

The default allocation of attention is broadly ahead of smooth pursuit

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When moving through our environment, it is vital to preferentially process positions on our future path in order to react quickly to critical situations. During smooth pursuit, attention may be directed ahead with either a focused locus or a broad bias. We examined the 2D spatial extent of attention during a smooth pursuit task using both saccade (SRT) and manual (MRT) reaction times as measures of attentional allocation. Targets were flashed at various locations around current eye position while subjects pursued a moving target. Subjects made a saccade or pressed a button as soon as they perceived the target. Both SRTs and MRTs were shortest to targets flashed ahead of compared to behind the direction of pursuit across half of the visual field ahead of pursuit direction. Furthermore, we found an increase specific to SRTs at small target eccentricities directly ahead of pursuit, which may be related to an additional saccade trigger strategy; small saccades take longer to execute if smooth pursuit brings the eyes close to the target. In summary, both SRTs and MRTs revealed that attention is by default broadly allocated in the visual hemi-field ahead of the line of sight during smooth pursuit eye movements. This attentional bias may serve a predictive purpose for facilitating the processing of upcoming events.

Keywords: spatial attention, saccade latency, manual reaction time, eye movements

Citation: Khan, A. Z., Lefèvre, P., Heinen, S. J., & Blohm, G. (2010). The default allocation of attention is broadly ahead of smooth pursuit. *Journal of Vision*, 10(13):7, 1–17, <http://www.journalofvision.org/content/10/13/7>, doi:10.1167/10.13.7.

Introduction

A natural visual scene can contain abundant information, all of which the brain may not be capable of processing simultaneously. In addition, many objects in our environment are moving, appearing or disappearing rather than remaining static. To maximize the potential information we can acquire from the scene, the visual system prioritizes information by selectively attending to locations of interest (James, 1890). For example, the visual system might take advantage of predictive situations by extrapolating where an object will be in the future and allocating attention to that location. This would allow new information to be processed as quickly as possible. Eye movements are predictive in that we can anticipate the future location of gaze before the eyes even begin to move (Barnes, 2008; Kowler, 1989; Schall & Boucher, 2007). In the case of saccades, many previous studies have

shown that attention shifts before saccades to the future goal of the movement (e.g., Crawford & Muller, 1992; Deubel & Schneider, 1996; Dore-Mazars, Pouget, & Beauvillain, 2004; Gersch, Kowler, & Doshier, 2004; Godijn & Theeuwes, 2003; Hoffman & Subramaniam, 1995; Kowler, Anderson, Doshier, & Blaser, 1995), thus taking advantage of this information. It has recently been suggested that saccades and pursuit eye movements may involve similar processes in the brain (Krauzlis, 2004, 2005; Orban de Xivry & Lefèvre, 2007) and therefore it is reasonable to consider that pursuit eye movements may also direct attention. The question is where and how attention is allocated during an ongoing smooth pursuit movement when the eye position is constantly updated.

There are a number of studies that have investigated attentional allocation during pursuit movements (Blohm, Missal, & Lefèvre, 2005; Kanai, van der Geest, & Frens, 2003; Kerzel, Born, & Souto, 2009; Khurana & Kowler, 1987; Lovejoy, Fowler, & Krauzlis, 2009; Souto &

Kerzel, 2008; Tanaka, Yoshida, & Fukushima, 1998; van Donkelaar & Drew, 2002). These studies can generally be grouped into two categories according to the behavioral measurement of attention during pursuit: (1) movement reaction times to targets flashed around the pursuit stimulus (Blohm et al., 2005; Kanai et al., 2003; Tanaka et al., 1998; van Donkelaar & Drew, 2002) and (2) discrimination of targets at or around the pursuit stimulus (Khurana & Kowler, 1987; Lovejoy et al., 2009). These two categories may reflect different attentional aspects (Prinzmetal, McCool, & Park, 2005). Indeed, attention at a certain location can speed up the detection of objects (Posner, 1980), which can lead to shorter latency saccades to that location (Clark, 1999; Findlay, 2009; Hoffman & Subramaniam, 1995; Shepherd, Findlay, & Hockey, 1986) or can improve the discrimination of targets at that location (Castet, Jeanjean, Montagnini, Laugier, & Masson, 2006; Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Khurana & Kowler, 1987; Lovejoy et al., 2009) or both (Hoffman & Subramaniam, 1995; Prinzmetal et al., 2005).

In the present study, we chose to focus on reaction times to investigate how attention is allocated by default across 2D space during a simple pursuit task, without explicit manipulation of attention, e.g., through cues. Many studies have used reaction times as a behavioral correlate of attention with the following logic: if certain spatial locations are attended, a target appearing at that location should be detected faster, leading to faster reaction times, compared to targets flashed at non-attended locations (Findlay, 2009; Hoffman & Subramaniam, 1995; Posner, 1980; Shepherd et al., 1986). Previous studies on pursuit have shown a decrease of reaction times ahead of pursuit compared to behind pursuit (Blohm et al., 2005; Kanai et al., 2003; Tanaka et al., 1998; van Donkelaar & Drew, 2002). These studies indicate that, when there is no specific task or location to be attended, attention is by default allocated ahead of pursuit. However, there are a number of questions that remain unanswered. First, it remains unclear how attention is allocated during pursuit across two-dimensional (2D) space, i.e., across both distance and direction. Studies have shown that both saccade reaction times (Blohm et al., 2005; Kanai et al., 2003; Smeets & Bekkering, 2000; Tanaka et al., 1998) and manual reaction times (van Donkelaar & Drew, 2002) are shorter to targets presented in the direction of pursuit compared to targets presented in the opposite direction. Some of these studies presented targets only along the horizontal meridian (Tanaka et al., 1998; van Donkelaar & Drew, 2002), implying that attention may be constrained along a narrow horizontal range and following the pursuit path (Figure 1A). Other studies presented targets at different directions relative to pursuit and found that saccade reaction times were shorter in some or all directions ahead of pursuit (Blohm et al., 2005; Kanai et al., 2003). Their results could be interpreted as a focus of attention ahead of pursuit (Figure 1B) that is somewhat

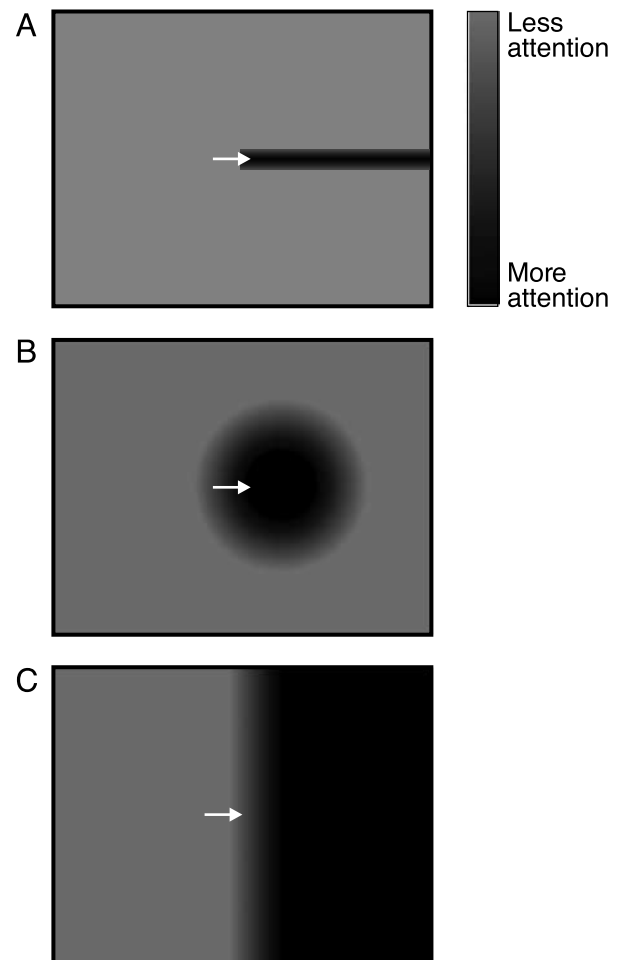


Figure 1. Possible attentional allocation patterns during pursuit. (A) Narrow range of attentional focus. Attention could be directed to a narrow range of directions ahead of pursuit. (B) Attentional focus ahead of pursuit. Attention could be directed to a location ahead of pursuit with a limited focus. (C) Attention could be broadly biased to the entire hemi-field ahead of pursuit. Color code ranges from gray (less attention) to black (more attention). The white arrow depicts the direction of pursuit and the arrowhead represents current eye position.

diffuse or a large overall bias in the entire field ahead of pursuit (Figure 1C). The focus of attention hypothesis is also supported by van Donkelaar and Drew (2002) who showed that *manual* reaction times are reduced shortly ahead of pursuit but increase further ahead. On the other hand, other studies showed a decrease of *saccadic* reaction times at both short (Kanai et al., 2003) and at further (Tanaka et al., 1998) distances ahead suggesting that attention may bias the entire visual field ahead of pursuit (Figure 1C). In summary, the results of these studies are inconclusive because they were limited by a small set of potential target locations. Furthermore, the saccade reaction time studies produced conflicting results both with each other, and with those studies that used manual reaction time as a readout of attention allocation during

pursuit, possibly because the experimental conditions were different in the different studies.

These conflicting findings lead to a second related question, which is whether some of the differences between studies mentioned above may be due to differences in the behavioral measure, i.e., saccadic vs. manual reaction times.

Here, we set out to determine whether default attention during pursuit is focused narrowly to small regions, or if it can be allocated broadly across the visual field using either the saccadic or hand motor system. We used a pursuit task, in which subjects were asked to either make a saccade or to press a button in response to a flashed target as soon as it appeared during ongoing pursuit. We evaluated saccade (SRT) and manual (MRT) reaction times as behavioral measures of attention. We tested whether reaction times varied as a function of direction and distance relative to pursuit direction by comparing reaction times to flashed targets presented randomly across a two-dimensional (2D) region centered on the current eye position. We controlled for SRT and MRT distance effects using tasks without pursuit. In doing so, we showed that both SRTs and MRTs to targets presented across the entire visual field ahead of the current eye position were shorter during pursuit. SRTs showed an additional effect at small target eccentricities that may reflect a saccadic trigger mechanism that interacts with pursuit eye movements. In summary, during pursuit attention is by default allocated to a broad region ahead of the eye position in the pursuit direction.

Methods

Task 1: Saccade reaction time

Subjects

We recorded the eye movements of eight healthy human subjects whose ages ranged between 23 and 38 (6 males, 2 females, all right handed). All subjects had normal or corrected-to-normal vision and did not have any history of neurological disorders. All procedures were approved by the Université catholique de Louvain Ethics Committee, in compliance with the Declaration of Helsinki.

Apparatus

Subjects sat in a completely dark room with their heads restrained by a chin rest. They sat facing a 1-m distant tangential translucent screen on which we presented a green pursuit target and a red saccade flash target. The green pursuit target was 0.5° in diameter and was generated by a Tektronics (Beaverton, OR, USA) 606A oscilloscope and was back-projected through custom

optics. The red flashed target was a 0.2° diameter laser spot that was back-projected via two M3-Series mirror galvanometers (GSI Lumonics, Billerica, LA, USA). Movements of the right eye were measured using the scleral coil technique (Skalar Medical BV, Delft, The Netherlands, 500 Hz).

Procedure

Each trial began with the green pursuit target (green dot in Figure 2) presented stationary for 500 ms at a random position on a 20° circle (not visible) centered on the screen (Figure 2). Next, the target jumped away and immediately moved toward the center at a velocity that randomly varied between $10^\circ/\text{s}$ and $40^\circ/\text{s}$. Subjects were asked to pursue the target as soon as it began moving. At a random time 500–1,500 ms after pursuit target onset, a red saccade target (star shape in Figure 2) was flashed (10-ms duration) at a random position within a 20° square (not visible, shown by the dotted square in Figure 2) around the current pursuit target position (at each trial, a random number generator independently generated a horizontal and vertical position within the 20° square centered around the pursuit target position). Subjects were instructed to saccade to the flashed location as soon as it appeared. Subjects also performed an additional control experiment, in which no pursuit target was present. In these trials, subjects were instructed to fixate the green target that remained at center and then make an eye movement to the flashed saccade target as soon as it appeared. The timing of the saccade target was the same as in the experimental condition. Subjects ran 4–8 sessions that were approximately 1/2 h long on different days. The first 2 blocks of recording during each session were control trials. Subjects performed approximately 10 blocks per session with 30 trials per block.

Data analysis

We collected a total of 3,771 valid trials in which saccades were executed toward the flash within 100–500 ms of the flash appearance and calculated SRTs to these flashes. We also recorded 4,117 control trials (without pursuit). The positions of the right eye and targets were sampled at 500 Hz using NI-PXI-6025E (National Instruments, Austin, TX, USA) data acquisition boards and stored on hard disks for off-line analysis using Matlab (Mathworks, Natick, MA, USA). In order to measure latencies for saccades directed to the flashed target, we first low-pass filtered eye position (zero-phase digital autoregressive forward-backward filter, cutoff frequency: 50 Hz). Second, we differentiated (central difference algorithm) eye position twice to obtain eye acceleration. Finally, saccades were detected using a 500 deg/s^2 acceleration threshold. Using an acceleration threshold instead of a velocity threshold for saccade detection

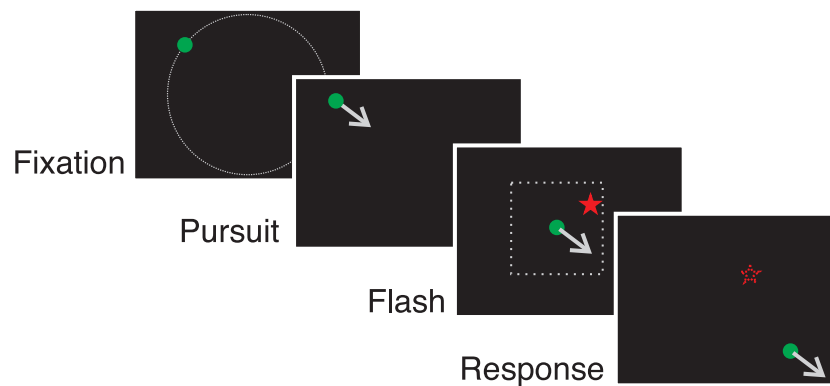


Figure 2. Experimental task. SRT task: Each trial began with a 500-ms fixation target (white cross, 1st panel) presented at a random position on a 20° circle (dotted circle) centered on the screen. The target jumped away and immediately moved toward the center at a velocity that randomly varied between 10°/s and 40°/s (green dot with arrow depicting direction of pursuit). Subjects were asked to pursue the target as soon as it began moving (2nd panel). At a random time 500–1,500 ms after pursuit target onset, a saccade target (red star shape) was flashed (10-ms duration) at a random position within a 20° square (shown by the dotted square) around the current pursuit target position (3rd panel). Subjects were instructed to discontinue pursuit and make a saccade to the flashed location as soon as it appeared (4th panel). MRT task: The task was the same as the SRT task with the following differences: subjects pushed a button as soon as they saw the flashed target, pursuit speed was constant at 10°/s, and the flashed target appeared at a random position within a 10° square around current pursuit target position.

during smooth pursuit allowed us to get an unbiased estimate of SRT, since the acceleration threshold proves to be independent of pursuit eye velocity (which is not the case for a velocity threshold; de Brouwer, Missal, Barnes, & Lefèvre, 2002). We performed repeated-measures ANOVAs or paired *t*-tests with each subject providing one data point. For each subject, data were normalized according to individual fits to the non-movement control data.

Task 2: Manual reaction time

Subjects

A separate group of seven subjects took part in this experiment. Their ages ranged from 24 to 39 (3 males, 4 females, 2 left-handed). Subjects had normal or corrected-to-normal vision and had no history of neurological disorders. Procedures were pre-approved by the Internal Review Board at the Smith-Kettlewell Eye Research Institute in compliance with NCPHS, USA.

Apparatus

Subjects were seated in front of a 17-inch high-resolution Nanao color monitor (1.76 min arc/pixel) with a refresh rate of 60 Hz that was controlled by a Macintosh computer and viewed from a distance of 48 cm. Stimuli were presented using Matlab (The Math Works, Natick MA) and functions from the PsychToolbox (Brainard, 1997; Pelli, 1997). Eye movements were recorded using a video-based Eyelink 1000 (SR Research, Mississauga, Canada) at 1,000 Hz. A chin rest maintained the viewing

distance and stabilized the head for accurate eye tracking. Subjects held a response box in the right hand and pressed a button with the right index finger.

Procedure

Subjects repeated the same experiment as in the SRT experiment with the same timings (Figure 2) except for a smaller range of possible target locations around pursuit position (10°). During the trial, they were asked to continue pursuing the target (green dot = 0.5° diameter) with their eyes and to press a button as soon as they perceived a flashed red target (without making any saccades). In this experiment, the flashed target (red dot = 0.5° diameter) was presented at a random position within a 10° square (not visible, shown by the dotted square in Figure 2) around the current pursuit target position. The target position's *x* (parallel to pursuit) and *y* (perpendicular to pursuit) positions were randomly chosen in 1° intervals, 5° ahead/behind, and 5° perpendicular in either direction relative to the current pursuit target direction. Target speed was held constant at 10°/s. We had an additional control experiment, where the pursuit target did not move, but rather jumped to the position it would be at each time interval (500 to 1,100 ms) and remained there. The red target was then flashed around this stationary target and subjects were asked to press a button as soon as they perceived the flashed target while maintaining fixation on the green stationary target. All other procedures remained identical to the pursuit experiment. Subjects performed 4 blocks of 168–280 trials per block for the control experiment and 9–11 blocks of 112–168 trials for the pursuit experiment across 2–10 days.

The control blocks were performed after the pursuit blocks were completed.

Data analysis

We collected a total of 6,842 valid trials for the main experiment and 5,378 trials for the control (without pursuit) experiment, in which subjects did not make any saccades to the flash and pressed the button within 100–500 ms of flash occurrence. We used either repeated-measures ANOVAs or paired *t*-tests with each subject providing one data point. For each subject, data were normalized according to individual fits to the non-movement control data.

Results

Task 1: Saccade reaction time

Figure 3 shows examples of typical performance during a trial. Figures 3A–3C show an example of a trial in which the red target was flashed behind pursuit. Figure 3A plots the vertical position of the pursuit target (dashed diagonal line), the flashed target (dotted horizontal line), and the vertical eye position trace (gray trace) for a trial in which the pursuit target moved vertically from the bottom of the screen to the top. As can be seen, the eye position trace first followed the pursuit target and then deviated (bold lines are saccades) shortly after the occurrence of the flash to land on the flashed target position. The highlighted saccade in black shows the saccade whose latency was measured. Figure 3B plots the vertical velocity of the eye and target movements over time, with the relevant saccade highlighted in black. Figure 3C shows the 2D trace (spatial representation as on the screen) of the targets and the eye position. As can be seen, the flashed target (red star) was presented behind (relative to the direction of pursuit) the pursuit target position (as shown by the solid gray line). The black trace represents eye position with one dot every 6 ms. The eye continued to pursue the target for a short interval before initiating the saccade to the flashed target (latency of saccade after flash = 226 ms). Figures 3D–3F show a trial where the target was flashed ahead of pursuit. This can be seen clearly in Figure 3F. In this case, saccade latency was shorter, at 168 ms. These trials are examples of our overall findings, where saccades made to targets further ahead of pursuit generally had the shortest latencies, compared to saccades made to targets behind pursuit. This is quantified next.

We investigated how SRTs vary as a function of both distance and direction relative to pursuit. It was necessary to first remove any additional effects that may modulate SRT. It is known from previous work that SRTs during

fixation are highly spatially dependent showing strong eccentricity effects (Kalesnykas & Hallett, 1994). This can be seen in Figure 4A, which plots saccade latency as a function of the absolute distance from the current eye position to the target during the *control* trials across all subjects. There were no pursuit movements during these trials, but rather simply fixation at the central location. At target onset, subjects made a saccade from the central fixation to targets at various positions within a 10° square. We fitted an exponential function to the SRTs (shown by the dotted line), which we then subsequently used to normalize the pursuit data. To do so, we subtracted the predicted control saccade latency (computed from the exponential function fit) from the measured saccade latency during the pursuit experiment by using the measured retinal error of the target at flash presentation as the eccentricity input to the fit function.

The normalized SRTs during the pursuit experiment are shown in Figure 4B plotted as a function of parallel (*x*-axis) and perpendicular (*y*-axis) distances relative to pursuit direction from current eye position (white cross in Figure 4B). The SRTs are color coded and mapped onto the corresponding target locations. As can be seen, overall latencies are shortest at eccentricities approximately >5 deg ahead of the current eye position across all vertical positions (bluest regions), compared to behind eye position. Compared to the control latencies (0 ms—normalized), latencies well ahead of the current eye position were decreased by about 10 ms. In contrast, latencies behind the current eye position were increased by approximately 40–50 ms compared to the control condition.

We first quantified how SRTs varied as a function of the angle of the target relative to pursuit direction (Figure 4C). A narrow distribution of attention would predict shorter latencies only in the direction ahead of pursuit. In general saccades made to targets ahead of pursuit had shorter reaction times (ahead—black), whereas those made opposite to the direction of pursuit had longer reaction times (behind—gray) across all directions. We binned SRTs in to 30° bins, e.g., 0° to 30° clockwise, etc., and performed a 1-way repeated-measures ANOVA on the 12 SRT bins with target direction as an independent factor. We found that target direction significantly modulated SRT ($F(11, 77) = 14.0$, $p < 0.001$). Overall latencies for all ahead directions were shorter than behind ($t(8) = -7.17$, $p < 0.001$). Bonferroni corrected post-hoc tests showed that SRTs for single directions were not significantly different from neighboring directions either ahead or behind pursuit ($p < 0.05$).

Next we quantified the normalized SRTs as a function of parallel distance by averaging across all positions perpendicular to pursuit direction. (Note: we arbitrarily chose Cartesian coordinates instead of polar coordinates, as our data cannot statistically distinguish between the two; however, both are theoretically possible.) In Figure 4B, a small focus of attention would predict shorter latencies ahead of pursuit and longer latencies well ahead of

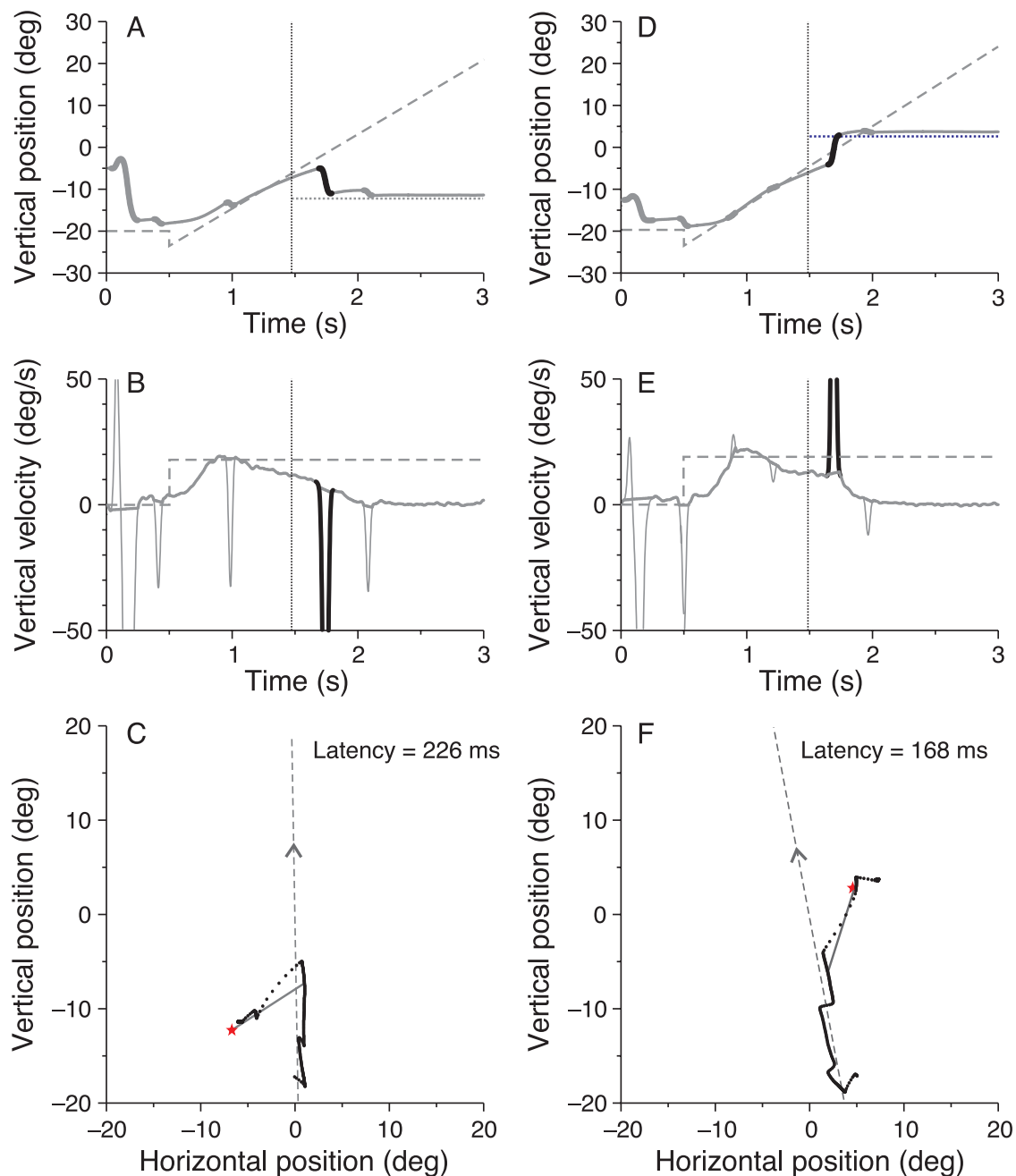


Figure 3. Typical trials. Trial with target flashed behind pursuit. (A) The position of the pursuit target (dashed diagonal line), the memorized flash location (horizontal dotted line), and the eye (solid gray traces, bold segments depict saccades) for the vertical component of the movement. Pursuit target motion started 500 ms after trial begin and the flash was presented around 1 s later (dotted vertical line) during ongoing pursuit. The first saccade toward the flash had a latency of 226 ms and is highlighted in bold black. (B) The velocities of the same trial. The smooth velocity with saccades (thin) and without saccades (thick) is shown. The relevant saccade is highlighted in black. (C) The spatial evolution of the trial. The pursuit target (dashed) and the flash (red star) are shown. The black dots represent eye position over time. Each dot is separated by 6 ms. The solid gray line links eye and flash position at the moment of flash appearance. (D–F) Trial with target flashed ahead of pursuit. The first saccade latency was 168 ms. Same representation as (A)–(C).

pursuit. We grouped the data into bins of 1° in the direction of pursuit, collapsing across all directions perpendicular to pursuit, i.e., from Figure 4B we binned data at each x position across all y positions. Figure 4D shows normalized SRTs as a function of parallel distance

from current eye position. Overall, normalized SRTs were longer during pursuit than during fixation (approximately 50 ms). Within the pursuit task, SRTs were shortest when the target was well ahead of current eye position (compared to those behind current eye position at the

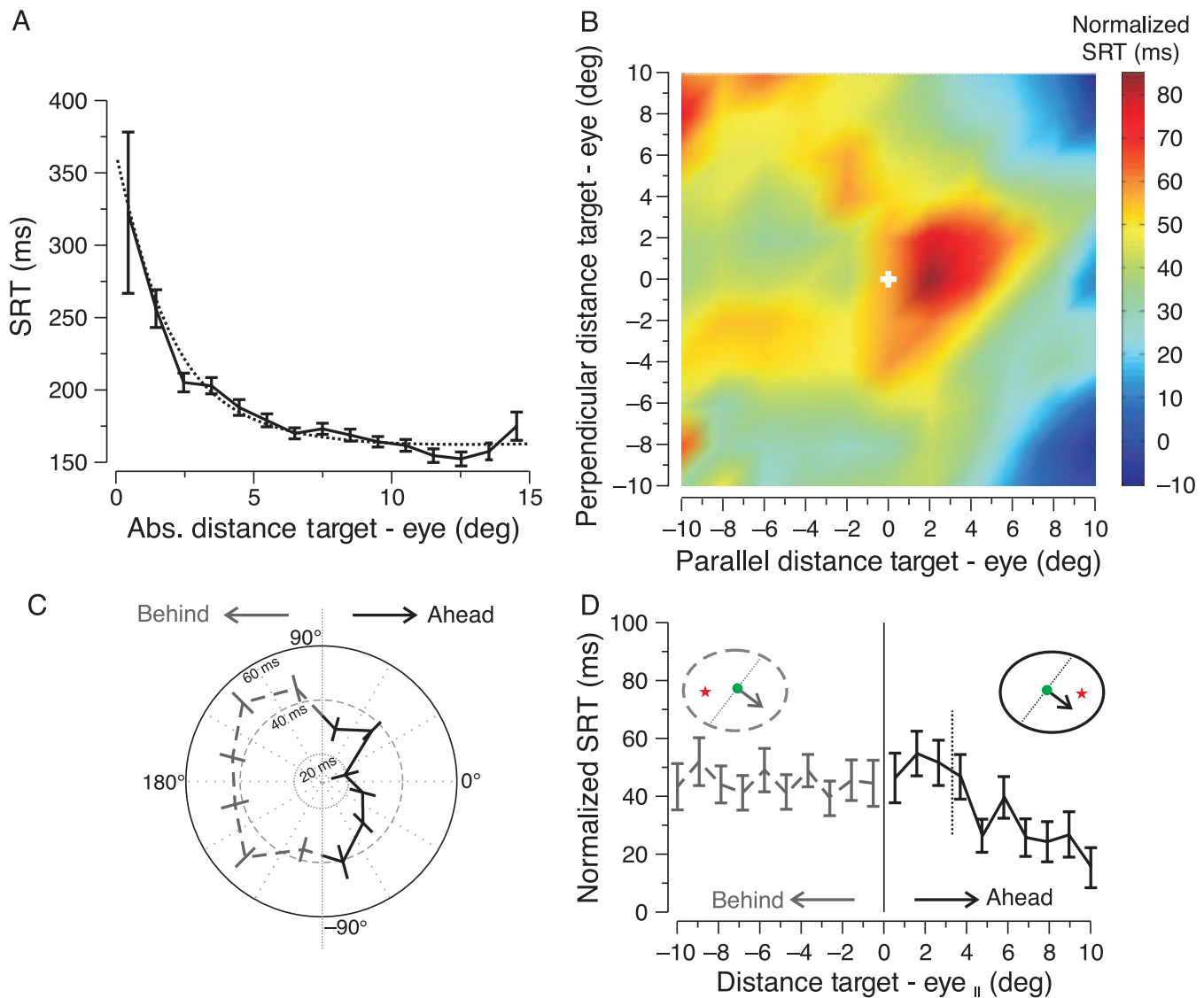


Figure 4. SRT as a function of target direction and distance (A) Relationship between SRT and absolute flash distance from current eye position in control trials during fixation (no pursuit movement) in 1-deg bins (mean $\pm$ SEM). The dotted line represents the exponential function fitted to the raw data: $y = 162 + 351 \cdot \exp(-(x + 1.113) / 2.021)$. This fit was used to normalize the test data during pursuit for (B) (see text). (B) Two-dimensional plot of normalized saccade latencies as a function of parallel and orthogonal flash position relative to the eye and normalized in pursuit direction, i.e., pursuit direction was always rightward (0°). The color code shows normalized saccade latencies. (C) SRTs are plotted as a function of the angle between the vector linking eye position to the flashed target position (black dotted line in Figures 3C and 3F) and the vector of current eye velocity in 30° bins. The latencies are shown for saccade targets flashed ahead (black lines: 0° $\pm$ 90°) and behind (gray lines: >90°). The normalized latencies associated with each circle are shown (inner dotted circle—20 ms, middle dashed circle—40 ms, and outer solid circle—60 ms). The bars depict SEM. (D) Normalized saccade latencies plotted as a function of distance between flash and eye position measured in direction of eye velocity (negative values mean behind current eye position). The vertical solid line shows target position at 0° = current eye position. Standard error bars are shown. The short dotted vertical line depicts the location where latencies for the ahead group switched from being longer than the behind group (at the same distance) to shorter. The mean eye velocity at the moment of flash presentation was 15.7°/s.

same distance). We observed the longest reaction times when the saccade target was ahead but closer to current eye position (again compared to those behind current eye position at the same distance).

We performed a two-way repeated measures ANOVA with group and absolute distance as factors. We found a

significant effect of group, with SRTs in the ahead group being significantly shorter than those in the behind group ($F(1, 7) = 20.7, p < 0.01$), of absolute distance ($F(9, 63) = 20.8, p < 0.001$) and a significant interaction effect between the two ($F(9, 63) = 21.1, p < 0.01$). The significant interaction effect can be seen in the figure,

where SRTs were longer for the ahead group compared to the behind group for small eccentricities and shorter for the ahead group for larger distances.

In summary, SRTs were shorter for the ahead vs. behind group when the saccade flash was ahead of the location of current pursuit by more than 3° (dashed vertical line). Closer to current eye position, SRTs were longer for the ahead vs. behind group.

We were interested in determining whether this pattern of long/short reaction times was dependent on pursuit speed, i.e., whether the pattern varied as a function of time—do reaction times become faster depending on pursuit speed—or location—do reaction times become faster at a certain distance ahead of current eye position, independent of pursuit speed. This is because in general SRTs depend on eye velocity as well as retinal slip, as was also the case in our data (see [Supplementary Figure 1](#)). The data in [Figure 4D](#) is made up of trials that are collapsed across different pursuit speeds. We separated the different pursuit speeds into three intervals as shown in [Figures 5A–5C](#) and plotted the normalized SRTs for the ahead and behind groups as a function of the absolute distance between the target and the eye. Since the SRTs are plotted against distance, a time-based effect would be revealed in a horizontal shift of the vertical dashed line (which depicts the point at which saccade latencies become faster for the ahead group compared to the behind group), whereas a location-based effect would predict no shift. We plotted the distance at which the ahead saccade latencies became shorter than the behind saccade latencies at corresponding eye–target distances (dotted vertical lines in [Figures 5A–5C](#)). When eye velocity was slow, the switch from being slower to faster ahead compared to behind occurred very close to current eye position (at 2.2° —dotted vertical line in [Figure 5A](#)). On the other hand, with faster pursuit speeds, this switch occurred at further and further distances (the vertical dotted line is at 3.4° for [Figure 5B](#) and at 6.0° for [Figure 5C](#)). We divided the distance of reversal by the average pursuit speed. This gave a reversal time that is an estimate of the time needed by the pursuit trajectory to cross the parallel distance corresponding to the distance of reversal. The resulting reversal time was 299 ms, 260 ms, and 320 ms for the slow ([Figure 5A](#)), medium ([Figure 5B](#)), and fast ([Figure 5C](#)) pursuit speeds, respectively.

In addition, we analyzed whether this pattern of latencies varied as a function of pursuit direction. We therefore split the data into the 8 directions of pursuit and plotted the 2D plot for each of the 8 directions ([Figure 6](#)). In general, the pattern remained the same, with shortest latencies ahead of pursuit compared to behind for all 8 pursuit directions. We performed a two-way repeated measures ANOVA with pursuit direction and group (ahead vs. behind current eye position) and found shorter SRTs in the ahead group across all directions ($F(1, 7) = 55.62, p < 0.001$) but no direction ($p > 0.05$) or interaction ($p > 0.05$) effect. In summary, SRTs were shortest well ahead of

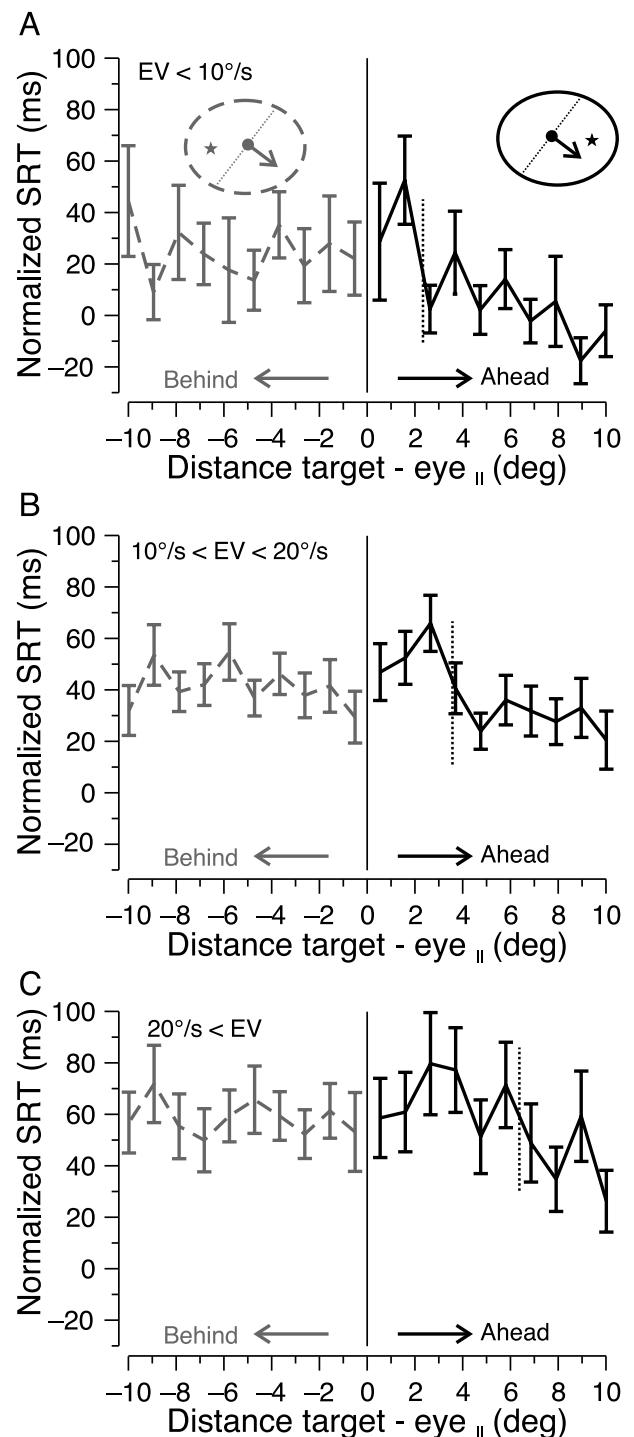


Figure 5. Difference plots separated by pursuit speed. Normalized saccade latencies are plotted as a function of the parallel distance between target and current eye position for eye velocities (EVs) (A) less than $10^\circ/\text{s}$ (mean EV = $7.4^\circ/\text{s}$), (B) between 10 and $20^\circ/\text{s}$ (mean EV = $14.5^\circ/\text{s}$), and (C) greater than $20^\circ/\text{s}$ (mean EV = $25.7^\circ/\text{s}$) plotted in the same manner as [Figure 4D](#).

pursuit across all directions perpendicular to pursuit. This reduction in SRTs was similar across all pursuit directions and varied as a function of pursuit speed.

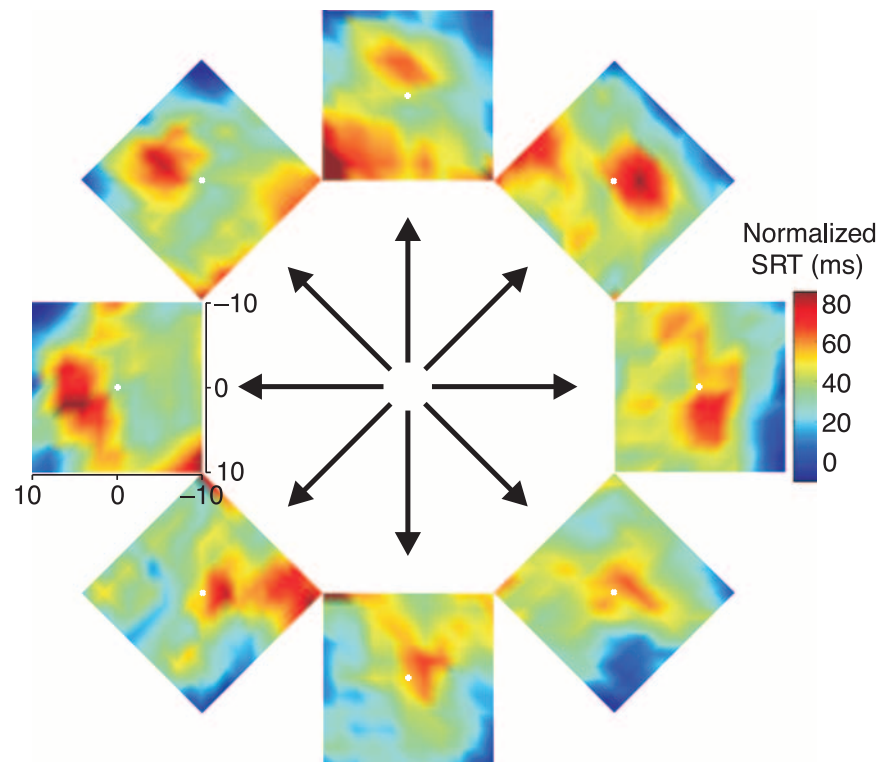


Figure 6. SRT separated by pursuit direction. Two-dimensional plots of normalized saccade latencies as a function of parallel and orthogonal flash position. Plots (and axes) are rotated according to pursuit direction (black arrows) and are plotted in the same manner as Figure 4B. In the x-axis, negative values mean behind current eye position (white cross) and in the y-axis negative values mean counterclockwise orthogonal to current eye position.

These findings support a general bias ahead of pursuit as opposed to a narrow attentional bias or a small focus of attention ahead of pursuit. However, the findings could still be interpreted in two ways. First, it could reflect a bias of attention *well ahead* of pursuit that is dynamic and varies as a function of pursuit speed. On the other hand, there could be an attentional bias as well as a secondary effect related to the interaction between saccadic and pursuit eye movements.

We repeated the same experiment using manual reaction times (button presses) instead of saccades. We hypothesize that if any SRT effects were due to attention, we should also find them in MRT patterns.

Task 2: Manual reaction time

MRT increases as a function of target eccentricity have previously been reported (White, Kerzel, & Gegenfurtner, 2006), likely reflecting visual eccentricity effects. To account for this, we plotted MRTs from the control manual reaction time task as a function of the absolute distance between the flashed red target and current eye position (rounded to 1° intervals). As can be seen in Figure 7A, MRTs showed a slight increase as a function of target eccentricity. We fitted this pattern with an exponential function, shown by the dotted line. We then

used this function to normalize MRTs in the pursuit task and plotted the normalized MRTs as a function of the 2D distance from current eye position (Figure 7B), as we did for the SRT analysis. As can be seen, MRTs overall showed shorter latencies ahead of pursuit direction across the entire visual hemi-field. In contrast to SRTs, we found that there was no increase in reaction times at small eccentricities ahead of pursuit. In addition, compared to SRTs, MRTs showed a similar decrease of about 10 ms when targets were presented ahead of the current eye position. MRTs behind the current eye position were also increased compared to control MRTs but to a much smaller degree than SRTs (2 ms compared to 45 ms).

As can be seen, MRTs also showed a tendency for shorter reaction times ahead of compared to behind pursuit (Figure 7C). We performed the same statistical analysis as for SRTs, binning reaction times into 30° bins, e.g., 0° to 30° clockwise, and performing a one-way repeated measures ANOVA analysis on the 12 MRT bins with target direction as an independent factor. Target direction significantly modulated MRT ($F(11, 66) = 3.7$, $p < 0.01$). A Bonferroni post-hoc test showed however that no single target directions were significantly different from neighboring target directions ($p < 0.05$). When averaged, all directions ahead of pursuit had shorter latencies compared to directions behind pursuit ($F(1, 6) = 41.5$, $p < 0.01$).

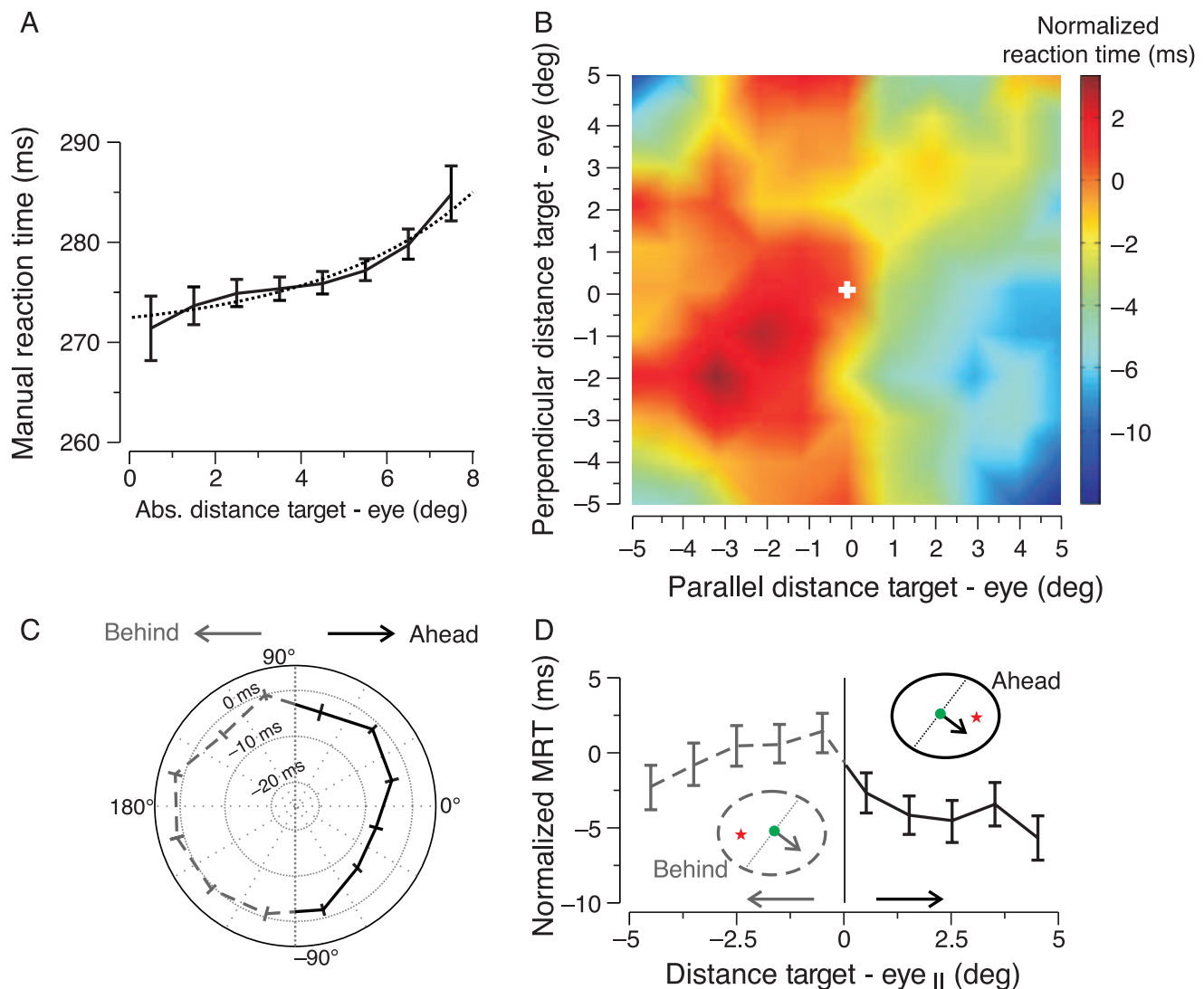


Figure 7. MRT as a function of target direction and distance. The same conventions as in Figure 4 apply. (A) MRT as a function of flash distance from the eye for control trials during fixation (no pursuit). The exponential fit function to the raw data (dotted curve) was: $y = 270.88 + 1.11 * \exp((x - 1.36) / 3.678)$. (B) Two-dimensional plot of MRT as a function of parallel and orthogonal flash position relative to the eye and normalized with respect to pursuit direction (pursuit direction was rightward, 0°). The color code shows the normalized MRT data. (C) Normalized MRT as a function of the angle between vector of the retinal error of the flash and pursuit direction. (D) Normalized MRT as a function of the distance between the flash and current eye position parallel to pursuit direction.

We plotted MRTs as a function of the distance in the direction parallel to pursuit (ahead vs. behind) across all positions perpendicular to pursuit. MRTs were reduced ahead of pursuit compared to behind pursuit (Figure 7D). A two-way repeated measures ANOVA with group and absolute parallel distance revealed a significant reduction in MRTs in the ahead group ($F(1, 6) = 22.46, p < 0.01$) compared to the behind group but no effect of distance ($F(4, 24) = 0.12, p > 0.05$) and no interaction effect ($F(4, 24) = 0.14, p > 0.05$), showing a consistent reduction across all distances in the ahead group compared to the behind group. The figure clearly shows a reduction of MRTs even at the smallest eccentricity (0.5°). This

reduction remained across the entire extent of our tested target distances (5°). To summarize, the MRT results support the hypothesis of a broad attentional facilitation in the whole hemi-field ahead of pursuit.

Comparing saccadic and manual reaction times

We found that both SRTs and MRTs show shorter reaction times ahead of the direction of pursuit, which we interpret as an attentional bias. However, we found a difference at very short eccentricities ahead of pursuit for

SRTs compared to MRTs. Specifically, MRTs showed an immediate decrease in reaction times ahead of pursuit whereas SRTs first showed an increase in reaction times that varied with pursuit speed followed by a decrease. We postulate that because we did not find a similar increase in MRTs this increase is not related to the default allocation of attention during pursuit but rather may be specific to the saccade trigger mechanism.

We hypothesized that this increase in SRTs (which is not due to a target eccentricity effect, as this was accounted for—see Figure 4A) may be due to the

interaction between saccades and pursuit (Orban de Xivry & Lefèvre, 2007). Indeed, de Brouwer, Yuksel, Blohm, Missal, and Lefèvre (2002) have shown that saccades during pursuit have very long reaction times for targets that have small eccentricities (relative to the current eye position) ahead of pursuit. They hypothesize that the eye movement system withholds saccades within a small region ahead of current pursuit, which they call the smooth zone. This may be an economical strategy used by the eye movement system; because the eyes are moving in that direction in any case, they are likely to

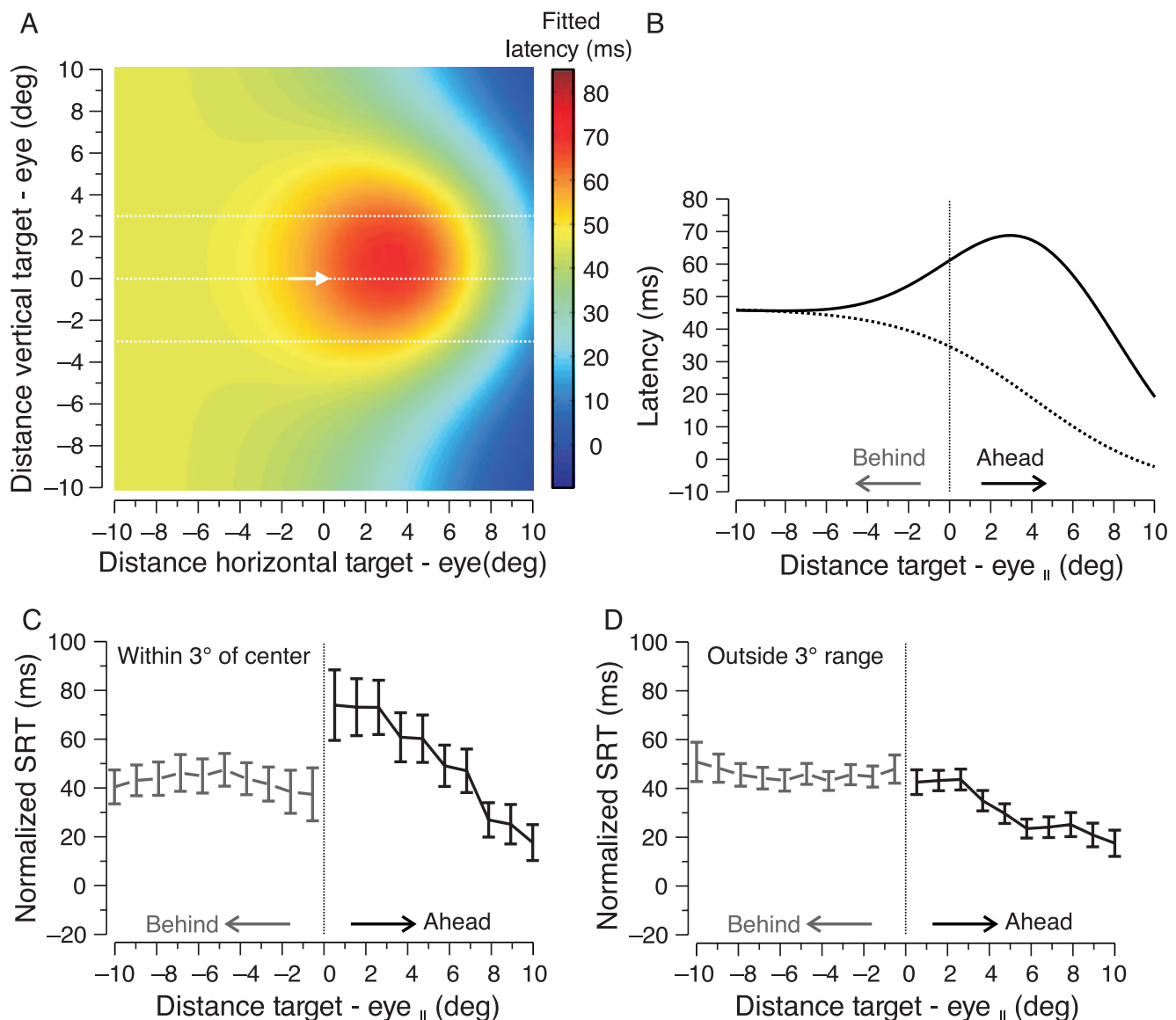


Figure 8. Data fitting for SRTs. (A) Results of a 2D sigmoid and superimposed Gaussian fit to the normalized SRT data: $z = -0.010 + 0.065 / (1 + \exp(0.328 * (x - 4.24))) + 0.05 * \exp(-(x - 4.734)^2 + (y - 0.81)^2 / 5.803^2)$. Horizontal dotted lines indicate the limits used to plot (C) and (D). The arrow depicts direction of the pursuit movement. Current eye position is represented by the arrowhead. (B) Side view of the fit function (solid line) along the eye-flash distance parallel to pursuit (x-axis in (A)). The dotted line depicts the sigmoid component of the fit function. (C) Normalized saccade latencies for orthogonal flash distances (relative to pursuit direction) <3 deg. (D) Normalized saccade latencies for orthogonal flash distances >3 deg.

catch up to the target with the ongoing pursuit movement and therefore the saccadic system waits to see if a saccade is necessary, a strategy that results in longer latencies in case a saccade is nevertheless needed. This would imply two mechanisms that could explain our pattern of SRTs. First, an attentional mechanism, which like in the MRT data, should show an overall decrease in SRTs in the ahead group compared to the behind group across all eccentricities and, in addition, a smooth zone effect at small eccentricities ahead and specific to the direction of pursuit. On the basis of this hypothesis, we fitted the SRT 2D data with a combination of a sigmoid and a Gaussian function centered on small eccentricities ahead in the direction of pursuit. This is shown in [Figure 8A](#), where the fitted SRT is plotted as a function of the parallel (x) and perpendicular (y) distances from current eye position (arrowhead; same representation as in [Figures 4B](#) and [7B](#)).

[Figure 8B](#) shows a 2D cut across [Figure 8A](#) along the central horizontal dotted line. The figure shows the fit of SRTs across this 2D cut (0 deg perpendicular distance) along the parallel distance from current eye position (the solid line). The dotted line shows the prediction of SRTs without the hypothesized smooth zone. Further, we hypothesized that if this mechanism applies to our data, we would expect only a small region around current eye position to show higher eccentricities and not regions that are further away, especially for regions perpendicular to pursuit direction. Therefore, we split the SRT data from the 2D plot into two zones, depicted by the top and bottom dotted horizontal lines in [Figure 8A](#). The SRT data from the region within these lines (3° away in either direction perpendicular from current eye position) is plotted in [Figure 8C](#) with SRTs in the ahead and behind groups plotted as a function of absolute parallel distance. This figure resembles that of [Figure 4D](#), with an increase in SRTs followed by a decrease at further target eccentricities. In contrast, [Figure 8D](#) plots the SRT data from outside the horizontal dotted lines in [Figure 8A](#). Here, we see that there is no increase of SRTs at small target eccentricities, but rather an overall decrease in the ahead group comparable to our observations in the MRT data.

Discussion

We employed saccadic and manual reaction times as behavioral correlates of attentional allocation during smooth pursuit eye movements and showed that reaction times for both saccades and manual button presses were shortest to targets presented ahead of the direction of pursuit. These reduced reaction times spread across the entire 2D visual hemi-field, suggesting a broad focus of attention that is predictively allocated with respect to pursuit direction and speed. In addition, saccadic reaction times were longest at short eccentricities ahead of pursuit,

which we propose is due to an interaction with catch-up saccade trigger mechanism (de Brouwer, Missal et al., 2002) in addition to the overall attentional effect.

Is this attention?

In our experiment, we made use of the well-established relationship between attentional shifts and movement reaction times to indicate the region of attentional allocation during smooth pursuit eye movements. A decrease in reaction times for both saccades and manual button presses executed to a recently cued region of space has been well established (Clark, 1999; Crawford & Muller, 1992; Klein, 2000; Posner & Cohen, 1984; Sheliga, Riggio, & Rizzolatti, 1995; Shepherd et al., 1986). It has been suggested that this decrease results from (covert) attention being allocated to a certain region in space, and therefore, a subsequent event in that region is detected faster (Findlay, 2009). Typically, for saccades attention is allocated to a certain location in space using an exogenous cue (Posner & Cohen, 1984), but endogenous cues such as arrows at the current fixation have also been shown to decrease saccade latencies toward peripheral locations (Hoffman & Subramaniam, 1995; Shepherd et al., 1986). In the case of pursuit, it could be that the pursuit target acts in a similar way to an endogenous cue in that it directs where attention should be allocated. Support for this comes from Kanai et al. (2003), who showed decreased reaction times for saccades ahead of pursuit except in the condition when the saccade target predictably jumped backward.

In our task, the red saccade/button press target is a bright, salient object. Therefore, it is very likely that this abrupt target onset captures attention (Abrams & Christ, 2003; Fecteau & Munoz, 2005; Lovejoy et al., 2009; Theeuwes, 1994; Yantis & Jonides, 1984, 1990) consistent with attentional frameworks of salience (Bundesen, Habekost, & Kyllingsbaek, 2005; Desimone & Duncan, 1995; Fecteau & Munoz, 2005). We propose however that this attentional modulation by the target occurs in addition to some default attentional bias that has already been allocated to the area ahead of pursuit, reminiscent of top-down attentional baseline increases in activity in visual areas in the absence of visual stimuli (Bundesen et al., 2005; Luck, Chelazzi, Hillyard, & Desimone, 1997; O'Connor, Fukui, Pinsk, & Kastner, 2002). If it were only the case that the abrupt target attracts attention, then we would expect the same reaction times regardless of whether the abrupt target appeared ahead or behind pursuit because presumably it would capture equal amounts of attention regardless of its location in space. We believe that the differences in reaction times ahead vs. behind reflect the degree of pre-allocated attention to the region ahead of pursuit in addition to attentional capture subsequent to the target flash, i.e., a combination of top-down and bottom-up attentional factors (Beck & Kastner,

2009; Bundesen et al., 2005; Desimone & Duncan, 1995; Fecteau & Munoz, 2005).

How do manual reaction times compare to saccadic reaction times?

We found reduced reaction times to targets ahead of the direction of pursuit for both manual and saccadic reaction times, i.e., different types of motor actions with different processing pathways in the brain. The similar patterns (taking the saccade trigger mechanism into account for small eccentricities; de Brouwer, Missal et al., 2002) support our proposal that we are measuring attentional allocation during pursuit. Conversely, it also suggests the presence of a single attentional system that is—at least partially—dependent of the motor output. Nevertheless, we found that the attentional effect was smaller on MRTs than on SRTs. This could be due to inherent differences between the two tasks. Specifically, task 1, with saccadic reaction times, could be viewed as a task switching paradigm, where subjects first have to stop actively pursuing before beginning the saccade movement. In contrast, task 2, with manual reaction times, is reflective of a dual task paradigm—subjects are not required to stop the pursuit movement to begin the button press. Thus, the greater difference in attentional modulation between ahead and behind trials might be related to a greater involvement of attention in stopping active pursuit, detecting a target and producing a new saccade plan compared to simply detecting a target for a button press. However, the fact that we found consistent effects for MRTs and SRTs despite these differences strongly supports our interpretation of a common attentional system acting on both motor systems.

How is attention allocated in 2D space?

Our results concur with and expand on previous findings that show an attentional bias ahead of pursuit (Blohm et al., 2005; Kanai et al., 2003; Tanaka et al., 1998) by showing that this attentional allocation was not limited to specific directions and distances but rather spread across a diffuse range that spread to the entire hemi-field ahead of the direction of pursuit (at least 10°, as we did not measure larger eccentricities), with the exception of an additional catch-up saccade trigger effect for a small region directly ahead of pursuit (Figure 1). We wish to emphasize that our findings are consistent with a predictive allocation of attention ahead of pursuit. In the task, we asked subjects to pursue a target that moved in one of eight possible directions. In our analysis, we calculated the position of the flashed target relative to pursuit direction and consistently found that attention was allocated ahead of the pursuit direction. Further, the MRT

analysis showed that the decrease of reaction times occurred at locations immediately ahead of pursuit and spread toward the entire hemi-field. Even at 0.5° target eccentricities (Figure 7D), MRTs were lower in the ahead condition compared to the behind condition.

We show that during the pursuit of a simple stimulus without the presence of objects for attentional focus, attentional resources are allocated by default to a broad region ahead of pursuit. Although our results are similar to most previous findings, they differ from other studies that found shorter reaction times just ahead of pursuit (van Donkelaar & Drew, 2002) or improved perceptual discrimination at the pursuit target in addition to slight improvement slightly ahead of pursuit when the likelihood of the target appearing at that location increased (Lovejoy et al., 2009) but not further ahead of pursuit. These differences may be explained by differences in attentional allocation. For example, with no specific task or object for attentional focus, attention may by default be spread out (Eriksen & St James, 1986), whereas the presence of a group of stimuli to pursue might focus attention (Shepherd & Müller, 1989). Alternatively, the differences may also be explained by the notion that attentional allocation is highly task-dependent. Pursuing a single target presumably does not require much attention and so it can be directed ahead of pursuit, perhaps a default attentional allocation due to the predictive nature of the eye movement. On the other hand, if a challenging task requires more attention at the pursuit location (Khurana & Kowler, 1987), it is directed there. Finally, it is possible that discrimination tasks and reaction time tasks measure different types of attention (Prinzmetal et al., 2005). One possibility is that reaction time tasks such as the current pursuit task or tasks with endogenous cues (Hoffman & Subramaniam, 1995; Posner & Cohen, 1984; Shepherd et al., 1986) may involve a combination of top-down and bottom-up attention, whereas discrimination tasks involve mainly top-down attention (Deubel & Schneider, 1996; Prinzmetal et al., 2005; Schneider & Deubel, 2002). However, further studies are necessary to investigate differences or similarities in attention during discrimination and detection tasks for both pursuit and saccadic eye movements.

Why would attention be allocated ahead of pursuit and be broadly tuned?

We found that the region of highest default attention was ahead of current eye position. This allocation of attention may facilitate processing events ahead in time. Doing so for locations ahead of movement direction (i.e., in an anticipatory manner in time) would allow an enhanced performance when acting upon potential upcoming events, e.g., to avoid obstacles or intercept objects. As such, this phenomenon could thus reflect a default

mechanism for predictively allocating attention to anticipated locations in space. Predictive mechanisms have been shown to be used by the brain to compensate for delays in processing. For example, it is known that even simple tracking of a target with the eyes involves some predictive mechanisms because of the time needed to visually process the target before commands are planned (e.g., de Brouwer, Missal et al., 2002; de Brouwer, Yuksel et al., 2002; Nijhawan, 1994; Schlag & Schlag-Rey, 2002) by the time the movement commands are sent, the target is no longer at the original position used to calculate them. Moreover, actions on moving objects such as for example, hitting a ball with a bat, have to predict the future location of the objects in order to successfully interact with them (Land & McLeod, 2000; McBeath, Shaffer, & Kaiser, 1995). Attention may therefore serve as an aid for the brain to predict future locations of objects or to speed up processing of unexpected events at these future locations (Bennett, Orban de Xivry, Barnes, & Lefèvre, 2007; Orban de Xivry, Bennett, Lefèvre, & Barnes, 2006; Orban de Xivry, Missal, & Lefèvre, 2008).

The broad tuning of this attentional bias could be considered to be similar to that shown by previous imaging studies on humans, where activity is shown to be increased across an entire endogenously cued hemi-field, even though there is no visual stimulus present (Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Kastner & Ungerleider, 2001). Additionally, studies with neglect patients have often shown attentional deficits with respect to the entire visual hemi-field, usually the left one (Heilman & Van den Abell, 1980; Karnath, 1988; Mesulam, 1981, 1999). These findings suggest the presence of neuronal mechanisms that bias an entire visual field, often at the expense of the other. A similar mechanism that biases an entire hemi-field might be involved during a predictive pursuit movement.

Possible neurophysiological mechanisms

The question of how these predictive attention shifts take place in the brain remains to be investigated. There is some evidence that areas such as the posterior parietal cortex and the frontal eye fields are involved in directing spatial attention (Bisley & Goldberg, 2003; Goldberg, Bisley, Powell, Gottlieb, & Kusunoki, 2002; Leigh & Zee, 1999; Schall, 2004; Tehovnik, Sommer, Chou, Slocum, & Schiller, 2000). These same areas have also been shown to be involved in predictive remapping (Duhamel, Colby, & Goldberg, 1992; Umeno & Goldberg, 1997). Whether the predictive shifts during pursuit rely on the same mechanisms as during saccades remains to be investigated (Blohm, Optican, & Lefèvre, 2006) but there is evidence that posterior parietal areas and regions of the frontal eye fields—analogueous to corresponding saccade regions—also show activity during pursuit (Bremmer, Distler, & Hoffmann, 1997; Gottlieb, Bruce, & MacAvoy, 1993;

Krauzlis, 2004; Tanaka & Lisberger, 2002). Therefore, these predictive shifts could be used to direct attention ahead of pursuit by modifying baseline activity of neurons in earlier extra-striate visual areas (Beck & Kastner, 2009; Bundesen et al., 2005; Luck et al., 1997; O'Connor et al., 2002) or by modifying baseline activity in areas purported to represent salience maps such as the LIP, the FEFs, or the superior colliculus (Bichot & Schall, 2002; Bisley & Goldberg, 2003; Bundesen et al., 2005; Fecteau & Munoz, 2005; McPeck & Keller, 2002; Thompson & Bichot, 2005).

Conclusions

In summary, we have shown that reaction times for both saccades and manual button presses are reduced when targets are presented in the hemi-field ahead of pursuit, with the exception of increased saccade latencies just ahead of pursuit. We propose that a broad default focus of attentional facilitation arises for events occurring ahead of a pursued target. Thus, when pursuing moving objects, attention is oriented so as to facilitate interaction with our environment at anticipated future locations in the entire upcoming hemi-space.

Acknowledgments

We would like to thank RM McPeck for helpful comments on this manuscript. This work was supported by the Fonds de la Recherche Scientifique (Belgium), Interuniversity Attraction Poles funding (Belgium), internal research grants (Université Catholique de Louvain, Belgium), Natural Sciences and Engineering Research Council of Canada, and the Botterell Foundation (Queen's University, Canada). AZK was supported by a Canadian Institutes of Health Research fellowship. GB was supported by a Marie Curie Fellowship (European Union).

Commercial relationships: none.

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