

Flexibility of foveal attention during ocular pursuit

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Smooth pursuit of natural objects requires flexible allocation of attention to inspect features. However, it has been reported that attention is focused at the fovea during pursuit. We ask here if foveal attention is obligatory during pursuit, or if it can be disengaged. Observers tracked a stimulus composed of a central dot surrounded by four others and identified one of the dots when it dimmed. Extinguishing the center dot before the dimming improved task performance, suggesting that attention was released from it. To determine if the center dot automatically usurped attention, we provided the pursuit system with an alternative sensory signal by adding peripheral motion that moved with the stimulus. This also improved identification performance, evidence that a central target does not necessarily require attention during pursuit. Identification performance at the central dot also improved, suggesting that the spatial extent of the background did not attract attention to the periphery; instead, peripheral motion freed pursuit attention from the central dot, affording better identification performance. The results show that attention can be flexibly allocated during pursuit and imply that attention resources for pursuit of small and large objects come from different sources.

Keywords: motion, eye movements, peripheral retina, pursuit system, dual task, fovea

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Introduction

Smooth pursuit is a type of eye movement used to follow moving objects and has been studied widely with a small, moving, spot stimulus. Despite being modeled as exclusively driven by visual motion (Krauzlis & Lisberger, 1989; Robinson, Gordon, & Gordon, 1986), smooth pursuit is also under cognitive control (Kowler, 1990). Attention is an important cognitive factor at work during pursuit since diverting attention during it impairs pursuit performance (e.g., Acker & Toone, 1978; Brezinova & Kendell, 1977; Souto & Kerzel, 2008). Furthermore, more attention is allocated to pursuit stimuli than background stimuli (Khurana & Kowler, 1987) and attention during maintained pursuit is focused within a small 2° region centered on the fovea and decreases sharply at more eccentric locations (Lovejoy, Fowler, & Krauzlis, 2009). However, most objects we pursue in the natural environment are different from the spot in that they extend beyond the fovea into the periphery. Moreover, it would be beneficial to be able to attend to eccentric features that require inspection, which could not occur if attention remained focused at the fovea. In the current study, we ask whether attention at a foveal target is obligatory or not.

It has been shown that extinguishing a fixation point before saccade target onset reduces saccade latency, a finding referred to as the gap effect (Saslow, 1967). There is evidence that the gap effect on saccades to static targets occurs because attention is released from the fixation point (Fischer & Weber, 1993; Jin & Reeves, 2009; Mackeben & Nakayama, 1993; Pratt, Lajonchere, & Abrams, 2006). The gap effect has also been observed with the pursuit system. It has been shown that during pursuit, saccade latency to a moving or static target is reduced after a gap is imposed (Boman, Braun, & Hotson, 1996; Knox, 1996; Krauzlis & Miles, 1996; Tanaka, Yoshida, & Fukushima, 1998). The occurrence of the gap effect during pursuit suggests that the gap might also release attention from the pursuit target, since attention is allocated to the fovea while pursuit is in progress (Lovejoy et al., 2009).

Motivated by the previous work, we used the gap paradigm to test whether attention at the fovea is obligatory or not. In the experiments, we employed a secondary, attention-demanding identification task on peripheral targets to allow direct assessment of attentional resource allocation. When a temporal gap was introduced before the target was specified, performance on the identification task during pursuit improved. In a second manipulation, we added peripheral motion consistent with the target motion to provide an alternative driving signal for

pursuit. This manipulation also produced better performance on the identification task, suggesting that the mere presence of the central target does not necessarily capture attention. Taken together, the results suggest that attention at the fovea during pursuit can be released for allocation to other locations, and its engagement at the fovea is not obligatory even when a foveal stimulus is present.

Methods

Observers

Altogether, nine observers participated in the current study. Each experiment had four observers and some observers participated in more than one experiment. Among the nine observers were two of the authors; each participated in one experiment (SW in the main experiment and ZL in the [Supplementary experiment](#)). The remaining observers were naive to the purposes of the experiments. All observers had normal or corrected-to-normal visual acuity. All experiments were approved by the Smith-Kettlewell Institutional Review Board and all observers gave informed consent before participating.

Stimuli

All stimuli were generated on a Macintosh computer using Matlab (The MathWorks, Natick, MA) and functions from the PsychToolbox (Pelli, 1997) and were displayed at 60 Hz on a 17-inch high-resolution Nanao color monitor (1.76 min arc/pixel). Viewing distance was 48 cm. An identification task was performed on stimuli that were constructed of 5 small bright dots (0.2 deg diameter, 40.0 cd/m²) arranged in the shape of a plus sign (+) that spanned 6 deg vertically and horizontally. The stimulus was either presented alone on a dark screen (0.07 cd/m², 99% Michelson contrast) or was superimposed on a large field of background dots (22.6 × 37.7 deg). The background dots were the same size as the target dots (0.2 deg diameter), but of slightly lower luminance (2.63 cd/m², 94% Michelson contrast), and were displayed at a density of 1 dot/deg². When present, the background dots appeared and disappeared with the task stimuli and when background dots moved off screen, new random dots were generated to maintain a constant dot density over the entire background region. Background dots were restricted from a square region surrounding the target whose borders extended one dot width beyond the target dots (see [Figure 1B](#)). Observers were initially tested on the identification task during pursuit with no background to individually set the dim level (range: 13.2 cd/m² to 24.4 cd/m²) so that their performance was

65–75% correct. This ensured that identification task performance for every observer had room to increase or decrease with experimental manipulations.

Procedure

Basic task

The general procedure was the same for all experiments ([Figure 1](#)). Each trial began with only the center dot of the 5-dot target illuminated, which served as a fixation point. After a pseudo-random fixation interval (300–600 ms), the task phase of the trial began, which lasted 1000 ms. At the start of the task phase, the remaining four spots appeared, as well as the background dots if present, and after a random time, one of the dots became the identification target and was dimmed (i.e., decreased in luminance) for 167 ms. The target location and dim onset time were selected randomly on each trial. At the end of the trial, the observer was required to identify which dot dimmed by pressing a button on the computer's numeric keypad. The spatial arrangement of the response buttons corresponded to that of the 5-dot target (i.e., 2 = bottom, 4 = left, 5 = center, 6 = right, 8 = top).

For pursuit trials, the stimulus moved from left to right along the horizontal meridian. The fixation point appeared 3.5 deg away from the left edge of the display, and the stimulus began moving at a constant velocity when the other dots appeared. The speed of the stimulus was selected randomly on each trial to be 10, 20, or 30 deg/s. In the gap experiment, the target dimmed 300 or 500 ms after the stimulus began to move and the central spot either remained on or was extinguished 0, 100, or 200 ms before the target dimmed and remained off. The center dot did not dim in this experiment, and therefore, only the surrounding four dots were potential targets. No background-on condition was used in the gap experiment. In the background-on/off pursuit experiment, the target dimmed 100, 300, or 500 ms after the task stimulus began to move and the background moved at the same speed and in the same direction when present. Instead of only the four surrounding dots, all five dots had an equal probability of being a target. All conditions were randomized, except for the background-on and -off conditions that were constant within a block.

We also had observers perform the identification task when the stimuli were static as a control condition both with and without the background. In static trials, the stimuli were displayed at the center of the monitor. However, when using the same luminance decrement values that were used during pursuit, the performance level of all observers was 100%. We therefore reduced the magnitude of the decrement in the static trials so that observer's performance was again 65–75% correct, allowing improvements or decrements caused by the independent variables to be detected. As in the background

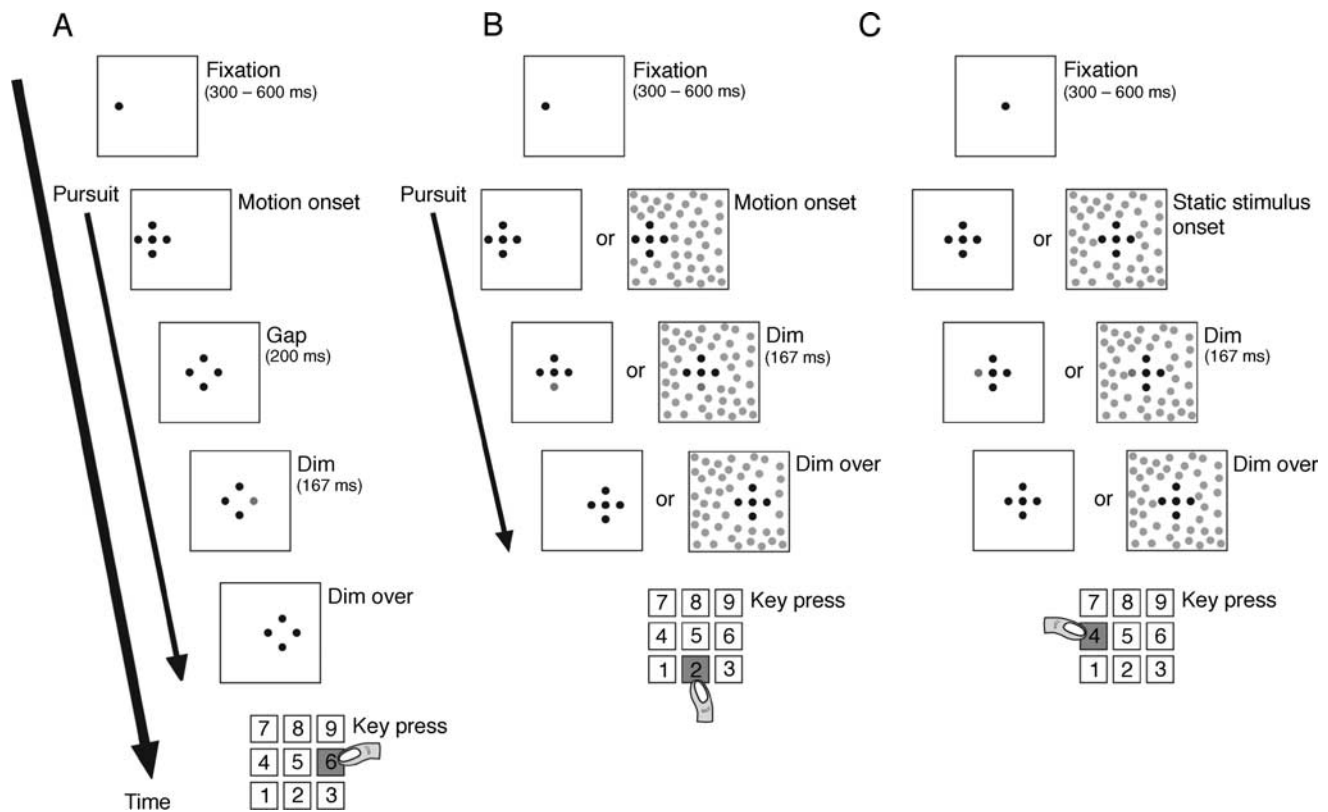


Figure 1. Experimental paradigms. In all cases, observers initially fixated for 300–600 ms. They next pursued the stimuli (except in the static experiment) that moved from left to right at 10, 20, or 30 deg/s, for a total duration of 1.0 s. A key press at the end of the trial indicated which dot dimmed. (A) Gap paradigm. The center spot was turned off 0, 100, or 200 ms before the dimming, which occurred either 300 or 500 ms after target motion onset. Only the four peripheral dots were dim candidates. (B) Pursuit task without a gap, with and without a textured background. Any one of the five dots could dim, either 100, 300, or 500 ms after target motion onset. When the background texture was present, it moved at the same velocity as the task stimulus. Note that the background texture was restricted from the region occupied by the 5-dot target. (C) Static task. The task was identical to that depicted in (B), but the stimulus and background were stationary.

experiment, all five dots had an equal probability of being a target.

Each observer completed a minimum of 5 blocks of the gap experiment, with 216 trials per block. For the background-on/off pursuit experiment, 15 blocks of 90 trials were run with the background on and the same number with the background off. For the static control, 4 blocks of 90 trials were collected with the background on and the same number with it off.

Eye movement measurement and analysis

Eye position was sampled at 1000 Hz using a video-based Eyelink 1000 eye tracker. Prior to each block of trials, the eye tracker was calibrated by having observers fixate at a series of 9 positions on the display (the center and 8 surrounding peripheral positions). Forehead and chin rests maintained a constant viewing distance and stabilized the head for accurate eye tracking. Eye velocity

was obtained by digital differentiation of eye position signals and filtered to reduce 60-Hz noise (2-pole Butterworth filter, cutoff = 50 Hz). Saccades were detected with an eye acceleration thresholding algorithm used in previous work (e.g., Badler & Heinen, 2006). Saccades were excised from the velocity traces when pursuit speed was characterized.

Pursuit initiation was first detected using an automatic algorithm that determined when eye velocity first exceeded 5 deg/s. All traces were visually inspected and the latency measure was manually adjusted when necessary. Pursuit initiation was analyzed in the interval 200–400 ms after motion onset to overlap the 100-ms target dim duration. Steady-state pursuit was analyzed in the interval 500–700 ms after task stimulus onset, an epoch consistent with that used in other work investigating pursuit with a background and with similar duration stimuli (Spering & Gegenfurtner, 2007). When comparing background-on and background-off pursuit conditions, trials in which a saccade potentially could interfere with target dimming detection because of saccadic suppression

were rejected from the analysis. For a trial to be rejected, a saccade had to be initiated in a time window that extended from 30 ms prior to target dimming until dimming ended. The reason for this criterion is that 3 deg saccades have durations of roughly 27.6 ms (Robinson, 1964); therefore, saccades that began within this temporal window would have overlapped the dimmed target.

Results

Gap experiment

Four observers participated in the gap experiment in which the central spot was turned off 0, 100, or 200 ms (gap) before the dot dimming, and gap duration was randomized within the same block to minimize the chances of a general warning effect. After being turned off, the central spot remained off. Since 200 ms is the optimum gap duration (Pratt, Bekkering, Abrams, & Adam, 1999), we defined the gap effect by the difference between the 0-ms and 200-ms gap durations. The 200-ms gap trials produced better task performance than 0-ms gap trials overall (gap 200 ms, 72.0% and gap 0 ms, 65.9%; an overall 6.1% change, Figure 2). A paired t -test showed that this difference in performance was significant ($t(3) = 4.708$, $p < 0.02$). We also applied Fisher's exact test to individual observer data with a hypothesis of higher performance in the gap condition and found significance for three of the four observers (HH, $p < 0.05$; JH, $p < 0.05$; AK, $p < 0.03$; KS, $p = 0.256$). The results of the gap

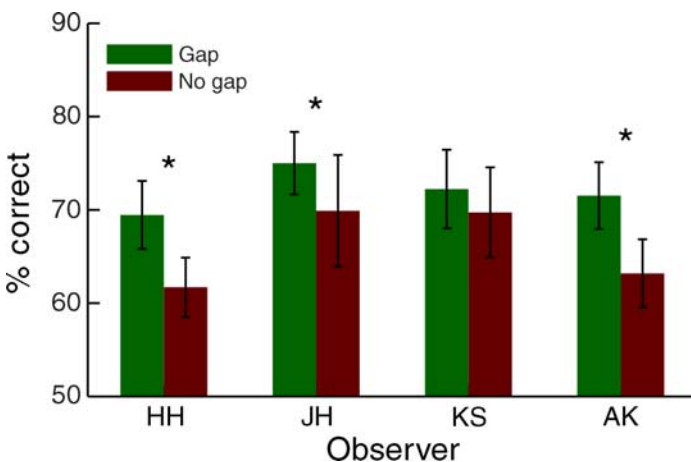


Figure 2. Identification performance with and without a temporal gap for four observers. The gap was 200 ms in duration and immediately preceded the target dimming. Note better performance overall when the gap was present. Error bars represent ± 1 standard error of the mean computed from variations across blocks. Asterisks indicate significantly better performance in the gap condition with $p < 0.05$.

experiment suggest that attention is not necessarily locked to the fovea during pursuit, at odds with the findings of Lovejoy et al. (2009).

It is known that the gap effect for saccades is partially due to the offset of the fixation point cuing observers as to when targets will appear (Kingstone & Klein, 1993; Pratt, Bekkering, & Leung, 2000). To test whether the gap could act as a temporal cue to the target blink, we performed a control experiment and found significantly better identification on our task when a gap was used as opposed to when a color change in the central target occurred 200 ms before the dimming (Supplementary material, S1). Furthermore, if observers could merely be cued to direct their attention to the periphery, and the fixation point did not pull attention toward the fovea, the optimum default strategy would be to spread attention to the periphery, since observers knew the task was only performed on the four peripheral dots. Yet, observers did not do this. This observation further supports our contention that in the gap experiment, the presence of the foveal target attracted attention, but that removing the target released it to perform identification on the peripheral spots.

It is possible that the eyes moved more freely during the gap and that they were positioned better relative to the peripheral spots to perform the identification (see van Donkelaar, 1999). Therefore, we compared horizontal eye position and velocity during the gap in 200-ms gap trials with those during the same period in no gap trials using a repeated-measures ANOVA. Neither eye position ($F(1, 3) = 0.243$, $p = 0.656$) nor eye velocity ($F(1, 3) = 2.427$, $p = 0.217$) differed between the gap and no gap trials, evidence that better performance in the gap trials was not due to changes in the pattern of eye movements.

Eye movements during pursuit with an RDC background

This result suggests that attention can be released from the fovea during pursuit. We wondered if reducing reliance on the foveal target as a pursuit drive can also free up attention to perform the identification task even if the foveal target remains present. Since large, moving, random-dot cinematograms (RDCs) are sufficient to drive pursuit (Heinen & Watamaniuk, 1998; Watamaniuk & Heinen, 1999, 2003), we added an RDC background to the 5-dot stimulus and moved the two together as a coherent unit (see Methods section). In the experiment, observers pursued the 5-dot stimulus with or without the background. Here, all five dots served as potential dimming targets with equal probability. Background-on and background-off trials were presented in separate blocks. Four observers participated in this experiment including two who had participated in the gap experiment.

First, we present a comparison of the eye movement data in the background-on and -off conditions because differences that we found in the eye movements between

these conditions are relevant to the hypothesis of the study and also affected how we analyzed the task performance data. During pursuit of a single spot, saccades are often made to correct for position errors that develop between the retinal image of the spot and the fovea. When pursuing large RDCs without a prominent central spot, the frequency of catch-up saccades when the target begins to move is reduced (Heinen & Watamaniuk, 1998). If the background reduces the necessity to use the spot to pursue, it should also reduce catch-up saccades even when the spot is present.

To investigate this, we compared the eye movements obtained in the background-on and background-off conditions (Figure 3). Figure 3A shows typical eye velocity traces for each condition from one observer. Fewer catch-up saccades can be seen in the background-on condition (blue traces) than in the background-off condition (red traces). Note that in general saccades are restricted to the horizontal traces, evidence that the saccadic intrusions were standard “catch-up” saccades largely used to correct for position error during pursuit of a spot stimulus (de Brouwer, Missal, Barnes, & Lefèvre, 2002). We analyzed the number of catch-up saccades during pursuit initiation (200–400 ms after target motion onset) and found fewer saccades in the background-on than the background-off condition at this time (Figure 3B; background off $M = 0.384$, background on $M = 0.256$; paired t -test $t(3) = -3.321$, $p < 0.05$). Furthermore, although not statistically significant, eye acceleration during pursuit initiation tended to be greater when the background was present (background off $M = 60.50 \text{ deg/s}^2$, background on $M =$

70.57 deg/s^2 ; paired t -test $t(3) = 2.529$, $p = 0.086$) in agreement with previous work comparing pursuit of an RDC alone and pursuit of a spot (Heinen & Watamaniuk, 1998). These findings suggest that pursuit depends less on the foveal spot when there is a background moving with it.

However, during steady-state pursuit (500–700 ms after target motion onset), the presence of the background did not affect pursuit. Saccade frequency during steady state was not different with the background (background off $M = 0.126$ saccade/trial, background on $M = 0.130$ saccade/trial; paired t -test $t(3) = -0.455$, $p = 0.680$) and paired t -tests for steady-state velocity gain and standard deviation also revealed no significant differences between the two background conditions (steady-state velocity gain, $t(3) = -1.119$, $p = 0.3446$; steady-state velocity standard deviation, $t(3) = -0.485$, $p = 0.661$), consistent with previous results (Niemann & Hoffmann, 1997). In addition, the standard deviation of the position error between the eye and the central dot during steady-state pursuit did not differ between the two conditions (background off $M = 0.162$, background on $M = 0.178$; paired t -test, $t(3) = 1.040$, $p = 0.375$), suggesting that the background did not better stabilize the eyes.

Task performance during pursuit with an RDC background

Next, we present the identification task performance results. The fact that more saccades occurred when the background was off could introduce a confound in

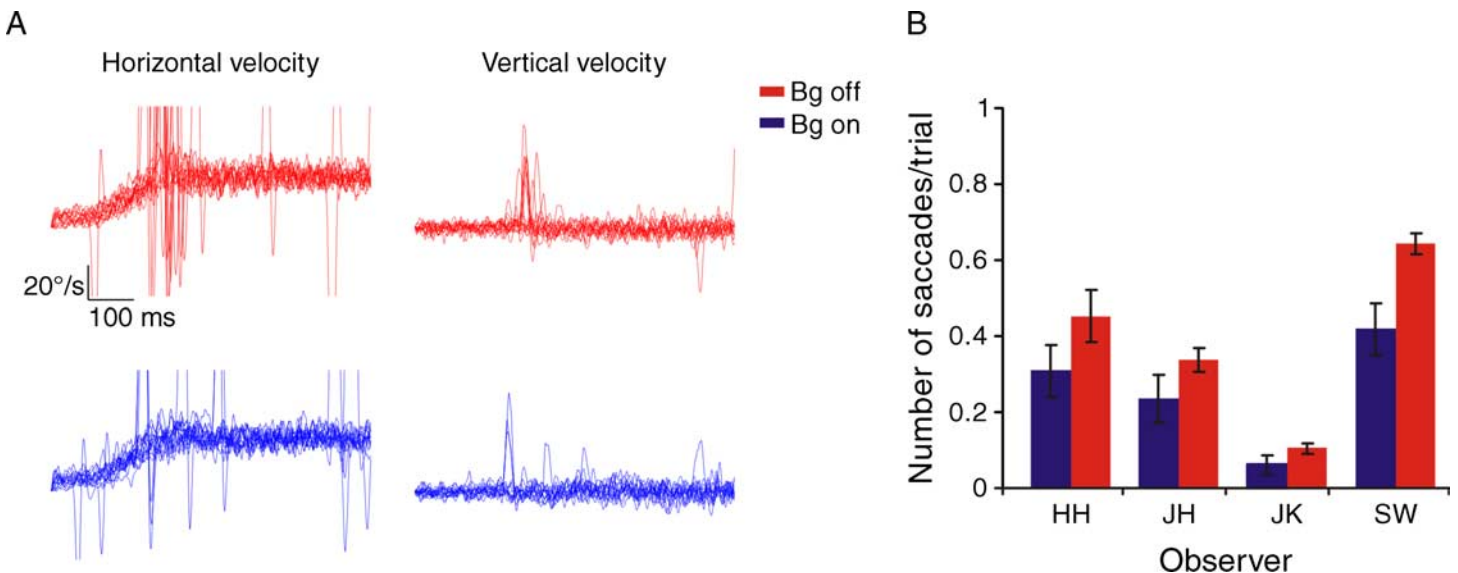


Figure 3. Eye movements while pursuing and performing the identification task with and without the RDC background. (A) Fifteen representative (left) horizontal and (right) vertical eye velocity traces for one observer (HH) randomly sampled from two blocks of trials, one in which the RDC background was on and another in which it was off. Target speed was 30 deg/s. Top traces (red) are from background-off trials; bottom traces (blue) are from background-on trials. Note fewer saccadic intrusions with the background on. Velocity traces were truncated at $\pm 50 \text{ deg/s}$ for ease of viewing. (B) Number of saccadic intrusions per trial for each observer averaged over all background-on/off trial blocks. Error bars represent ± 1 standard error of the mean.

	<i>F</i> -value	<i>df</i>	<i>P</i> -value
Background	45.164	1, 3	0.0067
Speed	9.349	2, 6	0.0143
Dim time	42.532	2, 6	0.0003
Target position	2.658	4, 12	0.0849
Background * speed	6.385	2, 6	0.0327
Background * dim time	2.809	2, 6	0.1377
Background * target position	2.029	4, 12	0.1541
Speed * dim time	0.927	4, 12	0.4805
Speed * target position	1.130	8, 24	0.3796
Dim time * target position	4.054	8, 24	0.0036
Background * speed * dim time	0.302	4, 12	0.8713
Background * speed * target position	0.489	8, 24	0.8658
Background * dim time * target position	0.636	8, 24	0.7400
Speed * dim time * target position	1.444	16, 48	0.1622
Background * speed * dim time * target position	1.057	16, 48	0.4196

Table 1. Results of the 4-way repeated-measures ANOVA on the percent correct identification data.

assessing task performance; if a saccade occurred when the target dimmed, the dimming might not be perceived because of saccadic suppression, i.e., an elevated luminance threshold during a saccade (Dodge, 1900). Therefore, we characterized identification performance only in trials in which no saccades occurred around the time of target dimming (see [Methods](#) section). We performed a 4-way repeated-measures ANOVA on the percent correct identification data with background (on, off), speed (10, 20, 30 deg/s), dimming onset time (100, 300, 500 ms), and target position (center, up, down, left, right) as the independent variables ([Table 1](#)). For all observers, accuracy on the task was higher when the background was present than when it was not ([Figure 4](#)). As the speed of stimuli increased, task performance decreased, which might be expected if more attention is required to pursue at higher speeds, but to our knowledge, this has not been shown in the literature. Task performance was also better the later the dimming onset occurred (averaged across speed: 53.9% at 100 ms, 89.0% at 300 ms, 90.9% at 500 ms). Since the early dimming began 100 ms after motion onset and lasted until 270 ms, it roughly overlapped pursuit initiation. Poorer task performance at this time is consistent with previous literature showing that attention is needed for pursuit initiation, manifesting about 150 ms after pursuit onset (Recanzone & Wurtz, 2000), with maximal effects on pursuit velocity 180–300 ms after motion onset (Souto & Kerzel, 2008). There was also a significant interaction between the background and speed such that the difference in performance when the background was and was not present was greater at higher speeds.

Previous studies have demonstrated that attention is preferentially allocated ahead of the target during pursuit (Blohm, Missal, & Lefèvre, 2005a, 2005b; Kanai, van der Geest, & Frens, 2003; Khan, Lefèvre, Heinen, & Blohm, 2010; Tanaka et al., 1998; van Donkelaar, 1999; van

Donkelaar & Drew, 2002), although other works found it to be focused on the target (Kerzel, Souto, & Ziegler, 2008; Khurana & Kowler, 1987; Lovejoy et al., 2009). To test which of these alternatives our results support, we compared identification performance for targets that dimmed in front of or behind the central spot. There was a tendency for better performance when the dimmed dot was presented ahead of the spot, although this improvement was not significant (ahead 79.9%, behind 73.5%;

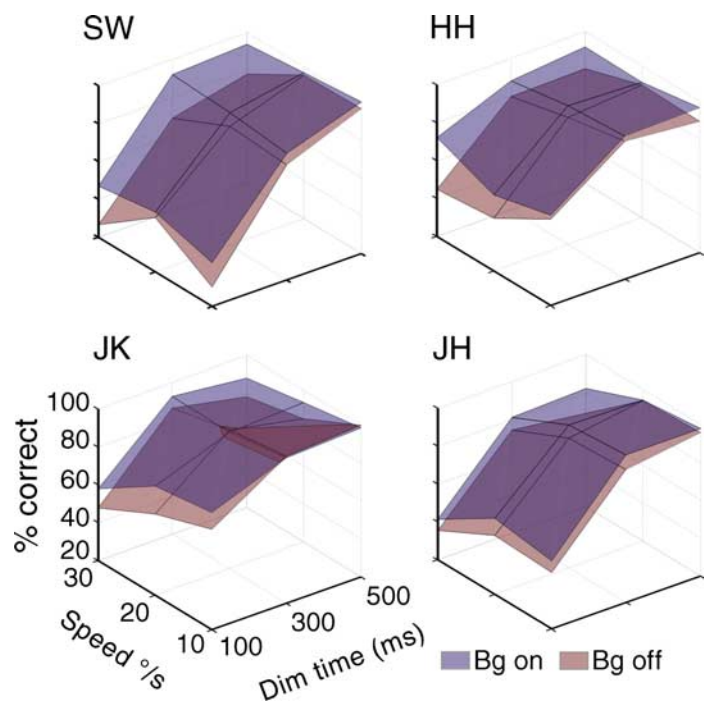


Figure 4. Task performance during pursuit with the RDC background on and off. Identification accuracy was better for all observers and at most target speeds and dimming times when the background was present.

paired $t(3) = 1.924$, $p = 0.1501$). We also tested for a difference in identification performance between the upper and lower dot-dimming positions and found none (upper 77.1%, lower 77.0%; paired $t(3) = 0.086$, $p = 0.9396$).

Does the RDC background release attention for the task?

The background appeared to release attention used to pursue the spot target by providing a sufficient signal to drive smooth pursuit, presumably because attention required to pursue peripheral motion is different from that required to pursue a spot. However, there are several alternative explanations. The first is that the background provided a better motion signal that led to better pursuit, and hence better image stabilization, which in turn enabled easier detection of the target dimming. In support of this, we found fewer saccades and higher acceleration during pursuit initiation in background-on trials. However, we only analyzed identification performance in trials where no saccades intruded on the dim time, and when looking at the gain of pursuit initiation as a function of identification performance for the 100 ms dim, we found no gain difference between correct and incorrect trials (gain correct = 1.03, gain incorrect = 1.02; paired $t(1) = 2.38$, $p = 0.25$). During steady state, we found no difference in saccade frequency or the quality of pursuit (see above). Therefore, better stabilization does not appear to account for our results.

Another possible explanation for the results is that the mere presence of the RDC provided a reference luminance that made it easier to detect the dimming of the target dot. If true, an RDC should also improve identification on a static target array as the reference luminance effect should not depend upon the presence or absence of motion. In our initial tests with a static array that had the same luminance decrement as did the one used in the pursuit trials, all observers performed the identification at 100% with the background either on or off, obscuring a potential benefit of the RDC by a ceiling effect. To eliminate this problem, we increased task difficulty by reducing the magnitude of the luminance decrement separately for each observer (see [Methods](#) section). All other task parameters were the same as in the previous experiment. A paired t -test on the static stimuli data showed that accuracy of dimmed target identification was not improved by the background ($t(3) = -0.090$, $p = 0.437$; [Figure 6](#)). Fisher's exact test was done on individual observer's data with a hypothesis of higher performance in the background-on than -off condition. This analysis yielded a significant result for only one subject (JH, $p < 0.01$) and insignificant results for the remaining three. Two of four subjects even showed significantly better performance on the identification task when no background was presented (SW, $p < 0.04$; JK, $p < 0.001$). These results suggest that the performance enhancement observed in the previous experiment in

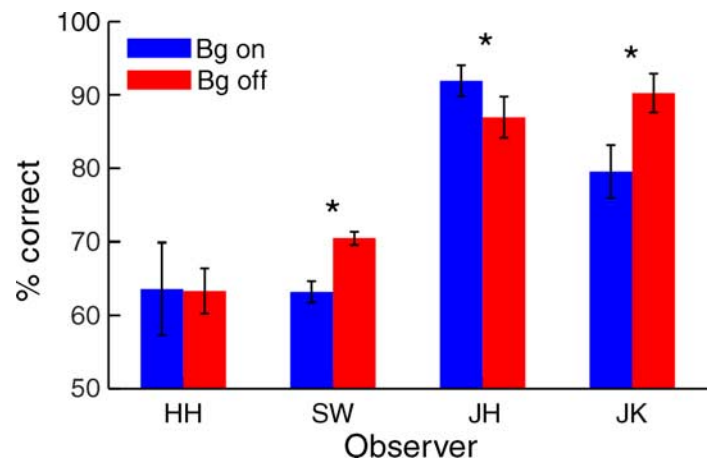


Figure 5. Identification performance in the static control condition. Note that there was no consistent difference in identification accuracy between the background-on and -off conditions. Error bars represent ± 1 standard error of the mean computed from variations over blocks. Asterisks indicate significance with $p < 0.05$.

which the background moved with the task stimuli did not occur because the background provided a reference luminance that facilitated dimming detection ([Figure 5](#)).

A potential explanation for better identification performance when the background is on is that the background attracts attention and therefore draws attention to the periphery. This would lead to the prediction that performance at the center dot would be either the same or even worse when the background was present than when not since spreading the attention could make it more diffuse. To investigate this possibility, we compared performance at the center dot in the background-on and -off conditions ([Figure 6](#)). As can be seen here, there is a tendency for performance to improve at the center dot with the background for all observers. This improvement was significant (background on: 84.51%, off: 80.05%, paired $t(3) = 4.305$, $p = 0.023$). In fact, the lack of a significant interaction between background and position (see [Table 1](#)) suggests that identification performance improved uniformly at all dot positions when the background was moved with the 5-dot stimulus.

Discussion

In the present study, we used a secondary identification task to manipulate attentional demands during smooth pursuit. We found that attention can be released from the fovea, as evidenced by an improvement in performance on the secondary task when the foveal stimulus was removed. Our results also demonstrate that during pursuit, the gap effect benefits a secondary perceptual task, and not just a saccadic one. In addition, we found that it is not

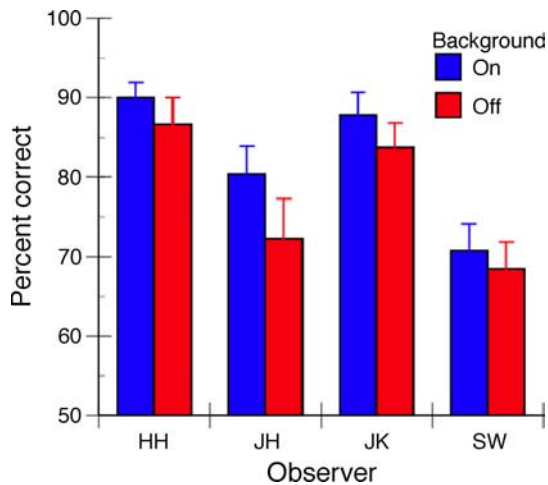


Figure 6. Identification performance at the central dot position. Note that performance was better in the background-on than background-off condition.

obligatory for the foveal target to capture attention if an alternative driving signal for pursuit is provided. This was evidenced by our finding that adding peripheral motion also boosted performance on the secondary task. Since there was less interference between the identification task and pursuit with the peripheral motion than with just foveal motion, attention required to pursue in each condition was apparently allocated differentially to different components of the pursuit system.

Previous work found that attention was narrowly allocated within a 2 deg region centered on the pursuit target (Lovejoy et al., 2009). However, in our study we found that attention was displaced away from the central target, allowing successful performance on a task that employed a stimulus that spanned 6 deg. Other work has found that attention is allocated ahead of the pursuit target (van Donkelaar, 1999; van Donkelaar & Drew, 2002). A commonality between this experiment and ours is that the targets were specified by a transient luminance change. Lovejoy et al. (2009) argued that transient targets outside of the foveal window could be detected during pursuit because they invoked attentional capture. This could explain the discrepancy between our results and theirs. Alternatively, the scope of attention is flexible and modulated by task demands. The pursuit target in Lovejoy et al.'s (2009) experiment was a number, and the task required discrimination of a letter or number that could appear at the fovea and therefore may have required more focused foveal attention. Our gap and background manipulations apparently both decreased attentional demands at the fovea to enable better performance on the task, consistent with this view.

Several studies have demonstrated that during smooth pursuit, the latency of saccades from a moving foveal pursuit stimulus to peripheral targets decreases with the gap (Boman et al., 1996; Knox, 1996; Krauzlis & Miles, 1996; Tanaka et al., 1998) as it does with static stimuli

(Fischer & Boch, 1983; Fischer & Ramsperger, 1984; Fischer & Weber, 1993; Saslow, 1967). It has been proposed that for static foveal stimuli, the gap reduces saccade latency because removing the fixation point allows for an earlier release of attention from the fovea (Fischer & Weber, 1993; Jin & Reeves, 2009; Pratt et al., 2006). This argument was also supported by improvement of performance on a peripheral vernier discrimination with the gap where no saccades were required (Mackeben & Nakayama, 1993). However, all studies showing a gap effect during pursuit used saccade tasks. Our results instead demonstrate a gap effect in a perceptual task during pursuit and provide direct evidence that the gap releases attention from a moving foveal target.

The peripheral motion provided by the RDC also appeared to reduce the amount of attention allocated to the central spot. This implies that while the spot is attended when it is the sole pursuit stimulus, its mere presence during pursuit does not necessarily usurp attention, since adding the RCD motion appeared to release attention from it. A potential reason that attention is required to pursue a spot in isolation is that the pursuit system must correct position error in order to keep the eyes foveated on the spot (Blohm et al., 2005a, 2005b; Pola & Wyatt, 1980). However, when the moving background is present, it may no longer be necessary to use position error as a drive for pursuit since motion provided by the background may be sufficient for this purpose. Therefore, although position error likely remains with the background present, it may be unnecessary to process it, thus reducing foveal attention and leaving the excess attention available for other tasks. Consistent with this idea, there were fewer catch-up saccades with the background (see Results section), which are largely used to correct for position error (de Brouwer et al., 2002).

There are several possibilities as to how the background affects attention allocation to improve task performance. One is that it redistributes attention spatially, thereby improving performance at the peripheral dots. This might occur if the background attracted attention to the periphery merely by stimulating peripheral retina. However, this alternative seems unlikely given that the presence of the background improved performance at the center dot (see Figure 6). If the mere spatial extent of the background drew attention to the periphery, performance on our task should also improve when the background moved in a different direction from the 5-dot stimulus. Preliminary data from our laboratory where subjects performed the task with background motion orthogonal to that of the 5-dot stimulus show no benefit of the background, consistent with this idea (Supplementary data 2).

Instead, we think that attention used to pursue the background arises from a different pool than that used to pursue the central spot and that the spot attention is shared with the identification task. Given this, pursuit of the background would free up attention from the spot and lead

to improved performance on the identification task. Different pools of attention may be exploited to pursue the spot and the background because different computations are performed for pursuit of these very different stimuli. When the spot is the goal of pursuit, it not only produces motion on the retina, but it can also introduce significant position error between it and the fovea, which is corrected by a position mechanism (Blohm et al., 2005a, 2005b). However, the RDC background alone produces no consistent position error, and therefore, it is likely to activate more exclusively motion-related mechanisms. Therefore, if it is used to drive the pursuit system, it might alleviate the need to correct position error that the spot might introduce. Our belief is that while the attention pool that is used to pursue the spot shares its resources with other cognitive functions such as the identification task in the current study, the attention pool used to pursue the background is outside the realm of attention used for such tasks.

Our results have implications for differential activation of structures in the pursuit system when large vs. small objects are pursued. When the main stimulus for pursuit is small and attention is directed toward it to drive pursuit, potential structures that are preferentially activated are the superior colliculus (SC), which processes position error (Krauzlis, Basso, & Wurtz, 2000), and possibly pursuit areas in frontal cortex that are not part of the classic motion processing pathway, such as the frontal eye fields (FEFs; Gottlieb, Bruce, & MacAvoy, 1993; MacAvoy, Gottlieb, & Bruce, 1991; Shi, Friedman, & Bruce, 1998; Tanaka & Lisberger, 2001) and the supplementary eye fields (Heinen, 1995; Lee & Tehovnik, 1995; Missal & Heinen, 2001; Schlag & Schlag-Rey, 1987; Schlag, Schlag-Rey, & Pigarev, 1992). In the current experiments, we supplemented the small stimulus that is normally foveated during pursuit with a large RDC that also stimulated peripheral retina. Since our results suggest that the RDC minimizes the necessity to attend to the spot in order to pursue, position error that develops between it and the fovea may be irrelevant for maintaining pursuit, and therefore, pursuit regions that are more specifically involved in processing motion might be preferentially activated when the RDC is present. These would include the main cortical motion areas that have been implicated in pursuit, including the middle temporal area (MT) and the medial superior temporal area (MST; Dürsteler & Wurtz, 1988; Newsome, Wurtz, & Komatsu, 1988). Also activated might be subcortical structures in the accessory optic system, such as the nucleus of the optic tract (NOT), that have been implicated in pursuit, peripheral motion processing and the more reflexive optokinetic reflex (OKR; Hoffmann & Distler, 1989; Ilg, Bremmer, Hoffmann, 1993; Inoue, Takemura, Kawano, & Mustari, 2000; Mustari & Fuchs, 1990).

However, the colliculus might still be activated since it has been shown to be active in the absence of a small spot when explicit correction of position error is not required

(Hafed & Krauzlis, 2008). In this study, observers pursued by maintaining gaze at the center of two peripheral spots that moved together as a unit. These authors interpreted the role of the colliculus as representing the goal of pursuit and not explicitly correcting for position error, since correcting position error would have placed the fovea on one of the peripheral dots. We speculate that the colliculus was active in this situation because it was correcting for “virtual” position error created by attempting to keep the fovea located between those spots, possibly because attention was directed here due to previous training. Given the hypothesis that the colliculus represents the goal of pursuit, we further speculate that it would not be active when a large RDC is used to drive pursuit, as was the case in our experiments, because an explicit goal is not inherent in the motion of the background.

How do our findings relate to ocular following, smooth eye movements that respond to full-field motion (Miles, Kawano, & Optican, 1986)? Natural pursuit objects, such as a colleague walking through the workplace, generally have a larger spatial extent than a small spot, as well as features that may require inspection. We believe that voluntary pursuit of the global motion of larger objects (simulated by our random-dot patterns) stimulates MT/MST, where pursuit neurons that respond to large texture motion are found (Komatsu & Wurtz, 1988), but also recruits circuitry in the system that generates the optokinetic reflex (OKR), a subsystem of ocular following that we think has been modified through evolution to follow an object selected for pursuit. The nucleus of the optic tract (NOT), commonly thought to drive OKR (Hoffmann, Distler, Erickson, & Mader, 1988; Kato, Harada, Hasegawa, & Ikarashi, 1988; Schiff, Cohen, & Raphan, 1988), also has neurons that respond during pursuit (Mustari & Fuchs, 1990). We think that this modern OKR circuitry performs a function of a larger object to allow inspection of its features using an attentional, foveate system that utilizes fixation and saccades.

However, pursuit of natural objects is critically different from primitive OKR. Primitive OKR is driven by motion of the global visual scene on the retina and is used to supplement the vestibuloocular reflex (VOR) in stabilizing that scene during self-movement in foveate animals such as fish (Cohen, 1974). OKR has been studied with textured stimuli, usually composed of gratings or random-dot stimuli such as those that we used in our experiments. However, in foveate animals, this primitive circuitry can be more of a hindrance than a benefit, at least during pursuit of an object in the visual scene. When pursuing an object in the natural world, motion driving the pursuit system is almost always directed opposite to that which would drive primitive OKR, and therefore, this reflex must either be inhibited or ignored.

Our results have implications for operation of the pursuit system outside of the laboratory. Specifically, they suggest that attention differentially activates different components of the pursuit system during pursuit of small,

foveal objects such as birds, or airplanes at a distance, and pursuit of larger objects that stimulate peripheral retina such as people or other animals in our proximity.

Conclusions

Previous work has shown that attention during smooth pursuit is restricted to a narrow region centered on the fovea. In this study, we perform two experiments that show that attention instead can be flexibly allocated during pursuit. Attention allocation was assessed by measuring identification performance on a dot-dimming task. Better performance on peripheral dot identification during pursuit was observed in a gap paradigm when the central dot was extinguished before the dot dimmed. Better performance was also found when consistent peripheral motion was provided as an alternative pursuit drive. Improved performance was not due to better image stabilization, or better visibility of the dimming in the presence of the background, rather the background appeared to free up attention from pursuit of the spot for the identification task. We conclude that attention can be flexibly allocated during pursuit and that attention for pursuit of peripheral motion comes from a different source from that required to pursue a small spot. Our results suggest that ocular pursuit in natural scenes may utilize neural mechanisms that require little conscious intervention, thereby allowing maximum allocation of resources to other tasks that require attention. Our work also has clinical implications for patients with age-related macular degeneration (AMD), as it suggests that oculomotor therapy for smooth pursuit should include peripheral motion.

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