. At random, one of the targets was dimmed briefly, and observers identified the dimmed target with a keypress. Consistent with the current results, performance was enhanced by the presence of the RDC. As in the current study, pursuit eye movements were similar with and without the RDC during steady-state pursuit, implying that better image stability did not account for the improved performance. Instead it was hypothesized that the RDC provided an alternative drive for smooth pursuit to that provided by the foveal target, releasing attention that had been used to pursue the target for the task. It followed then that the attention resources used in the identification task were shared with those used to pursue the spot.

The latency reduction observed in the present study provides further evidence that consistent motion afforded by an RDC releases attention from a foveal pursuit target, since it takes time to disengage attention from one target before a saccade can be made to another (Jin & Reeves, 2009; Posner et al., 1984). Additional support for the RDC releasing attention comes from our second experiment in which we manipulated attention directly. In it, observers identified a color change on the pursuit target, which was imposed to increase attention at the fovea and draw it away from the saccade targets. The change occurred 130 ms before the saccade target was specified, a time when attention is maximally attracted to the location of a brief stimulus (Nakayama & Mackeben, 1989). If the RDC improved saccade performance by releasing attention from the pursuit target, drawing attention back to the fovea should null its benefit, and this is what we found. The RDC benefit returned when the color change occurred 350 ms before the saccade target, a time by which attention to a brief stimulus has dissipated (Nakayama & Mackeben, 1989), evidence against a general cuing effect.

Previous work suggests that attention allocation during pursuit is rigid and spatially restricted. Most of these studies have found attention to be allocated ahead of the pursuit target (Kanai et al., 2003; Tanaka et al., 1998; van Donkelaar, 1999), and there is evidence that this forward allocation has a broad span (Khan et al., 2010). Other work suggests that attention is tightly centered at the foveal pursuit stimulus (Lovejoy et al., 2009). The results of the current study and Heinen et al. (2011) suggest that attention can be allocated flexibly either toward the fovea or away from it depending upon the type of stimulus used to drive pursuit and task demands. In our experiments, we think that the RDC released attention that is normally used to pursue the spot. Alternatively, the spatial extent of the RDC attracted attention outward to the peripheral saccade targets. However, a result from Heinen et al. (2011) argues against this interpretation. In that experiment, observers identified which of five spots, of which the pursuit target was one, dimmed briefly during pursuit. The RDC improved identification performance for all targets, including the foveal pursuit target, which would not have occurred if the RDC merely attracted attention away from the fovea.

Our results support the conclusions of other work showing that pursuit of foveal targets requires attention (e.g., Acker & Toone, 1978; Brezinova & Kendell, 1977; Heinen et al., 2011; Souto & Kerzel, 2008). Furthermore, because saccade latency was penalized during pursuit of the spot alone, the results suggest that attentional resources are shared by the foveal pursuit and saccadic systems, consistent with the observation that many saccade structures also subserve pursuit

(Krauzlis, 2004), most notably, the superior colliculus (SC). Our results predict that the SC, because it is involved in spot pursuit (Basso, Krauzlis, & Wurtz, 2000; Krauzlis, Basso, & Wurtz, 1997, 2000) and saccades (e.g., Robinson, 1972), and is activated by attention (Goldberg & Wurtz, 1972; Ignashchenkova, Dicke, Haarmer, & Thier, 2004), would be differently activated with or without the RDC in our task. Without the RDC, attention might modulate pursuit-related neurons in the SC, imposing an attentional penalty on the neurons involved in generating saccades. Differential RDC on/off effects might also be found in the FEF, which is active during pursuit (Gottlieb, MacAvoy, & Bruce, 1994; Tanaka & Lisberger, 2001) and saccades (Bruce & Goldberg, 1985), as well as the SEF, which also has pursuit (Heinen, 1995; Heinen & Liu, 1997; Missal & Heinen, 2001) and saccade-related activity (Schlag & Schlag-Rey, 1987).

However, a question remains: why did pursuit of the RDC require less attention than pursuit of the spot? We believe there exists a relatively reflexive and subconscious neural mechanism devoted to pursuing objects that extend beyond the fovea and stimulate peripheral retina. This mechanism is likely subserved by motion-processing circuitry in MT/MST, which contains pursuit neurons that respond to large textured motion stimuli (Komatsu & Wurtz, 1988), but may also recruit circuitry in the system that generates the optokinetic reflex (OKR). Indeed, the size of our RDC ( $22.6^\circ \times 37.7^\circ$ ) is in the range of those used to elicit OKR and ocular following in humans ( $20^\circ \times 15^\circ$  for small-field OKN, e.g., Dieterich, Bucher, Seelos, & Brandt, 2000;  $32^\circ \times 25.6^\circ$  for ocular following, e.g., Sheliga, Chen, FitzGibbon, & Miles, 2005). As a subsystem of ocular following, OKR circuitry may have been modified through evolution to pursue objects, such as another proximal person or animal, common in natural scenes. Supporting this notion, the nucleus of the optic tract (NOT), which is commonly thought to drive OKR (Hoffmann, Distler, Erickson, & Mader, 1988; Kato, Harada, Hasegawa, & Ikarashi, 1988; Schiff, Cohen, & Raphan, 1988), contains neurons that respond during pursuit (Mustari & Fuchs, 1990) and might be involved in pursuit of larger objects. This modern, yet still mostly automatic, OKR circuitry releases attention for the inspection of an object's features, which uses a foveate system of fixation and saccades.

The proposed mechanism relies on strong motion cues elicited by large objects and, analogously, RDCs. When less common small objects such as a laboratory spot or a distant airplane move, a different pursuit mechanism is enabled. Unlike the mechanism used to pursue larger objects, this mechanism attempts to keep objects foveated, and therefore uses not only motion circuitry, but also attention-demanding position-cor-

recting circuitry. While little is known about the non-foveal pursuit mechanism for which our current results provide evidence, there is support for the differential involvement of position and motion systems during pursuit of small spots and large RDCs. In a study where observers pursued either a spot or an RDC, it was found that the RDC increased pursuit gain during the open-loop period, and afforded better speed discrimination relative to the spot (Heinen & Watamaniuk, 1998). This suggested that the larger RDC produced a better motion signal than the spot, leading to the observed facilitated pursuit response. On the other hand, during pursuit of the spot, catch-up saccades, which at least partially correct for position error (de Brouwer et al., 2002), are common. These saccades are virtually absent during pursuit of RDCs (Heinen & Watamaniuk, 1998), indicating that the position system is relatively inactive in this situation. Furthermore, the SC, a structure involved in foveating targets and correcting position error (Wurtz & Optican 1994) is active during spot pursuit (Krauzlis et al., 1997, 2000).

*Keywords:* attention, smooth pursuit, saccades, eye movements

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