Vision Research

Effects of attention shifts to stationary objects during steady-state smooth pursuit eye movements

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Abstract

A number of studies have shown that stationary backgrounds compromise smooth pursuit eye movements. It has been suggested that poor attentional selection of the pursuit target was responsible for reductions of pursuit gain. To quantify the detrimental effects of attention, we instructed observers to either pay attention to background objects or to ignore them. The to-be-attended object was indicated by peripheral or central cues. Strong reductions of pursuit gain occurred when the following conditions were met: (a) the subject payed attention to the object (b) a salient event was present, for instance the onset of the target or cue and (c) the attended target produced retinal motion. Removing any of the three conditions resulted in no or far smaller decreases of pursuit gain. Further, decreases in pursuit gain were present with perceptual discrimination and simple manual detection.
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1. Introduction

Tracking a moving object across a stationary background produces global retinal motion of the background opposite to the motion of the pursuit target. Global retinal motion typically elicits optokinetic nystagmus (OKN) which stabilizes the retinal image by matching eye velocity to the retinal background velocity. As the OKN elicited by a stationary background would counteract voluntary smooth pursuit, it needs to be suppressed. More than a single mechanism may be involved in turning off OKN during smooth pursuit.

1.1. Mechanisms involved in OKN suppression

To facilitate smooth pursuit across a structured background, the sensitivity of the oculomotor system to background motion opposite to the direction of pursuit is reduced. Unpredictable changes of background velocity have a larger effect if they occur in the direction of pursuit compared to changes of equal magnitude opposite to the direction of pursuit (Lindner & Ilg, 2006; Schwarz & Ilg, 1999; Suehiro et al., 1999). While our ability to execute smooth pursuit in the presence of a background shows that OKN suppression works quite well, the suggested low-level mechanism is not perfect. In the presence of a textured background, steady-state pursuit gain (eye velocity/target velocity) decreases moderately by 5–10% (Collewijn & Tamminga, 1984; Hutton, Crawford, Kennard, Barnes, & Joyce, 2000; Yee, Daniels, Jones, Baloh, & Honrubia, 1983).

It was therefore suggested that effort and attentional control also contributed to OKN suppression. Kowler, Murphy, and Steinman (1978) reported that the pursuit gain of observers was not affected when they were trained to track a small target on a textured background. Therefore, Kowler et al. concluded that previously reported reductions of smooth pursuit gain were due to a lack of

effort or a failure to allocate sufficient attention to the target. Similar effects of effort were reported for OKN by Barnes and Crombie (1985). While Kowler et al.'s results suggest that optimal allocation of attention to the pursuit target improves performance, there are no studies that examined how exactly inefficient allocation of attention harms performance.

1.2. Tradeoffs between perception and smooth pursuit

The present study aimed at characterizing the effects of attending to stationary objects during steady-state pursuit. We presented cues that indicated which of two stationary objects was to be attended. Various tasks had to be performed and the performance difference between the cued and the uncued object served to describe the efficiency of attentional allocation to the non-pursued (background) object. If differences occurred, attention was allocated to the non-pursued objects and presumably, attention was also withdrawn from the pursuit target. A performance trade-off between the oculomotor and the secondary task is expected if the two rely on the same central resources, such as effort or attention (Navon & Gopher, 1979; Norman & Bobrow, 1975). Previously, Khurana and Kowler (1987) showed that perceptual accuracy was better for pursued than for non-pursued stimuli, indicating that perception and smooth pursuit share common resources.

In the present study, we asked observers to perform as well as possible on both the oculomotor and the secondary task. We hoped that observers would allocate as much attention as possible to the secondary task. To verify this expectation, we included a control condition with eye fixation which should allow for flexible allocation of attention to peripheral positions (e.g., Posner, 1980). Cueing effects in this condition are used as the standard for the dual task conditions. If cueing effects during smooth pursuit are as large as during fixation, we assume that the secondary task has received as much attention as when it is performed alone (i.e., during fixation). With attention fully allocated to the secondary task, the trade-off with smooth pursuit performance should produce a close-to-maximal decrease of smooth pursuit performance.

In addition to the fixation condition, we included a condition with background objects that moved along with the pursuit target which eliminated (or strongly reduced) retinal motion of the peripheral objects. As with stationary objects, observers were asked to attend the cued object. While only stationary background objects produce a conflicting motion vector, both moving and stationary background objects involve a shift of attention away from the foveal pursuit target. Thus, we are able to separate effects of changes in the spatial distribution of attention (attention to moving background objects) from effects of changes in the attended motion signals (attention to stationary background objects).

Further, we wanted to isolate decreases of pursuit gain that occurred because observers were engaged in a dual task. We therefore included a single task control condition in which observers could ignore the background objects and focus exclusively on the pursuit target. It is unclear whether a secondary visual task would improve or degrade performance. It has been known for some time that secondary visual tasks on the pursuit target improve pursuit (Shagass, Roemer, & Amadeo, 1976; Sweeney et al., 1994; Van Gelder, Lebedev, Liu, & Tsui, 1995), but we know of no study asking this question for peripheral background objects moving at the same speed as the pursuit target.

1.3. Types of cues

To facilitate efficient shifts of attention, the probability that the cue indicated the correct location was about 80%. This guaranteed that cueing effects would be present in accuracy as well as in reaction time measures (Prinzmetal, McCool, & Park, 2005). Two types of cues were used. Peripheral cues were presented at the possible locations of the peripheral target to directly indicate the to-be-attended object. Central cues were presented in the fovea and had to be interpreted before they could be acted upon. The shifts of attention elicited by peripheral and central cues are often referred to as exogenous and endogenous, respectively. The important difference between central and peripheral cues is the time course of the respective shifts of attention. Performance peaks earlier with peripheral cues than with central cues (Cheal & Lyon, 1991; Müller & Rabbitt, 1989). However, both cue types are effective within less than 100 ms.

1.4. Experimental tasks

As outlined above, our goal was to measure effects of dividing attention between a stationary background object and the smooth pursuit target. While the attentional demands of the smooth pursuit task will remain unchanged, the attentional demands of the secondary task will depend on the nature of the task. Tasks that use the same resources as the pursuit task are likely to impair smooth pursuit more strongly. We therefore varied the nature of the secondary task across experiments (see Fig. 1). In Experiments 1 and 2, a perceptual task was used. Cueing benefits in such tasks are believed to arise at least in part from signal enhancement (e.g., Bashinski & Bacharach, 1980; Cheal & Gregory, 1997; Henderson, 1996). If attention to stationary objects increases the gain of their neural representation, a relatively strong perturbation of pursuit is expected because the boosted representation of the respective motion signals are in conflict with those of the pursuit target.

In Experiments 3 and 4, we asked observers to detect a luminance decrement. While some have argued that cueing effects in reaction times are due to resource allocation to the cued location (Posner, Snyder, & Davidson, 1980), others have claimed that cues decrease the response criterion
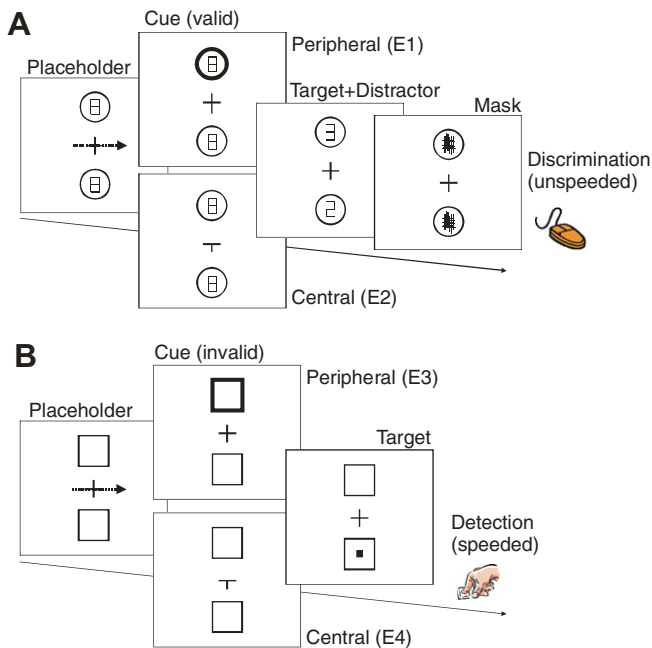
Fig. 1. Overview of experimental stimuli and tasks. (A) In Experiments 1 and 2, observers had to discriminate between the letter E and its mirror image. The numbers 2 and 5 served as distractors. A peripheral (Experiment 1) or central (Experiment 2) cue preceded pursuit target onset by 180 ms. (B) Observers were asked to detect target onset. Peripheral (Experiment 3) and central (Experiment 4) cues were presented. The onset of the cue preceded the target by 250 or 500 ms.

for stimuli appearing at the cued location (Shaw, 1984). The latter claim was recently supported by experiments showing that uninformative cues affect reaction times, but not accuracy (Prinzmetal, Park, & Garrett, 2005). Because cueing effects on reaction times arise at a late stage that is more related to decision-making or response selection, we expect the interference between smooth pursuit and the reaction time measures to decrease compared to perceptual discrimination. In fact, if the stage at which cueing effects arise in reaction time experiments is way downstream from perceptual processing, no detrimental effects of attention shifts on smooth pursuit are expected.

2. Experiments 1 and 2: perceptual discrimination with peripheral vs. central cues

In Experiments 1 and 2, two static or moving placeholders were replaced by the perceptual discrimination target and a distractor (see Fig. 2A). About 180 ms before target onset, a peripheral (Experiment 1) or central (Experiment 2) cue was presented. The peripheral cue was a luminance decrement of the peripheral placeholder. The central cue was a change of the pursuit/fixation target that indicated where the target most likely appeared. The target appeared with a probability of 80% at the cued location. A single task condition was included in which observers were asked to ignore the peripheral targets. We orthogonally varied retinal motion (absent, present) and eye movement type

(fixation, smooth pursuit). For ease of exposition, we refer to these conditions as conditions with and without retinal motion, despite that strictly speaking, there always was some retinal motion. The fixation conditions with or without retinal motion serve to gauge the cueing effects that may be obtained with similar retinal stimulation, but without concomitant smooth pursuit.

2.1. Methods

2.1.1. Participants

The same six observers participated in Experiments 1 and 2. In all experiments reported here, at least one and at most two authors participated. The authors' performance was not significantly different from the pattern of naïve observers. The remaining observers were undergraduate students in psychology. All subjects had normal or corrected-to-normal visual acuity and all were highly trained in smooth pursuit tasks. Except for the authors, the participants were naïve with respect to the experimental design and hypothesis.

2.1.2. Apparatus

The stimuli were presented on a 21 inch CRT display with a refresh rate of 100 Hz and a resolution of 1280 (H) × 1024 (V) pixels. Observers' head position was stabilized with a chin rest at 47 cm from the screen. Eye movements were recorded with a head-mounted, video-based eye tracker (EyeLink II, SR-Research, Osgoode, Ontario, Canada) at a sample frequency of 250 Hz using both pupil and corneal reflection.

2.1.3. Stimuli

The stimuli appeared on a uniform gray background of 32 cd/m^2. A 0.4 × 0.4 deg cross was used as foveal target (line thickness: 0.11 deg). Two outline circles (line thickness: 0.11 deg, radius: 2.25 deg, eccentricity: 7 deg) that contained the digit "8" (line thickness: 0.03 deg, dimensions: 0.5 deg (H) × 1.5 deg (V)) served as placeholders. The placeholders had a luminance of 25 cd/m^2. As a peripheral cue, the outline circle was dimmed for 50 ms to 0 cd/m^2 (Experiment 1). As a central cue, one branch of the fixation cross was erased for 50 ms (Experiment 2). The SOA between cue and flash was fixed at 180 ms. The peripheral target was the letter "E" or a "mirror E" (luminance: 12 cd/m^2). The digits "2" and "5" served as distractors (see Fig. 2A). Target and distractor stimuli were generated by removing two lines from the digit "8". In each trial, a peripheral target and a distractor were shown. In valid trials, the position of cue and peripheral target ("E" or "mirror E") were the same, while the distractor ("2" or "5") was shown in the non-cued location. In invalid trials, the position of the cue and distractor were the same, while the target was shown in the non-cued position. Both symbols were masked by randomly arranged horizontal and vertical lines that covered the target letter (luminance: 12 cd/m^2).
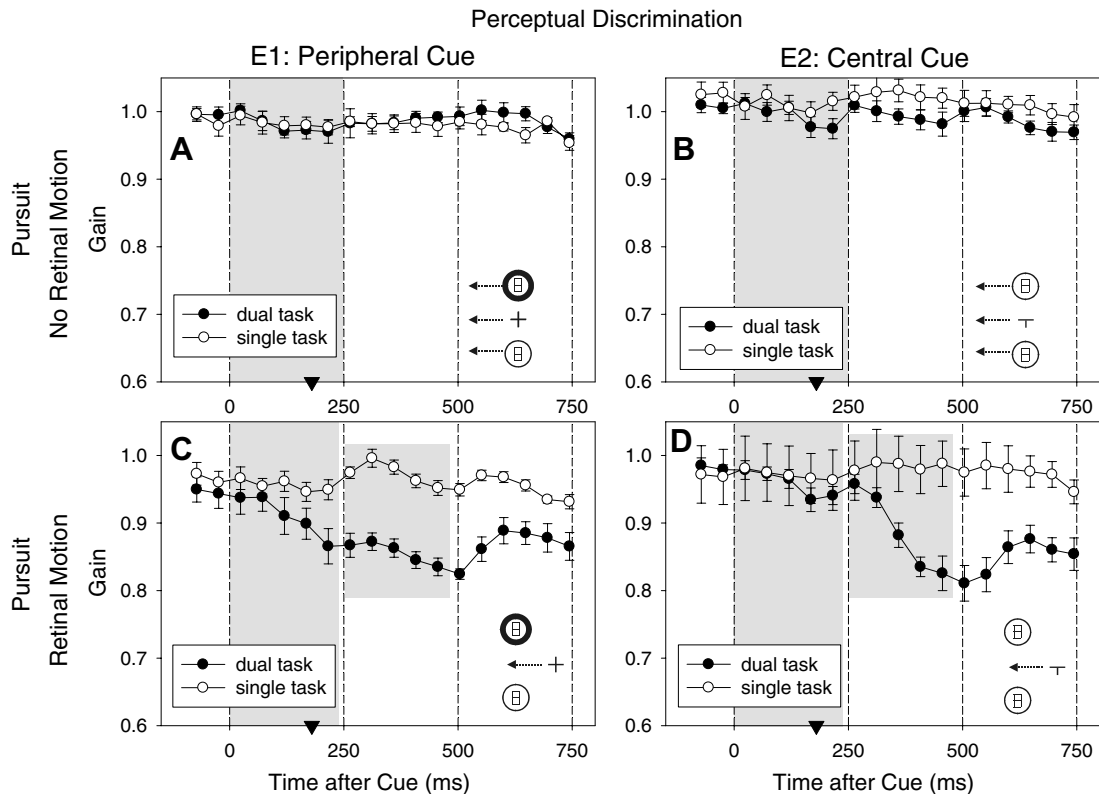
Perceptual Discrimination

Fig. 2. Eye movement gain (eye velocity/target velocity) in Experiments 1 and 2. (A and B) Pursuit gain in conditions without retinal motion of the peripheral objects. (C and D) Data from conditions with retinal motion. The time at the center of the bin is plotted (e.g., the bin 0–48 ms is plotted at 24 ms). Triangles on the *x*-axis indicate the time of target onset. Shaded areas indicate the time interval used to characterize the change of pursuit gain following cue or target onset. Error bars represent the between-subject standard error.

In conditions with smooth pursuit, the pursuit target moved for 2 s, starting randomly at an eccentric position in the left or right half of the monitor and passing the screen center after 1 s. Initial target motion was always towards the screen center and the target velocity was 7.05 deg/s. Presentation of the cue was random within a time interval of about 600 ms around the center of the trajectory. To induce retinal motion during pursuit, the placeholders remained stationary in the center of the screen. Otherwise, they moved directly above/below the foveal target. In conditions with fixation, the fixation target remained in the center of the screen, but the temporal parameters were as in the condition with smooth pursuit. To induce retinal motion during fixation, the placeholders were first shown in the left or right part of the screen and moved towards the screen center. At the start of a trial, the fixation or pursuit target was presented in its start position (eccentric with smooth pursuit or in the screen center with fixation).

2.1.4. Procedure

To initiate a trial, observers pressed a key with their left index finger. The key-press triggered a drift correction to correct for shifts of the head-mounted tracking system. When the drift correction was successful, the fixation cross turned red and 200 ms elapsed. Then, the foveal target started to move in trials with smooth pursuit. If observers

made a vertical saccade larger than 1.1 deg to one of the peripheral placeholders, an error message appeared at the end of the trial and the trial was discarded.

The task of the observer was to indicate whether the letter "E" or its mirror version had been shown. Responses were collected after offset of the pursuit target by means of a mouse click. Further, observers were instructed to attend to the cued location and to perform as well as possible on both tasks.

Before the experiment, the presentation time of the target was adjusted by means of a staircase procedure to yield 71% correct responses. This was done separately for trials with and without retinal motion during fixation. No cues were presented. The thus determined thresholds were also used in the respective smooth pursuit condition with and without retinal motion. In Experiment 1, peripheral target presentation varied between 50 and 90 ms ($M = 76$ ms) without retinal motion, and between 70 and 143 ms ($M = 99$ ms) with retinal motion. In Experiment 2, peripheral target presentation varied between 60 and 80 ms ($M = 67$ ms) without retinal motion, and between 60 and 160 ms ($M = 113$ ms) with retinal motion.

2.1.5. Design

The conditions with or without retinal motion were run in separate sessions. The order of sessions was balanced across subjects. The eye movement tasks (fixation, pursuit)

were run in alternating blocks of 40 trials. In each block, the different combinations of direction of motion (left, right), cue location (up, down), and target location (up, down) were randomly interleaved. The cue was valid in 80% of the trials, and invalid in the remaining 20%. After four blocks of 40 trials, the apparatus was recalibrated. For each of the four combinations of eye movement and retinal motion, 240 trials were collected. Thus, a total of 960 trials were run per observer and experiment. Additionally, observers completed 320 smooth pursuit trials without perceptual discrimination task for each experiment (160 with and 160 without retinal motion). In the single task condition, they were asked to pursue the target while ignoring cue and peripheral target.

2.2. Results

2.2.1. Perceptual discrimination performance

The eye movement traces were visually inspected. Trials in which the subject was not following the target, but fixated elsewhere, were excluded from analysis. Moreover, trials with blinks and unsolicited saccades to the peripheral targets (vertical component larger 1.1°) were excluded from further analysis (see Table 1). Less than 2% of the trials were discarded. Three-factorial, repeated-measures ANOVA (eye movement × retinal motion × validity) were carried out on the proportion of correct responses.

The ANOVA showed that the proportion of correct responses was higher with valid cues than with invalid cues. This was true for peripheral cues (.78 vs. .58), $F(1,5) = 41.07$, $p < .005$, and for central cues (.79 vs. .58), $F(1,5) = 57.04$, $p < .005$. For central cues, the interaction of eye movement condition and retinal motion was significant, $F(1,5) = 34.13$, $p < .005$, indicating that the proportion of correct responses was higher with retinal motion than without retinal motion during fixation (.72 vs. .62), but not during smooth pursuit (.68 vs. .70). No other main effects or interactions were significant. Inspection of the data pattern confirmed that the cueing effects were present for all combinations of eye movement and retinal motion.

2.2.2. Eye movements

Before calculating the gain, saccades and samples 16 ms before and after the saccade were removed from the eye movement trace. To identify saccades, the output of the EyeLink II eye movement parser was used. It classified episodes with acceleration larger than 4000 deg/s² and velocity larger than 22 deg/s as saccades. After removing saccades detected by the EyeLink parser, episodes in which the eye velocity deviated by more than two standard deviations from the average eye movement velocity, as well as 16 ms preceding and following this interval, were discarded. This was done to remove small saccades not detected by the EyeLink parser. Visual inspection confirmed that the algorithms worked well.

Preliminary analysis demonstrated that vertical pursuit gain was not affected by our manipulations. Therefore, the data were not considered any further.

Then, the horizontal gain (eye velocity/target velocity) was calculated for 48 ms bins (12 samples), starting 96 ms before cue onset. If more than 1/3 of the samples in a bin of a single trial were missing due to saccades, the bin was discarded.

Inspection of the gain shows that there was a rather linear decrease of pursuit gain across the initial ∼250 ms interval. To quantify the decrease of pursuit gain, a regression was run on the pursuit gain in the first five bins (i.e., 0–240 ms after cue onset). The slope of the regression quantifies if and how strongly pursuit gain decreased after presentation of the cue. The regressions were run on averaged data for each observer and experimental condition. Bins from 96 ms before to 48 ms after cue onset were averaged to have a robust estimate of baseline performance. Trials were averaged across valid and invalid trials as both imply shifts of attention. Negative slopes indicate that pursuit gain decreased. The unit of slope values is gain per second.

To evaluate whether observers traded smooth pursuit for perceptual performance on a trial-by-trials basis, we correlated the pursuit gain in each bin with the correctness of the perceptual judgment. Correlations were calculated for each observer separately. Then, individual correlations were converted to Fisher's z and the resulting values were compared to zero by a t-test. For clarity, correlations and not Fisher's z values are reported. We repeated this analysis with moving averages across more than a single bin, but this did not change the results substantially.

2.2.2.1. Initial decrease of pursuit gain.
Fig. 2 shows the eye movement data and Fig. 3 summarizes the slopes of the initial decrease. When there was no retinal motion during smooth pursuit, the initial decrease of pursuit gain was slightly stronger in the dual task compared to the single task condition. The difference was not quite significant with peripheral cues (−0.14 vs. −0.06), $t(5) = 1.99$, $p = .1$, but it

Table 1
Task, type of cuing, velocity (deg/s), number of subjects (N), percentage of false alarms (FA) in catch trials, percentage of misses in target-present trials (M) and the percentage of all rejected trials (R, including false alarms, misses, and bad traces) in Experiments 1–4

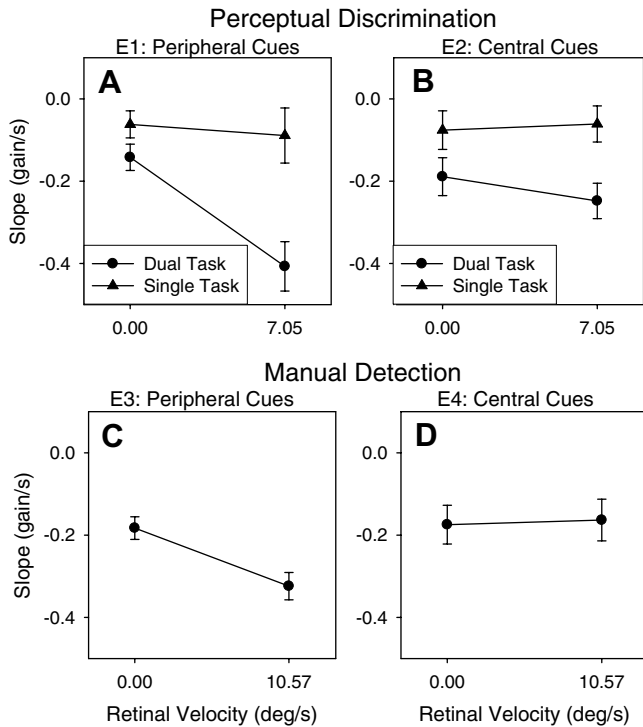|	Task	Cueing	Velocity	N	FA	M	R
Exp. 1	Perceptual discrimination	Peripheral	7.05	6	—	—	1.4
Exp. 2	Perceptual discrimination	Central	7.05	6	—	—	1.3
Exp. 3	Manual detection	Peripheral	10.57	8	5.2	2.3	4.5
Exp. 4	Manual detection	Central	10.57	6	2.0	2.1	4.6

Perceptual Discrimination

Fig. 3. Slopes characterizing the early change of pursuit gain following cue onset. Five bins following cue onset were used in Experiments 1 and 2 (i.e., 0–240 ms after cue onset) and four bins in Experiments 3 and 4 (i.e., 0–192 ms after cue onset). Negative slope values indicate that pursuit gain decreased. The titles refer to the secondary task or cue type employed in the respective experiment. Error bars represent the between-subject standard error.

reached significance with central cues (-0.19 vs. -0.08), $t(6) = 5.86$, $p < .005$. Similarly, when there was retinal motion during pursuit, pursuit gain decreased more in the dual task than in the single task condition. This difference was significant with peripheral cues (-0.41 vs. -0.09), $t(5) = 5.56$, $p < .005$, and with central cues (-0.25 vs. -0.06), $t(5) = 2.85$, $p < .05$. Inspection of Fig. 3A and B suggests that the effect of retinal motion in the dual task condition was particularly strong with peripheral cues. This impression was confirmed by separate two-factorial ANOVAs (task load × retinal motion) for peripheral and central cues.

For peripheral cues, the ANOVA showed that slopes were more negative in the dual compared to the single task condition (-0.28 vs. -0.08), $F(1,5) = 33.29$, $p < .005$. The effect of retinal motion approached significance, $F(1,5) = 6.25$, $p = .054$. Task load and retinal motion interacted, $F(1,5) = 11.17$, $p < .05$, indicating that the decrease due to retinal motion was stronger in the dual task condition than in the single task condition (difference of 0.26 vs. 0.03).

For central cues, the ANOVA showed that pursuit gain decreased more in the dual task compared to the single task condition (-0.22 vs. -0.07), $F(1,5) = 26.86$, $p < .005$. However, task load and retinal motion did not interact,

$F(1,5) = 0.89$, $p = .38$, showing that the effects of retinal motion were the same for single and dual task conditions.

Further, we directly compared the initial slope values of central and peripheral cues in the dual task conditions. Without retinal motion, the slope values did not differ between peripheral and central cues (difference of 0.05), $t(5) = 1.83$, $p = .13$. With retinal motion, the slope values were more negative with peripheral than with central cues (difference of 0.16), $t(5) = 3.82$, $p < .05$.

Finally, cue onset did not affect pursuit gain if it was ignored. In the single task condition, the initial slopes with and without retinal motion were not significantly different from zero, $t(5) < 1.89$, $p > .11$. In contrast, attention to the peripheral objects in the dual task conditions produced a significant decrease even when there was no motion on the retina: Slopes with and without retinal motion were significantly different from zero, $t(5) > 4.1$, $p < .01$.

2.2.2.2. Late decrease of pursuit gain. With central cues and retinal motion, smooth pursuit gain dropped dramatically about ~100 ms after target onset (i.e., 280 ms after cue onset) in the dual task condition. Only a far smaller decrease was visible with peripheral cues in the dual task condition (cf. Fig. 2C and D). To quantify the late decrease, we ran regressions from the bin centered on 264 ms to the bin centered on 456 ms in the conditions with retinal motion (see Fig. 4). With peripheral cues, the slopes were the same for single and dual task conditions (-0.16 vs. -0.19), $t(5) = 0.20$, $p = .85$. With central cues, pursuit gain decreased much more in the dual than in the single task condition (-0.77 vs. 0.02), $t(5) = 5.34$, $p < .005$.

2.2.2.3. Correlations. The correlations between pursuit gain and correctness of the perceptual judgment were small. If an alpha-level of .01 is accepted to correct for multiple comparisons, none of the mean correlations were significantly different from zero. Also, there was no systematic time course of the correlations.
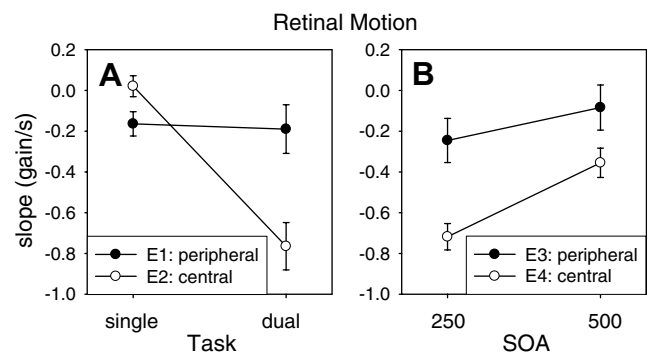

Fig. 4. Slopes characterizing the late change of pursuit gain from bins 264–456 ms in Experiment 1 and 2, and from bins 312–408 ms in Experiment 3 and 4. Only conditions with retinal motion were analyzed. Negative slope values indicate that pursuit gain decreased. Error bars represent the between-subject standard error.

2.3. Discussion

Our results confirmed that attention shifts, as estimated by the difference between cued and uncued locations in the perceptual task, were as efficient during fixation as during pursuit. We thus think that performance decrements in the pursuit task due to the perceptual task were as strong as they can get.

Background objects did not influence pursuit gain when they were not attended to. In the single task conditions, smooth pursuit gain was hardly affected by cue or target onset. This shows that the attentional filter, if set to ignore peripheral objects, works quite well. In contrast, pursuit gain decreased significantly in the interval following cue onset when the peripheral objects were task relevant. This decrease occurred even when there was no retinal motion of the peripheral objects. Thus, a secondary visual task associated with peripheral stimuli does not facilitate pursuit. Previously, facilitation of smooth pursuit has been reported when the secondary visual tasks was presented on the pursued object (Shagass et al., 1976; Sweeney et al., 1994; Van Gelder et al., 1995). If attention is conceptualized as a "spotlight" of variable diameter (Eriksen & St James, 1986), attention is expected to spread out when the secondary visual task is presented on peripheral objects, and to "zoom in" when the secondary visual task is presented on the pursuit target. Consequently, "zooming in" on the pursuit target improves pursuit performance and not performing a secondary visual task itself (cf. Madelain, Krauzlis, & Wallman, 2005).

Further, there was an early decrease of pursuit gain with peripheral cues and stationary objects. This result confirms that observers had to compromise pursuit performance when attending to a stationary object. However, they had to compromise smooth pursuit performance only to a certain degree. Even though attention was shifted efficiently (as confirmed by our comparison with the fixation condition), smooth pursuit performance only dropped by 10–15% to about 0.8–0.85. Despite the evidence for tradeoffs between pursuit and secondary task (i.e., comparison single vs. dual task), the lack of trial-by-trial correlations between smooth pursuit and perception suggest that the decrease of pursuit gain was not due to switching between extreme strategies. Observers did not attend to the pursuit target while neglecting the perceptual target on one trial, and attended to the perceptual target while neglecting the pursuit task on another. Rather, there was a general decrease in performance due to the secondary task that was independent of perceptual performance on a trial-by-trial basis. Another alternative for the lack of correlation may be the high noise of pursuit gain in bins of 48 ms. However, averaging across more than a single bin before running the correlation did not alter the results substantially.

Finally, our results suggest that the initial decrease of pursuit gain was stronger with peripheral than with central cues. Conversely, the late decrease of pursuit gain around ∼280 ms after cue onset was stronger with central than with peripheral cues. The different time course of peripheral and central cues is consistent with the literature on perceptual accuracy (Cheal & Lyon, 1991; Müller & Rabbitt, 1989) where it was demonstrated that perceptual accuracy peaks and drops earlier with peripheral than with central cues. However, the late decrease of pursuit gain with central cues and retinal motion was conspicuously abrupt. Typically, the build-up of attentional effects on accuracy is much more continuous. Therefore, we will consider the alternative hypothesis that the late decrease of pursuit gain with central cues was triggered by the onset of the target, and not by the late deployment of attention. In other words, the attention shift may have been incomplete after presentation of a central cue, and was finalized after presentation of an abrupt onset in the periphery. In contrast, peripheral cues draw most of the attentional resources immediately to their location and only few resources are allocated at target onset. Therefore, there is a strong early decrease and a small decrease later on.

3. Experiments 3 and 4: Manual detection with peripheral vs. central cues

To disentangle the two hypotheses (late attentional deployment vs. target as trigger) we varied the stimulus onset asynchrony (SOA) between cue and target between 250 and 500 ms. If late deployment of attention was responsible for the late decrease of pursuit gain, then the decrease should be comparable for 250 and 500 ms SOAs. In contrast, if target onset triggered the late decrease, the late decrease should be present with a SOA of 250 ms, but not with a SOA of 500 ms.

Further, we used a manual detection task (see Fig. 2B). Previously, it has been argued that cueing effects in this paradigm may be entirely due to changes in response thresholds. Participants may be more ready to respond to cued locations than to uncued locations (e.g., Prinzmetal et al., 2005). Consequently, it may be that participants do not have to compromise smooth pursuit performance for performance on the secondary task because the two use different processing resources.

3.1. Methods

3.1.1. Subjects

Eight subjects participated in Experiment 3 and six of those subjects participated in Experiment 4.

3.1.2. Apparatus and stimuli

The same apparatus and stimuli were used as in Experiments 1 and 2 with the following exceptions. Two gray outline squares (size = 2.1 deg, luminance = 25 cd/m², one pixel lines = 0.035 deg) were presented at 5 deg above and below the horizontal target trajectory (center-to-center) as placeholders for the peripheral target (see Fig. 2B).

The target for the location discrimination tasks was a small filled square (size = 0.35 deg, luminance = 12.5 cd/

m^2) that was presented in the center of one of the peripheral boxes and was visible until the end of a trial. As a peripheral cue, one of the two outline squares was dimmed to 0 cd/m^2 for 100 ms (Experiment 3). As a central cue, one branch of the foveal fixation cross disappeared for 100 ms (Experiment 4). The target moved horizontally at 10.57 deg/s.

3.1.3. Procedure

A simple detection task was used. Subjects were asked to press a button with their right index as soon as the target appeared. If the latency of the response was shorter than 100 ms or longer than 500 ms, the response was considered anticipatory or missed, respectively. In trials in which no peripheral target was presented (catch trials), responses were considered false alarms.

3.1.4. Design

The design was as in Experiments 1 and 2 with the following exceptions. When the eccentric target was presented, it was preceded by a cue on the same placeholder (valid cue) in 60% of all trials. In 20% of the trials, the cue and the target were presented on different placeholders (invalid cue). Thus, the cue had a validity of 75% (60/80). To avoid anticipations, no peripheral target was presented in the remaining 20% of the trials. No single task trials were run.

3.2. Results

3.2.1. Reaction times

A five-factorial ANOVA (eye movement × retinal motion × SOA × validity) was run on the reaction time data.

3.2.2. Peripheral cues

Reactions times were faster with valid than with invalid cues (287 vs. 310 ms), $F(1, 7) = 21.95$, $p < .005$, and were faster during fixation than during smooth pursuit (294 vs. 304 ms), $F(1, 7) = 7.69$, $p < .05$. The main effect of SOA, $F(1, 7) = 16.94$, $p < .005$, showed that reactions were faster with the long SOA than with the short SOA (293 vs. 305 ms). The interaction between SOA and cue validity approached significance, $F(1, 7) = 5.35$, $p = .054$, indicating that the advantage of valid trials was larger with the short than with the long SOA (28 vs. 19 ms, both means different from zero, ps < .005). There was no evidence that cueing effects were affected by eye movement or retinal motion.

3.2.3. Central cues

Reaction times were faster with valid than with invalid cues (269 vs. 297 ms), $F(1, 5) = 42.87$, $p < .005$, and were faster with the long SOA than with the short SOA (268 vs. 298 ms), $F(1, 5) = 221.43$, $p < .001$. The interaction of retinal motion and eye movement, $F(1, 5) = 24.69$, $p < .005$, showed that retinal motion speeded up responses during fixation (277 vs. 288 ms), but rather slowed down responses during smooth pursuit (286 vs. 280 ms). The interaction of eye movement and cue validity approached

significance, $F(1, 5) = 6.46$, $p = .052$, indicating that the advantage of valid trials was slightly reduced during smooth pursuit (32 vs. 23 ms, both means different from zero, ps < .01). Thus, attention shifts tended to be less efficient during smooth pursuit than during fixation. However, the reduction of the cueing effect was small (9 ms) and not quite statistically significant. We therefore chose to not interpret this finding any further.

3.2.4. Eye movements

3.2.4.1. Initial decrease of pursuit gain.
Eye movement data are shown in Fig. 5 and slope values are shown in Fig. 3. Without retinal motion, pursuit gain decreased. The slope values were significantly different from zero with peripheral cues (−0.18), $t(7) = 6.65$, $p < .001$, and central cues (−0.17), $t(5) = 3.7$, $p < .05$. Similarly, attending to stationary objects during pursuit led to a decrease of pursuit gain with peripheral cues (−0.32), $t(7) = 9.76$, $p < .001$, and central cues (−0.16), $t(5) = 3.22$, $p < .05$. For peripheral cues, the decrease of pursuit gain was larger with than without retinal motion, $t(7) = 3.16$, $p < .05$. This was not the case for central cues, $t(5) = 0.19$, $p = .86$. Thus, attention to stationary objects only reduced initial pursuit gain when peripheral cues were used.

3.2.4.2. Late decrease of pursuit gain.
Regressions were run on the bins centered on 312–408 ms which best reflect the late decrease (differences between adjacent bins were significant). Only conditions with retinal motion were considered because there were no differences between SOAs without retinal motion. Mean slope values are presented in Fig. 4B. With peripheral cues, there was no difference between the 250 and 500 ms SOA (−0.25 vs. −0.08), $t(7) = 1.48$, $p = .18$. With central cues, the decrease was larger with the 250 than with the 500 ms SOA (−0.72 vs. −0.36), $t(7) = 17.12$, $p < .001$.

3.2.4.3. Correlations.
The correlations between pursuit gain in individual bins and RT were again small and mostly not significant. With peripheral cues and retinal motion, they were highly significant with an SOA of 250 ms in the ∼150 ms following target onset ($p < .01$, see bins centered on 264, 312, and 356 ms in panel 5E). The significant positive correlations suggest that trials with a high gain were trials in which manual responses were slow. However, no such tendency was confirmed in the 500 ms SOA condition after target onset (i.e., from 500–700 ms after cue onset). With central cues, the correlations between pursuit gain and reaction time were small and mostly not significant ($p > .01$). There was one highly significant correlation for the bin centered on 216 ms. However, this was due to the extremely small variability in this bin which resulted in a significant t-value.

3.3. Discussion

We confirmed the results of Experiments 1 and 2. Peripheral cues resulted in a large early decrease of pur-
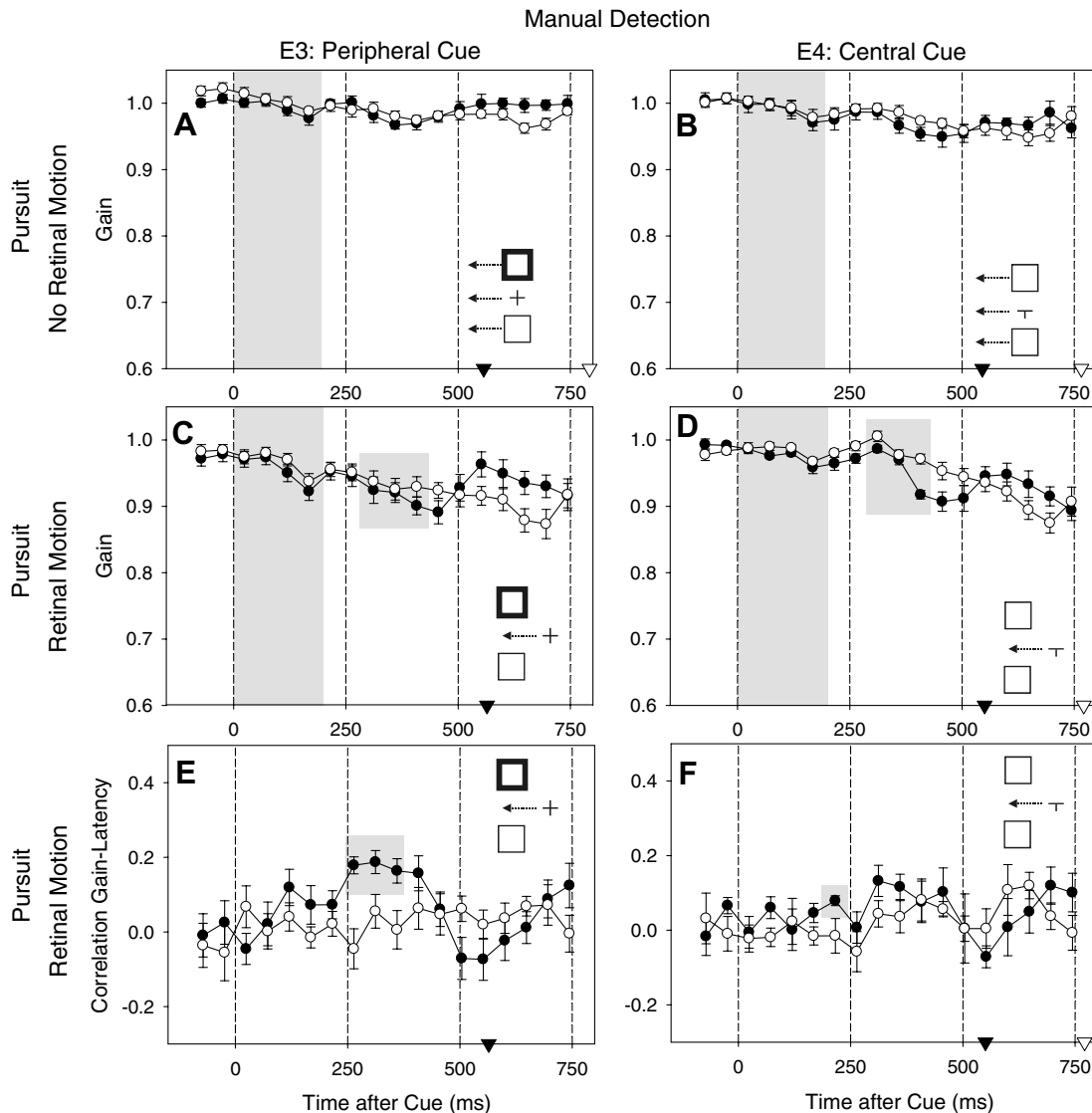
Manual Detection

Fig. 5. Eye movement gain (rows 1 and 2) and correlations between gain and reaction time (row 3) in Experiments 3 and 4 as a function of cue-target interval (250 or 500 ms). (A and B) Pursuit gain in conditions without retinal motion of the peripheral objects. (C–F) Data from conditions with retinal motion. Shaded areas indicate the time interval used to characterize the change of pursuit gain following cue or target onset (A–D), or significant correlations (E–F). The triangles on the x-axis indicate when the response occurred in the 250 ms (filled triangle) and 500 ms (open triangle) SOA conditions. In some cases, the response occurred outside the visible range (C and E). Correlations are only shown for the pursuit conditions with retinal motion. In the condition without retinal motion, correlations were essentially zero. Error bars represent the between-subject standard error.

suit gain when a stationary object was attended. The decrease was smaller when the peripheral cue indicated a moving object. Central cues produced a smaller initial decrease, but a larger late decrease. In particular, the late decrease with retinal motion was more pronounced for the SOA of 250 ms than for the SOA of 500 ms (see panel 5D). Thus, it is likely that the onset of the target after 250 ms, and not the late allocation of endogenous attention is responsible for the late decrease. If late allocation of endogenous attention was responsible, the decrease with retinal motion should have been the same for the 250 and 500 ms SOA. In sum, attentional resources seem to be allocated piecemeal whenever a salient event is present: One chunk at cue onset, and another chunk at target onset.

Even though the detection task was extremely simple and some have argued that cueing effects with detection are entirely due to response-related changes in threshold, we observed a pattern of results that was highly similar to the perceptual discrimination task in Experiments 1 and 2. The decrease of pursuit gain was stronger when stationary objects had to be attended than when the to-be-attended objects moved along with the pursuit target. Peripheral cues produced an immediate decrease, while central cues produced a small initial decrease and a large decrease later on.

4. General discussion

In the present study, we investigated effects of attention shifts to background objects on smooth pursuit. We used a

dual task paradigm and assured that the weight given to the secondary task was comparable to a single task condition (i.e., fixation). Therefore, the changes in pursuit gain are expected to be close to the maximal change that may be obtained. We were interested in whether the dual task itself produced changes of pursuit gain. In the absence of conflicting motion signals, the dual task condition produced a decrease of pursuit gain in all experiments. Thus, execution of two tasks at the same time involving different objects (a foveal pursuit target and peripheral discrimination targets) tends to degrade smooth pursuit gain. In contrast, a secondary visual task on the pursuit target is known to improve pursuit gain. Overall, changes of pursuit gain with peripheral objects producing no retinal motion were significant, but rather small.

Far larger changes were observed when the peripheral objects produced retinal motion. With retinal motion of the peripheral objects, we noted that exogenous cues produced an immediate decrease after cue onset, and a far smaller decrease after target onset. For central cues, the opposite was true. The decrease after cue onset was small, whereas the decrease after target onset was large. Our results may be summarized in the following way. Strong reductions of pursuit gain occur when the following conditions are met: (a) the subject pays attention to the object (b) a salient event is present, for instance the onset of the target or cue and (c) the attended target produces retinal motion. Removing any of the three conditions will result in no or far smaller decreases of pursuit gain.

Finally, we asked whether changes in pursuit gain depend on the nature of the secondary task. In the introduction, we presented evidence that cueing effects in the different tasks may arise at different stages (perceptual or response-related). Alternatively, one may conceptualize the differences in terms of task difficulty. The perceptual task required discrimination between two possible percepts at a given location, while the manual detection task required judging the presence or absence of an object. Thus, task difficulty decreased from Experiments 1 and 2 to Experiments 3 and 4. It has been demonstrated that deployment of attentional resources is not independent of task difficulty. More attentional resources are allocated to difficult than to easy tasks (Urbach & Spitzer, 1995). Therefore, more difficult secondary tasks should lead to larger perturbations of smooth pursuit than easy secondary tasks.

Consistent with this idea, Hutton and Tegally (2005) reported that effects of secondary non-visual tasks changed with task difficulty. With repetitive tapping, pursuit gain did not change compared to a single task condition, whereas it decreased when a spatial pattern had to be tapped. Presumably, the latter task was more difficult. In contrast, the present series of experiments showed that effects of various secondary tasks produced quite comparable effects on smooth pursuit. It was neither the case that secondary tasks involving perceptual judgments produced particularly strong decreases of smooth pursuit, nor was it the case that supposedly easy tasks such as simple detec-

tion could be executed at no cost. From looking at Fig. 3 one may get the impression that the effect of retinal motion was smaller in Experiment 3 (manual detection, peripheral cues) than in the other experiments. However, a *t*-test on the five subjects who participated in Experiments 1 and 3 did not confirm this impression. While this conclusion is certainly post-hoc and would require additional support from a direct comparison of perceptual discrimination and manual detection, there is no doubt about the similarity of the pattern of changes in pursuit gain.

The present results show that motion signals from the pursuit target and non-pursued objects are averaged. The degree to which averaging occurs depends on the attentional resources allocated to the non-pursued objects. When the background objects are ignored, pursuit gain is hardly affected by conflicting motion signals arising from background objects. When the background objects are attended, the motion signal is averaged with motion of the target, but the weight of the non-pursued motion signals is relatively low. This is evident in the high overall gain even with attention allocated to stationary objects. Therefore, the distribution of attention determines which motion signals drive pursuit and the weight given to different motion signals may vary. In other words, observers are able to compromise smooth pursuit in order to shift attention elsewhere, but the result of this compromise is gradual, and not all-or-none.

In contrast to the closed-loop pursuit responses observed here, studies investigating the role of opponent motion of a distractor on smooth pursuit initiation showed delayed latency but a winner-take-all pursuit response, even in conditions that strongly facilitated allocation of attention to the target: Ferrera and Lisberger (1995) instructed monkeys to pursue one of two objects (the target), while ignoring the other object (the distractor). They observed that a distractor moving in the same direction as the target shortened response latencies, while a distractor moving in the opposite direction increased response latency. The role attributed to attention was to bias the competition between motion signals. Once a specific motion signal is selected, it exclusively drives smooth pursuit (winner-take-all). The winner-take-all response contrasts with the vector-averaging of pursuit direction when distractors move in non-collinear directions (Lisberger & Ferrera, 1997). For instance, if one object moves from top to bottom, and the other from left to right, the eye will move toward the lower right, indicating that the direction of individual object motion was averaged. However, vector-averaging is strongly reduced if observers have advance knowledge of the to-be-selected target (Spering, Gegenfurtner, & Kerzel, 2006), showing that top–down processing may modulate vector averaging.

Activity in area MT/MST may underlie the gradual attentional modulations found here because this area provides direction and speed information for the pursuit system (reviewed in Krauzlis, 2004). For example, initial pursuit acceleration depends on the speed signal that can

be estimated from the population response in MT (Priebe, Churchland, & Lisberger, 2001).

It is well known that activity of neurons in the area MT/MST are modulated by spatial attention (Martinez-Trujillo & Treue, 2002; Recanzone & Wurtz, 1999; Seidemann & Newsome, 1999; Treue & Maunsell, 1996). Recanzone and Wurtz (2000) found that during the steady-state phase of smooth pursuit, attention may modulate the neural response in MT and MST by more than 50%. Previously, these authors had already demonstrated that the transition from an initial vector-average response at 150 ms after target onset to a winner-take-all response during the steady-state phase correlated with the winner-take-all or vector-average neural response. They suggested that attention may play a major role in the winner-take-all oculomotor outcome (Recanzone & Wurtz, 1999). However, direct comparisons between experiments are made difficult because of the strong differences in attentional modulation arising from apparently small differences in task difficulty or the nature of attentional components involved (overview in Treue, 2001). Coarsely speaking, the modulations observed in our study fit well with the time course of attentional effects in MT and the strength of the observed modulation. For instance, Seidemann and Newsome (1999) showed a mean modulation of ~9% by attention and a latency of ~300 ms due to the top-down allocation of attention (discussed in Treue & Maunsell, 1999). Although further direct comparison with neurophysiological and behavioural studies are needed to elucidate how attention modulates the read-out of distractor and target motion from MT for smooth pursuit, our study suggests that the pursuit response can return to vector-average by shifting attention to a peripheral object, just as attention may bias the oculomotor system away from the vector-average to a winner-take-all response during pursuit initiation (Recanzone and Wurtz, 1999; Recanzone and Wurtz, 2000). Altogether, the present study indicates that attention may bias the closed-loop pursuit response by differentially weighting the contribution of non-target motion signals.

Acknowledgments

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