

The coordinate system of endogenous spatial attention during smooth pursuit

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A central question in vision is whether spatial attention is represented in an eye-centered (retinotopic) or world-centered (spatiotopic) reference-frame. Most previous studies on this question focused on how coordinates are modulated across saccades. In the present study, we investigated the reference-frame of attention across smooth pursuit eye-movements using a goal-directed saccade task. In two experiments, participants were asked to pursue a moving target while attending to one or two grating stimuli. On each trial, one stimulus was constant in its retinal position and the other was constant in its spatial position. Upon detection of a slight change in stimulus orientation, participants were asked to stop pursuing and perform a fast saccade toward the modified stimulus. In the focused attention condition, they attended one, predefined, stimulus, and in the divided attention condition they attended both. In **Experiment 1** the angle of the orientation change marking the target event was constant across participants and conditions. In **Experiment 2**, the angle was individually adapted to equate performance across participants and conditions. Findings of the two experiments were consistent and showed that the enhancement of mean visual sensitivity in the focused relative to the divided attention condition was similar in magnitude for both retinotopic and spatiotopic targets. This indicates that during smooth pursuit, endogenous attention was proportionally divided between targets in retinotopic and spatiotopic frames of reference.

space in the cortex is predominantly retinotopic; that is, that the vast majority of neural receptor fields in the occipital and parietal cortex correspond to specific locations on the retina rather than to locations in space (Engel, Glover, & Wandell, 1997; Gardner, Merriam, Movshon, & Heeger, 2008; Tootell, Silverman, Switkes, & Devalois, 1982). Evidence for spatiotopic coding, that is, neurons that respond to specific space locations regardless of their retinal placement, is relatively sparse and focuses on specific areas of the posterior parietal cortex and the ventral intraparietal area (VIP) (Duhamel, Bremmer, BenHamed, & Graf, 1997; Galletti, Battaglini, & Fattori, 1993).

However, although it is widely accepted that the organization of the visual cortex is retinotopic, it is still an open question whether visual attention is also allocated in retinotopic coordinates or whether it is allocated spatiotopically. Although the retinotopic reference frame is evidently natural for the visual system, there is reason to hypothesize that allocation of attention in spatiotopic coordinates would be more suitable in certain contexts, such as when planning motor actions (Soechting & Flanders, 1992). Previous studies addressed this question by testing attentional allocation to target locations that were either *retinally* or *spatially* consistent across saccades. In these procedures, attention was directed to a certain location shortly before a saccade was performed. Perception of a test stimulus was assessed after the saccade, when the stimulus appeared either at the same retinal coordinates (*retinotopic*) or at the same spatial coordinates (*spatiotopic*) as the attended location. Findings of these studies were inconsistent: some found an attentional advantage for the spatiotopic frame of reference (e.g., Howe, Drew, Pinto, & Horowitz, 2011; Melcher & Morrone, 2003; Pertzov, Zohary, & Avidan, 2010; Szinte & Cavanagh, 2011); others found an advantage for the retinotopic frame of reference

Introduction

Despite the constant motion of our eyes, our perceptual experience remains stable and invariant to eye position. This ability of our visual system to preserve stability across eye movements is striking, especially considering that the representation of visual

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(e.g., Afraz & Cavanagh, 2009; Golomb, Chun, & Mazer, 2008; Golomb, Nguyen-Phuc, Mazer, McCarthy, & Chun, 2010; Golomb, Pulido, Albrecht, Chun, & Mazer, 2010; Knapen, Rolfs, & Cavanagh, 2009; Mathot & Theeuwes, 2010; McKyton, Pertzov, & Zohary, 2009); and others suggested that the preferred reference frame of attention depends on the characteristics of the specific context (Abrams & Pratt, 2000; Posner & Cohen, 1984).

Most previous studies manipulated the frame of reference using saccadic eye-movements. Saccades involve rapid shifts of gaze and consequently result in transient and abrupt changes of the retinal coordinates. It could be hypothesized that when retinal coordinates change continuously, such as during smooth pursuit eye-movements, it would be advantageous to allocate attention according to a stable spatiotopic reference frame rather than to continuously update the retinotopic coordinates. A study by Niebergall, Huang, and Martinez-Trujillo (2010), examined the reference-frame of spatial attention during smooth pursuit. In their study, participants were asked to attend to stationary or moving targets and discriminate transient changes in their orientation, while smoothly pursuing a moving object. The targets were either spatiotopic (i.e. stationary on the screen and therefore moving in retinal coordinates during pursuit) or retinotopic (i.e., moving on the screen to retain constant retinal position during pursuit). On some of these trials, participants were asked to attend solely to a single target, either the retinotopic or the spatiotopic, and on other trials they were asked to divide their attention between the two targets. The goal of this procedure was to estimate the perceptual cost of dividing attention to targets of different reference frames relative to focusing attention on a target of a single reference frame. This approach was based on previous findings showing that dividing attention between two targets impairs perception of both stimuli relative to focusing attention on one stimulus at a time (Braun & Julesz, 1998; Lee, Itti, Koch, & Braun, 1999; Lee, Koch, & Braun, 1997). The findings of Niebergall et al. (2010) showed that the cost of dividing attention was similar for retinotopic and spatiotopic targets, indicating that attention was equally allocated to both reference-frames. These findings suggest that the attentional system uses effectively, and to a similar extent, retinotopic and spatiotopic coordinates when pursuing a moving object.

In the study by Niebergall et al., orientation discrimination performance was measured using manual responses. However, previous studies have shown that the mode of response could modulate the reference-frame of attention (e.g. Abrams & Pratt, 2000). Therefore, there is reason to speculate that in tasks that involve an immediate goal-directed response, such as a saccade task, the attentional system would favor a certain coordinate system over the other.

One possible hypothesis is that in an attention task that involves an eye-movement towards a target, attention will be encoded in spatiotopic reference frame. Saccades are a type of an orienting response, similar to movements of the head and the body toward external stimuli. Since the positions of the eyes, head and body are all interdependent and coordinated, it could be hypothesized that they would share a single, spatiotopic, frame of reference (Soechting & Flanders, 1992). A possible neural substrate that could enable such a general spatiotopic orienting representation is the Superior Colliculus (SC). Deep layers of the SC contain supramodal maps where input from different modalities is aligned according to its spatial location (Knudsen, 1982; Meredith, Nemitz, & Stein, 1987; Soechting & Flanders, 1992). Such supramodal maps could theoretically support a spatiotopic allocation of attention. A second possible hypothesis is that in an attention task involving eye movements, attention will be encoded in retinotopic reference frame. Since eye movements are goal-directed visually-driven actions, it could be hypothesized that they would be represented primarily by a retinotopic reference frame, which is hard-wired to the neural structure of the visual cortex and most oculomotor brain regions.

A previous study focused on exogenous attention and showed that the abrupt onset of peripheral cues at target location, modulated the processing of retinotopic targets more than spatiotopic targets (Souto & Kerzel, 2009). This finding supported a retinotopic dominance for the exogenous attention system. However, the endogenous attentional system is believed to be more flexible and more easily modulated by task demands than the exogenous system (Barbot, Landy, & Carrasco, 2012). It is an open question whether the endogenous attention system would demonstrate a retinotopic or spatiotopic dominance, or alternatively whether the dominant coordinate system would depend on task demands.

The goal of the present study is to examine whether endogenous attention uses both reference frames equally or whether it is based mainly on one of them when the required response is a goal-directed action. Participants were asked to smoothly pursue a moving object while attending targets—consistent in either their retinotopic or spatiotopic coordinates. The *retinotopic* target moved along the horizontal axis at the same speed as the pursued object, so that its spatial location constantly changed but its location relative to the pursuit target remained fixed throughout the trial. The *spatiotopic* target remained in its original spatial location, so that its location relative to the pursued object constantly changed but its spatial location was constant throughout the trial. Participants were requested to either focus their attention on one of the two presented targets (focused-attention condition) or divide their attention between these

targets (divided-attention condition). On detection of a small orientation change in the attended target (or one of the two attended targets), participants were asked to perform a fast saccade toward that target.

In two experiments, we evaluated the perceptual cost of dividing attention by comparing perceptual performance when attention was divided between two targets (retinotopic and spatiotopic) to when it was focused on one of them. These perceptual costs were obtained separately for the retinotopic and the spatiotopic targets and were compared to evaluate the preferred reference frame of attention. The retinotopic cost (performance on a retinotopic target in the focused attention task, minus performance on a retinotopic target in the dual attention task), reflects the extent to which performance was degraded by the addition of a spatiotopic task. Finding high retinotopic cost would indicate that the spatiotopic task required high amount of attentional resources. Similarly, the spatiotopic cost (performance on a spatiotopic target in the focused attention task, minus performance on a spatiotopic target in the dual attention task), reflects how much performance was degraded by the addition of a retinotopic task. Finding high spatiotopic cost would indicate that the retinotopic task required high amount of attentional resources. There are three possible outcomes of this analysis: (A) finding that retinotopic cost is larger than spatiotopic cost would indicate that the spatiotopic task required more resources than the retinotopic task, suggesting dominance of the retinotopic reference frame; (B) finding that spatiotopic cost is larger than retinotopic cost would indicate that the retinotopic task required more resources than the spatiotopic task, suggesting dominance of the spatiotopic reference frame; or (C) finding no substantial difference between the two cost values would suggest that neither of the two reference frames is more dominant than the other. In the two following experiments we found the third outcome—near-equal costs for the two type of stimuli. These findings suggest that both reference frames can be similarly used by the attention system, depending on context and task demands.

Experiment 1

Methods

Participants

Twenty-four participants (mean age = 26.3, $SD = 4.04$, 17 females) participated in the experiment for credit or payment. All participants reported normal or corrected-to-normal vision and no history of neurologic disorders. They signed written consents for the study,

which was approved by the ethical committees of Tel-Aviv University and of the School of Psychological Sciences.

Apparatus

The experiment was conducted in a sound-attenuated room. Visual stimuli were presented on a 24-inch LCD monitor (ASUS VG248QE) with 1920*1080 resolution and 120 Hz refresh rate. A chin and forehead rest supported the participant's head at a viewing distance of 98 cm from the monitor throughout the experimental session. The experiment was programmed using Matlab-based Psychtoolbox-3 (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007).

Stimuli

Background color was mid-gray. The response target was a tilted Gabor grating patch (1° diameter, 3 cpd, 0.8 Michelson contrast) placed within a red or a blue square (size $1.2^\circ \times 1.2^\circ$). The fixation/pursuit target consisted of a mid-gray dot (diameter 0.15°) placed within a black annulus (diameter 0.5°).

Procedure

A trial began with the presentation of a fixation target at 7° left or right from screen center on the central horizontal axis, and two response targets: one placed above and the other placed below the central horizontal line (Figure 1). After fixation at the fixation target was established for 500 ms, as verified by online monitoring of gaze position, the cue was presented for 300 ms. The cue consisted of a color change of the fixation target: (1) In the focused attention conditions, either the top or the bottom half of the surrounding annulus changed color to indicate which response target should be attended. In this case, both the location of the color change (top/bottom) and the color itself (red/blue) represented redundant 100% valid cues for the attended target (upper or lower target, red or blue target); (2) In the divided attention condition, both top and bottom halves changed color to indicate that both response targets should be attended.

Following cue presentation, the fixation target started to move smoothly along the horizontal axis at a speed of $2^\circ/s$, towards the opposite side of the screen (i.e. becoming the pursuit target). The *retinotopic* response target moved at the same speed as that of the fixation target, maintaining a constant distance with regard to the observer, whereas the *spatiotopic* response target remained in a fixed spatial position throughout the trial. The color of the square surrounding the Gabor patch of each target indicated whether it is a retinally-preserved or a spatially-preserved target. For half of the participants red represented the retinally-preserved targets and blue represented the spatially-preserved

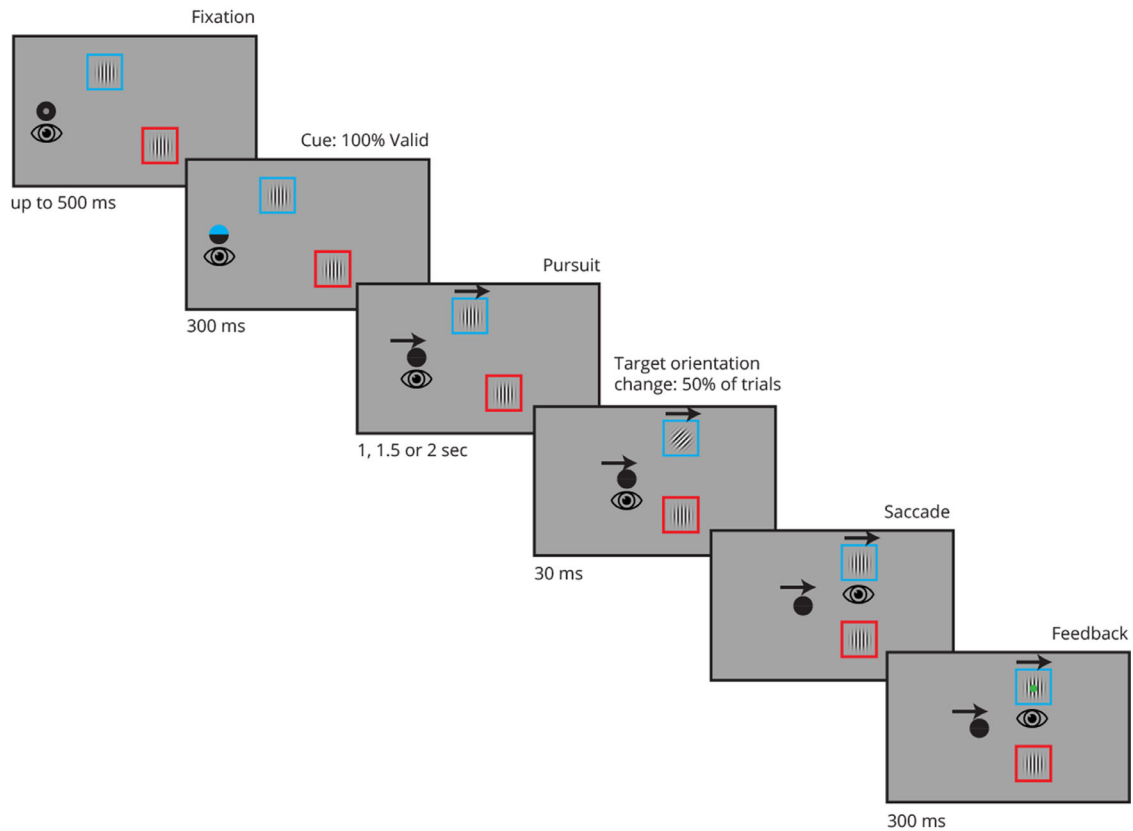


Figure 1. Schematic illustration of a trial of the focused-attention retinotopic condition. The arrows and the eye images are presented for demonstration purposes and did not appear in the experiment. The arrows represent motion of the stimuli and the eye image represents the location of fixation. After fixation is established at the fixation target, fixation target changes its color to indicate which response target should be attended (in this case blue, the retinotopic). This is followed by movement of the fixation target along with the retinotopic target (blue). The spatiotopic target (red) remains stationary. The participant is required to pursue the fixation target while focusing attention to the (blue) response-target. After a varying pursuit duration, the response target changes its orientation for a brief duration in 50% of the trials. The participant is requested to stop the pursuit and make a saccade to the response target upon detection of an orientation change. The response is followed by a feedback presented at the center of fixation (in this case, green to represent a correct response). For illustration purposes, the sizes of the stimuli in this figure are not up to scale.

targets for the entire session, and for the other half the colors were opposite. In separate blocks, the cues indicated which target should be attended: the retinally-preserved (*focused-attention retinotopic condition*), the spatially-preserved (*focused-attention spatiotopic condition*) or both (*divided attention condition*).

The pursuit target moved for one to two seconds (randomly drawn, with steps of 500 ms) until either the trial ended (in 50% of the trials; no-target trials) or the grating changed its orientation by 45° clockwise from vertical for 30 ms and then returned to its original orientation (50% of the trials; target trials). This orientation shift never occurred in the first 500 ms following the motion onset of the pursuit target, and always occurred when the response target was at 6° or 8° away from it. These distances between response-target and pursuit target were balanced across conditions. Therefore the foveal distances of the retinotopic and the

spatiotopic response-targets were the same on average across all trials of session.

In the focused-attention retinotopic and focused-attention spatiotopic conditions, the orientation shift was always at the cued response target. In the divided attention condition, the orientation change could occur at either one of the two response targets with an equal probability. Participants were asked to pursue the pursuit target with their gaze and attend to the cued response target(s). Upon detection of an orientation shift, participants were asked to respond to it by rapidly shifting their gaze towards the shifted response target. The trial ended as soon as a response was detected, or after two seconds with no response. Trials were classified online as correct or incorrect trials, by online examination of gaze positions. Visual feedback was provided accordingly at the end of each trial at the center of fixation: green circle (1.3° presented for 100 ms) for correct responses and red circle (same

size and duration) for incorrect responses. A correct response in a target trial, was considered as such when, following the target's orientation change, gaze was shifted toward the square surrounding the response target and landed within it during the time interval allowed for responding (2 seconds). A correct response in a non-target trial was considered as such when there were no gaze shifts of more than 2° from the pursuit target for more than 10 continuous samples during the trial. The rest of the trials were considered as incorrect.

Each participant completed one experimental session that consisted of a total of 512 trials divided equally into four blocks: focused-retinotopic attention condition block; focused-spatiotopic attention condition block; and two divided attention blocks. The order of the blocks was counterbalanced except that the two blocks of the divided-attention condition never appeared in succession.

Eye-tracking

Recording: Binocular eye-movements were recorded at 1 kHz sampling rate using a remote infrared video-oculographic system (Eyelink 1000 Plus; SR Research Ltd., Kanata, Ontario, Canada) with a spatial resolution of 0.01° and 0.25° to 0.5° average accuracy when using a head-rest, as reported by the manufacturer. A nine-points calibration procedure was performed at the beginning of each block and repeated when necessary. Throughout the experiment, a gaze-contingent procedure was used to monitor eye movements in real time. When participants shifted their gaze away from the fixation target by more than 3° before the target could potentially appear (in the first 1000 ms of the pursuit) a warning message (“fixation was broken” in Hebrew) was presented in the center of the screen. Trials with fixation breaks were aborted, discarded from analysis, and repeated at the end of the block to maintain equal number of trials per condition.

Saccade detection: Saccade were detected in real-time using the SR research detection algorithm and offline using a published algorithm (Engbert & Kliegl, 2003) and an inhouse-developed toolbox based on Matlab (MathWorks) available at <https://github.com/Rinatmer/Pursuit-Analyzer.git>. Before the offline saccade detection, gaze-data was segmented at 0 to 5000 ms relative to the time of pursuit onset and then low-pass filtered (cutoff frequency at 60 Hz). Saccade detection threshold was defined as six times the standard deviation (*SD*) of the eye movement velocity using a median-based estimate of *SD* (Engbert & Kliegl, 2003). Saccade detection was subjected to offline manual inspection and corrected if necessary. Segments of data were excluded from all analyses if a saccade equal or larger than 1° was detected during the interval of the smooth pursuit before the target could potentially appear (1, 1.5, or 2 seconds).

Pursuit gain: The quality of the smooth pursuit was assessed by examining the ratio between the horizontal velocity of gaze positions and velocity of the pursuit target (pursuit gain ratio). Time epochs containing saccades of all sizes, including microsaccades, were removed from this analysis. After saccade exclusion, the horizontal velocity of gaze positions during smooth pursuit was computed on different time-windows of length Δt using Equation 1. In this equation, x_i is the horizontal gaze position at time point i .

$$vel_{horizontal}(i, \Delta t) = \frac{x_{(i+\Delta t)} - x_i}{\Delta t} \quad (1)$$

To calculate the pursuit gain ratio, we divided the horizontal velocity by the velocity of the pursuit target (2 degrees per second). We calculated the pursuit gain ratio in two separate time-windows: (A) At 700 to 800 ms after pursuit onset, which was always before target onset ($i = 700$ ms relative to pursuit onset, $\Delta t = 100$ ms); and (B) the last 100 ms of pursuit, shortly before target onset ($i = -100$ ms relative to target, $\Delta t = 100$ ms). With these two time-windows we could assess the quality of pursuit both during the trial (first interval) and shortly before the target event (second interval).

Smooth pursuit accuracy: In this study the pursuit was always horizontal. Therefore, for each participant, smooth pursuit accuracy on each trial was assessed by computing the distance between the horizontal coordinate of eye position and the location of the pursuit target center at each time point during the pursuit segment and then averaging across all time points.

Saccade density: For each participant, the number of saccades (x_i) were counted for each time-point i across trials, separately for each condition. The saccade density time series was then calculated and smoothed by a sliding window of 50 ms (Δt), using Equation 2.

$$sac_{density}(i, \Delta t) = \frac{\sum_{j=1}^{\frac{\Delta t}{2}} (x_{(i+j)} + x_{(i-j)}) + x_i}{\Delta t + 1} \quad (2)$$

Analysis

Trial rejection: Mean percent of excluded data segments because of saccades was 0.13% (*SD* = 0.04%). After this exclusion, trials in which the pursuit gain was lower than 0.5 or higher than 1.5 within the first examined time-interval were excluded from further analysis (Mean percent of excluded trials: focused-retinotopic condition = 0.007% [*SD* = 0.023%], focused-spatiotopic condition = 0.007% [*SD* = 0.012%], divided condition = 0.008% [*SD* = 0.016%]). After trial rejection, mean pursuit accuracy was 0.77° (*SD* = 1.03°) in the focused-retinotopic condition, 0.58° (*SD* = 0.22°) in the focused-spatiotopic condition and 0.79° (*SD* = 0.76°).

Behavioral analysis: Trials were classified according to condition and response correctness: when a saccade followed an orientation shift and landed on the shifted target, the trial was classified as a Hit; when a saccade was not preceded by an orientation shift target, or when it was directed toward to the target that did not show the orientation shift, the trial was classified as false alarm (FA). Visual sensitivity (d') was calculated as the difference between standardized Hit rate and standardized FA rate. Trials were divided into four conditions: *focused-retinotopic* (attention was focused on the retinotopic stimulus), *focused-spatiotopic* (attention was focused on the spatiotopic stimulus), *divided-retinotopic* (attention was divided between both stimuli and the target was the retinotopic stimulus), and *divided-spatiotopic* (attention was divided between both stimuli and the target was the spatiotopic stimulus). Note that, since the distinction between the divided-spatiotopic and divided-retinotopic conditions existed only for target trials, the FA rate used for the d' calculation was identical in both of these conditions.

Bayesian statistics: To test the null hypothesis that there is no difference between attentional cost for the retinotopic and spatiotopic conditions in comparison to the alternative hypothesis, we conducted a two-way Bayesian repeated measures analysis of variance (ANOVA) and computed the Bayes factor (BF_{10}) using JASP computer software (JASP Team, 2017; Version 0.8.3.1). Cauchy distribution was centered on zero and default JASP prior width was used for all Bayesian analyses [$r = 0.707$]. The Bayesian repeated measures analysis compares different models of the data (e.g., including various combinations of main effects or interactions of interest) with the null model (model without main effect or interaction), allowing to draw inference about which model best explains the data. In practice, BF_{10} represent the evidence for a model of interest relative to a null model (main effect of subject; 1 versus 0). BF_{10} greater than 1 indicates that the model of interest performs better than the null model; a Bayes factor smaller than 1 constitutes evidence in favor of the null model. The magnitude of the BF_{10} can be used as an index to interpret the strength of evidence in favor of the null model: this evidence is considered anecdotal when $1 < BF_{10} < 3$, substantial when $3 < BF_{10} < 10$, strong when $10 < BF_{10} < 30$, very strong when $30 < BF_{10} < 100$ and decisive when $BF_{10} > 100$ (Jeffreys, 1961).

Results

Pursuit gain

Figure 2 depicts the grand average pursuit gain across the entire pursuit segment for each attention condition. Gain levels in all conditions reflect that pursuit was fairly accurate: gains values in all conditions start

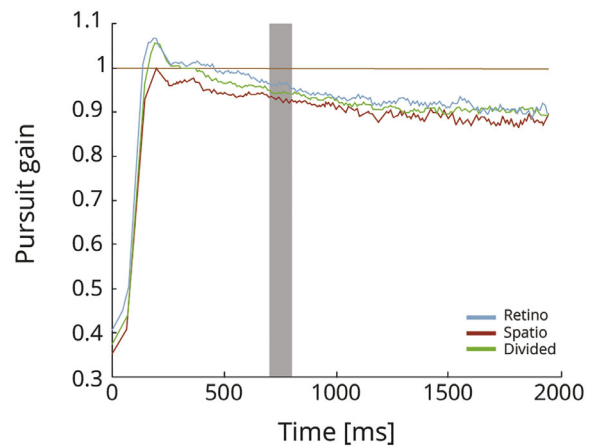


Figure 2. Grand average pursuit gain in Experiment 1. The orange horizontal line at 1 represents gain 1, reflecting that gaze is moving at the same velocity as the target. The shaded gray area corresponds to the time-interval over which pursuit gain was analyzed. Time zero represents the onset of pursuit target.

slightly above 1 and go down to around 0.9 throughout the trial. Consistently with previous research (Kerzel, Souto, & Ziegler, 2008), pursuit was slightly slower in the spatiotopic condition relative to the retinotopic condition but this trend was small and insignificant (see below). For the first examined time-interval (700–800 ms after pursuit onset), mean pursuit gain was 0.94 in the divided condition, ($SD = 0.039$), 0.93 in the focused-spatiotopic condition ($SD = 0.062$) and 0.96 in the focused-retinotopic condition ($SD = 0.058$). One-way ANOVA revealed no evidence for differences in pursuit gain between conditions during this time-interval ($F[2,69] = 1.768$, $p = 0.178$). For the second examined time interval (–100 to 0 ms relative to the orientation change), mean pursuit gain was 0.89 in the divided condition ($SD = 0.066$), 0.88 in the focused-spatiotopic condition ($SD = 0.089$) and 0.91 in the focused-retinotopic condition ($SD = 0.076$). One-way ANOVA revealed no evidence for differences in pursuit gain between conditions shortly before the orientation change ($F[2,69] = 0.93$, $p = 0.4$).

Saccade density

Figure 3 depicts the grand average saccade density across the entire pursuit segment for each attention condition. Although there were some differences in saccade density between conditions at the initiation of the pursuit, these were found mainly in the first 500 ms of the pursuit, long before the presentation of the target event. By the first examined interval (700–800 ms after pursuit onset), there was no significant difference between conditions ($F[2,69] = 0.025$, $p = 0.97$; focused-retinotopic: mean 2.09, $SD = 1.12$; focused-spatiotopic: mean 2.06, $SD = 1.18$; divided: mean 2.2, $SD = 0.99$). Similarly, no significant difference

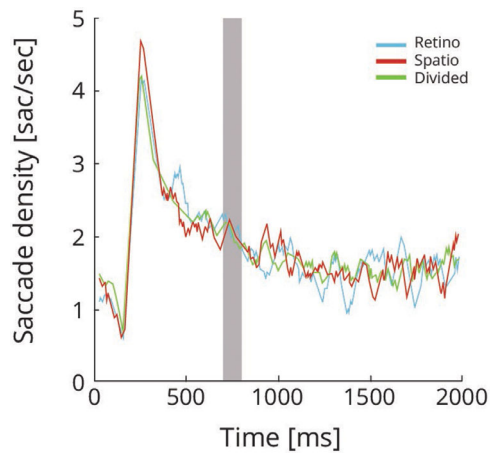


Figure 3. Grand average of saccade densities in Experiment 1. Time zero represents the onset of pursuit target.

between conditions was found in the second interval (-100 to 0 relative to target onset) ($F[2,69] = 0.53$, $p = 0.59$; focused-retinotopic: mean 1.83 , $SD = 1.05$; focused-spatiotopic: mean 1.5 , $SD = 1.02$; divided: mean 1.65 , $SD = 1.2$), confirming there was no difference between conditions by the time the target event occurred.

Hit rate

Mean hit rate was 0.92% in the focused-retinotopic condition ($SD = 0.082\%$), 0.77% in the focused-spatiotopic condition ($SD = 0.122\%$), 0.88% in the divided-retinotopic condition ($SD = 0.125\%$) and 0.62% in the divided-spatiotopic condition ($SD = 0.186\%$).

Mean visual sensitivity

A two-way repeated measures ANOVA with factors: attention condition (focused/divided attention) and target's coordinate system (spatiotopic/retinotopic) was performed on the sensitivity index d' . There was a significant main effect of attention ($F[1,23] = 14.76$, $p = 0.001$, $\eta^2 = 0.39$) resulting from higher d' in the focused attention relative to the corresponding divided attention condition. This finding validated the attentional manipulation, suggesting that dividing attention to both targets resulted in a perceptual cost. There was also a significant main effect of coordinate-system ($F[1,23] = 53.09$, $p < 0.001$, $\eta^2 = 0.70$), resulting from higher d' for the retinotopic relative to the spatiotopic stimuli. There was no evidence for an interaction between the two factors ($F[1,23] = 0.023$, $p = 0.88$), suggesting that despite the global perceptual advantage for the retinotopic stimuli, the attentional cost of dividing attention relative to focusing it, did not differ between the two coordinate systems (Figure 4A).

Bayesian analysis was used to examine the null hypothesis of no interaction between attention condition and coordinate system. Results showed that the model with the highest explanatory power was a model containing the two main effects and no interaction ($BF_m = 12.93$). Comparing this model to the null model showed strong support for the null model (BF_{10} ratio = $3.196e^{10}$). These results suggest that there was no reliable interaction between coordinate system and attention condition and that the effects of these two manipulations are additive.

In a follow-up analysis, we examined the effect of the peripheral response-target distance on performance, using a two-way repeated measures ANOVA with factors: coordinate system (focused retinotopic/spatiotopic) and distance ($6^\circ/8^\circ$ away from the pursuit target) on the sensitivity index d' . For the closer target location condition (6°), mean visual sensitivity was 3.27 ($SD = 0.85$) for retinotopic targets and 2.91 for spatiotopic targets ($SD = 0.85$). For the farther target location condition (8°), mean visual sensitivity was 3.22 ($SD = 0.82$) for retinotopic targets and 1.97 for spatiotopic targets ($SD = 0.79$). As in the previous analysis, there was a significant main effect of coordinate system ($F[1,23] = 29.65$, $p < 0.001$, $\eta^2 = 0.56$), resulting from a higher d' in the retinotopic condition than in the spatiotopic condition. As expected, there was a significant effect of distance ($F[1,23] = 29.64$, $p < 0.001$, $\eta^2 = 0.59$), resulting from higher d' when the peripheral response-target was closer to the foveated pursuit target (6°) compared to when it was farther away from it (8°). There was a significant interaction between coordinate system and distance ($F[1,23] = 7.12$, $p = 0.014$), resulting from a larger effect for difference in the spatiotopic condition than in the retinotopic condition.

Reaction-times (RTs)

RT were computed for correct ("Hit") trials only. For each participant and condition, trials in which RT exceeded the participant mean RT in that condition by more than 3 SD were excluded from analysis. On average, this resulted in the removal of 2.04% of trials in the focused-retinotopic condition ($SD = 0.015\%$), 1.6% in the focused-spatiotopic condition ($SD = 0.01\%$), 2.23% in the divided-retinotopic condition ($SD = 0.016\%$) and 2.14% in the divided-spatiotopic condition ($SD = 0.02\%$). Following this procedure, RTs were averaged across participants. For the focused-attention condition, mean RT was 530 ms ($SD = 98.09$ ms) for retinotopic targets and 595 ms for spatiotopic targets ($SD = 102.13$ ms). For the divided-attention condition, mean reaction-time was 560 ms ($SD = 98.15$ ms) for retinotopic targets and 643 ms for spatiotopic targets ($SD = 126.19$ ms). The RTs results were consistent

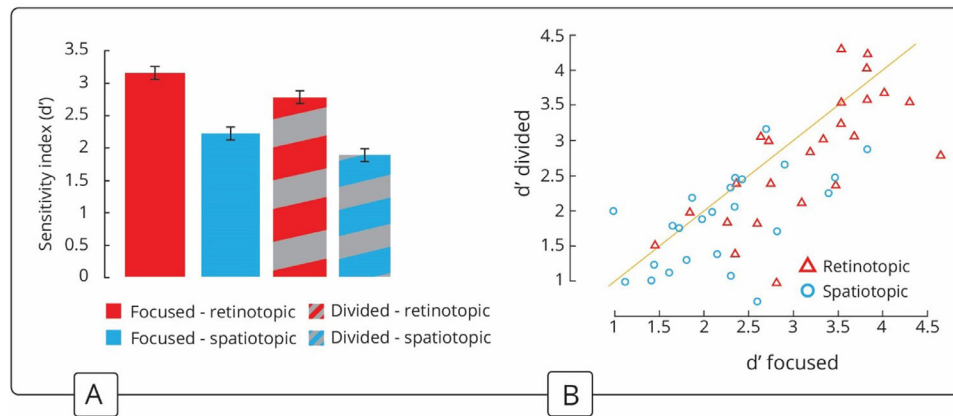


Figure 4. Visual sensitivity results of [Experiment 1](#). (A) Grand averages ($N=24$) of d' values. (B) Visual sensitivity (d') when dividing vs. focusing attention on targets in the two reference frames. A single data point represents the d' values during focused attention and divided attention tasks, per reference frame condition and per participant. Each participant contributes with two data points: one representing the retinotopic (red triangles) and the other the spatiotopic (blue circles) condition. Error bars represent ± 1 within-subject standard error calculated separately for each condition ([Cousineau, 2005](#)).

with the d' results, and there was no evidence for accuracy-speed trade-offs.

A two-way repeated measures ANOVA with factors: attention condition (focused/divided attention) and target's coordinate system (spatiotopic/retinotopic) was performed on the reaction times. There was a significant main effect of attention ($F[1,23] = 7.65$, $p = 0.011$, $\eta^2 = 0.25$) resulting from faster responses in the focused attention relative to the divided attention conditions. There was also a significant main effect of coordinate-system ($F[1,23] = 20.39$, $p < 0.002$, $\eta^2 = 0.47$), resulting from faster responses for the retinotopic relative to the spatiotopic stimuli. The interaction between the two factors was not significant ($F[1,23] = 0.59$, $p = 0.45$), suggesting that, despite higher perceptual facilitation for the retinotopic stimuli, the cost of dividing attention relative to focusing it, did not differ between the two coordinate systems.

Results of the Bayesian repeated measures ANOVA showed that the model with the highest explanatory power was a model containing the two main effects and no interaction ($BF_m = 3.16$). Comparing this model to the null model showed a strong support for the null model (BF_{10} ratio=181). These results suggest that there was no reliable interaction between coordinate system and attention condition and that the effects of these two manipulations are additive.

Results summary

[Experiment 1](#) examined the cost from dividing attention between a retinotopic and a spatiotopic target relative to focusing it on either one of them. The findings show that this cost is similar for retinotopic and

spatiotopic targets, suggesting the attentional system can use both reference-frames to a similar extent.

However, results also indicated that there was an inherent difference in detection level between retinotopic and spatiotopic targets: performance for retinotopic targets was substantially higher, regardless of whether the condition was focused or divided attention. For some of the participants the difference in d' between conditions was more than two, with the retinotopic condition reaching ceiling level performance at a hit rate of 92% on average.

The main finding of this experiment is based on the assumption that comparing divided and focused attention controls for global differences between the two types of targets across the attentional conditions. However, this assumption does not necessarily hold when the perceptual performance is extremely low or extremely high. In these cases, the lower and upper limits of performance-level could account for a lack of interaction between attention type (divided vs. focused) and reference frame (retinotopic vs. spatiotopic). Presumably, if performance measurements could vary more, a larger attentional effect could have been found for the retinotopic condition resulting in an interaction.

[Experiment 2](#) was conducted to examine this question by equating the perceptual performance for the retinotopic and the spatiotopic targets. The experiment was identical to the first experiment, except that the perceptual thresholds were adjusted individually using a staircase procedure for each participant and separately for retinotopic and spatiotopic targets. By equating task difficulty between the two attention conditions, we avoided the ceiling effect in the retinotopic condition while maintaining above-floor effect in the spatiotopic condition, thus making the two conditions more comparable than they were in the first experiment.

Experiment 2

Methods

The Methods of [Experiment 2](#) were identical to those of [Experiment 1](#) except when indicated otherwise.

Participants

Eighteen participants (mean age = 25.4, $SD = 4.15$, 8 females) participated in the experiment for credit or payment.

Pretest session

Before their participation in the main experiment (at least one day before but no more than a week), participants performed a pretest session in which their perceptual thresholds were determined separately for the retinotopic and the spatiotopic tasks. During this pretest, participants performed two experimental blocks, one of the *focused-retinotopic task* and another of the *focused-spatiotopic task*. In these blocks, the target's tilt was modified using two-up one-down staircase procedure ([Garcia-Perez, 1998](#)). Each block ended upon reaching 12 reversals and the perceptual threshold was determined to be the average of the two last reversals. The order of the blocks in the pre-test session matched the order of blocks assigned to that participant in the main experiment. The tilt of spatiotopic and retinotopic targets remained fixed throughout the entire experiment (on both single and divided blocks). The averaged threshold tilt ($N = 18$) in the *focused-retinotopic* condition was 15.7° (Min: 11.8° , Max: 31° , $SD = 4.4^\circ$) and the averaged threshold tilt in the *focused-spatiotopic* condition was 32.7° (Min: 28.4° , Max: 37.8° , $SD = 3^\circ$).

Analysis

Trial rejection procedure was as in [Experiment 1](#). Mean percent of excluded data segments was 0.14% ($SD=0.04\%$). Following this exclusion, trials in which pursuit gain deviated from the target velocity by more than 0.5 were removed from all analyses (Mean percent of excluded trials: focused-retinotopic condition = 0.005% ($SD = 0.012\%$), focused-spatiotopic condition = 0.009% ($SD = 0.016\%$), divided condition = 0.008% ($SD = 0.012\%$). After trial rejection was completed, mean pursuit accuracy was 0.59° ($SD = 0.13^\circ$) in the focused-retinotopic condition, 0.6° ($SD = 0.13^\circ$) and 0.64° ($SD = 0.14^\circ$) in the divided condition.

Results

Pursuit gain

[Figure 5](#) shows the grand average pursuit gain across the entire pursuit segment for each attention condition.

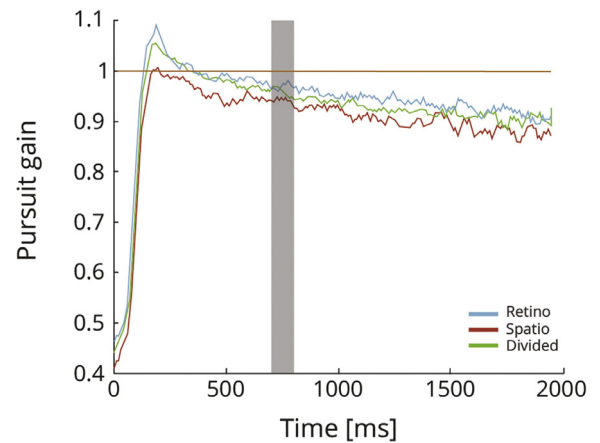


Figure 5. Grand average pursuit gain in [Experiment 2](#). The orange line at 1 represents gain 1, in which gaze is moving at the same velocity as the target. The shaded gray area corresponds to the time-interval over which pursuit gain was analyzed.

For the first examined time-interval (700–800 ms relative to pursuit onset), mean pursuit velocity value was 0.96 in the divided condition ($SD = 0.05$), 0.97 in the focused-retinotopic condition ($SD = 0.03$) and 0.94 in the focused-spatiotopic condition ($SD = 0.07$). One-way ANOVA revealed no evidence for differences in pursuit gain between conditions ($F[2,17] = 0.023$, $p = 0.88$).

For the second time-interval (–100 to 0 relative to target onset), mean gain velocity value was 0.9 in the divided condition ($SD = 0.06$), 0.87 in the focused-spatiotopic condition ($SD = 0.06$) and 0.91 in the focused-retinotopic condition ($SD = 0.05$). One-way ANOVA revealed that the difference in pursuit gain between conditions around the time of orientation change was not significant ($F[2,17] = 1.63$, $p = 0.21$).

Saccade density

[Figure 6](#) depicts the grand average saccade density across the entire pursuit segment for each attention condition. Although there were some differences in saccade density between conditions at the initiation of the pursuit, these were found mainly in the first 500 ms of the pursuit. Similarly to [Experiment 1](#), examination of the first time-interval shows that there were no reliable differences between conditions 700 to 800 ms after pursuit onset: mean saccade density was 2.26 in the focused-retinotopic condition ($SD = 0.98$), 2.08 in the focused-spatiotopic condition ($SD = 1.3$) and 2.27 in the divided condition ($SD = 1.14$). One-way ANOVA revealed no evidence for differences in saccade density between conditions during this time-interval ($F[2,17] = 0.152$, $p = 0.86$).

Examination of the second time-interval shows that by the time the target event occurred, saccade density was similar between conditions: mean saccade density was 1.43 in the focused-retinotopic

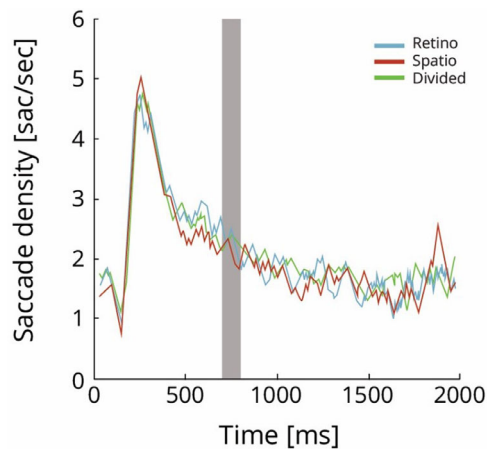


Figure 6. Grand average of saccade densities in Experiment 2. Time zero represents the onset of pursuit target.

condition ($SD=1.11$), 1.92 in the focused-spatiotopic condition ($SD=1.54$) and 1.67 in the divided condition ($SD=1.07$). One way ANOVA revealed no evidence for differences in saccade density between conditions ($F[2,17]=0.71$, $p=.5$).

Hit rate

The mean hit rate was 0.74% in the focused-retinotopic condition ($SD = 0.15\%$) and 0.72% in the focused-spatiotopic condition ($SD = 0.15\%$), confirming that the adaptive staircase procedure worked as expected. Performance on the divided attention conditions was lower, as expected: 0.69% in the divided-retinotopic condition ($SD = 0.13\%$) and 0.67 in the divided-spatiotopic condition ($SD = 0.14\%$).

Mean visual sensitivity

A two-way repeated measures ANOVA with factors: attention condition (focused/divided attention) and target's coordinate system (spatiotopic/retinotopic) was performed on the sensitivity index d' . The results of Experiment 2 were consistent with those of Experiment 1. There was a significant main effect of attention ($F[1,17] = 14.81$, $p = 0.001$, $\eta^2 = 0.466$), resulting from higher d' in the focused attention relative to the corresponding divided attention condition. The main effect of coordinate system ($F[1,17] = 0.035$, $p = 0.85$) was not significant, and the interaction between the two factors was not significant ($F[1,17] = 0.61$, $p = 0.45$), suggesting that the attentional cost of dividing attention relative to focusing it did not differ between the two coordinate systems (Figure 7A). Bayesian analysis was used to examine the null hypothesis of no interaction between attention condition and coordinate system. Results showed that the model with the highest explanatory power was a model containing

the main effect of attention alone ($BF_m = 5.05$). Comparison of this model to the null model showed a substantial support for the null model (BF_{10} ratio = 2.8) (Jeffreys, 1961), thus supporting the lack of a reliable interaction between coordinate system and attention.

In a follow-up analysis, two-way repeated measures ANOVA with factors: coordinate system (focused retinotopic/spatiotopic) and distance ($6^\circ/8^\circ$ away from the pursuit target) was performed on the sensitivity index d' . For the closer target location condition (6°), mean visual sensitivity was 2.02 ($SD = 0.79$) for retinotopic targets and 1.86 for spatiotopic targets ($SD = 0.89$). For the farther target location condition (8°), mean visual sensitivity was 1.44 for retinotopic targets ($SD = 0.86$) and 1.52 for spatiotopic targets ($SD = 0.53$). The main effect of coordinate system was not significant ($F[1,17] = 0.43$, $p = 0.84$). The main effect of distance was significant ($F[1,17] = 27.76$, $p < .001$, $\eta^2 = 0.62$), resulting from a higher d' when the response-target was closer to the pursuit-target than when it was farther away from it. Unlike Experiment 1, the interaction between the two factors was not significant ($F[1,17] = 0.87$, $p = 0.36$), suggesting that differences in performance between the retinotopic and spatiotopic conditions cannot be attributed to the distance of the peripheral response-target.

Reaction times

Outlier removal procedure was identical to that of Experiment 1. On average, this resulted in the removal of 3.76% of the data in the focused-retinotopic condition ($SD = 0.04\%$), 2.63% in the focused-spatiotopic condition ($SD = 0.02\%$), 3.73% in the divided-retinotopic condition ($SD = 0.05\%$) and 2.66% in the divided-spatiotopic condition ($SD = 0.02\%$). After this procedure, RTs were averaged across participants. For the focused-attention condition, mean reaction-time was 671 ms for retinotopic targets ($SD = 0.126$ ms) and 671 ms for spatiotopic targets ($SD = 136$ ms). For the divided-attention condition, mean reaction-time was 681 ms for retinotopic targets ($SD = 113$ ms) and 713 ms for spatiotopic targets ($SD = 90$ ms).

A two-way repeated measures ANOVA with factors: attention condition (focused/divided attention) and target's coordinate system (spatiotopic/retinotopic) was performed on the RTs. Results indicate that there was no accuracy-speed tradeoff: the main effect of attention was not significant ($F[1,17] = 1.52$, $p = 0.235$), indicating that participants did not respond faster on the focused conditions than on the divided-attention condition. The main effect of coordinate was not significant ($F[1,17] = 1.23$, $p = 0.284$), indicating that participants did not respond faster to a retinotopic

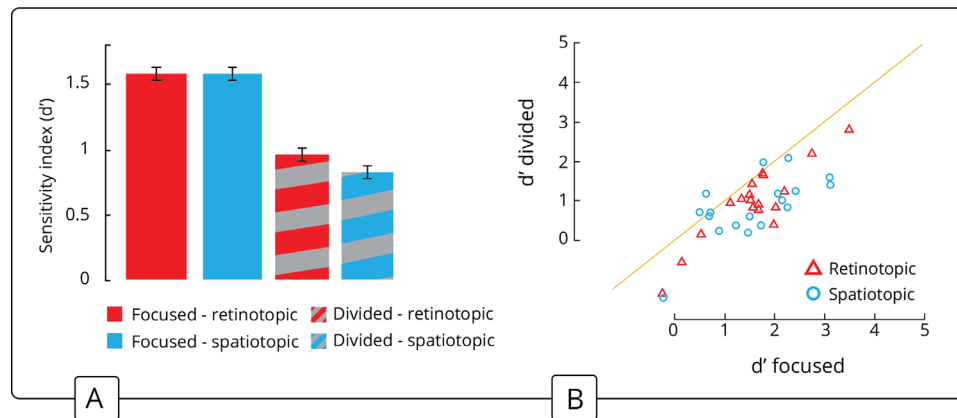


Figure 7. Visual sensitivity results of [Experiment 2](#). (A) Grand averages ($N=18$) of d' values. (B) Visual sensitivity (d') when dividing vs. focusing attention on targets in the two reference frames. A single data point represents the d' values during focused attention and divided attention tasks, per reference frame condition and per participant. Each participant contributes with two data points: one representing the retinotopic (red triangles) and the other the spatiotopic (blue circles) condition. Error bars represent ± 1 within-subject standard error calculated separately for each condition ([Cousineau, 2005](#)).

target than to a spatiotopic target. There was no significant interaction between attention and coordinate system ($F[1,17] = 0.51, p = 0.48$). Analysis of the Bayesian repeated measures ANOVA revealed that the model with the highest explanatory power was the null model ($BF_m = 3.6$). Comparison of the model with two main effects and no interaction with the model containing the interaction (5.6/13.3) showed that the model with the two main effects was favored by a Bayes factor of 2.4 to the interaction model, thus proving a substantial support for the model that does not contain an interaction. ([Jeffreys, 1961](#)).

Results summary

Consistently with the results of [Experiment 1](#), we found that there was no difference between retinotopic and spatiotopic targets in the cost of dividing attention versus focusing it on one target. After the individual adjustment of target tilt in this experiment, there were no ceiling or floor effects, and perceptual performance was similar between the two conditions.

General discussion

This study examined which reference frame is used by the attentional system during smooth pursuit, when the required response to the target is a goal-directed action, i.e. a saccade to a peripheral attended target. Findings showed that there was no interaction between the target's coordinate system and the attentional requirements of the task; that is, the enhancement of visual sensitivity in the focused relative to the divided attention condition was similar

in magnitude for retinotopic and spatiotopic targets. These findings were obtained even when the overall detection performance for retinotopic and spatiotopic targets was equated using an adaptive procedure ([Experiment 2](#)). These findings suggest that during smooth pursuit, attention can be allocated in both the retinotopic and the spatiotopic coordinate systems. The finding that attention allocation is neither dominantly retinotopic nor dominantly spatiotopic stresses the importance of context and the flexibility of the spatial attention mechanism: the attention system may under some conditions favor either a retinotopic or a spatiotopic reference frame, yet under other conditions, it can effectively and adaptively use both reference frames.

These findings are consistent with a similar study by [Niebergall et al. \(2010\)](#). In that study, participants performed a smooth pursuit task on an object moving in a circle while they attended a peripherally presented target. As in the present study, the target was either fixed in its retinotopic or in its spatiotopic coordinates, and the task was either divided or focused attention on one of these targets. That study differed from the present one both in the mode of response (manual response vs. saccade, correspondingly) and in the type of task (orientation discrimination vs. detection, correspondingly). The present findings suggest that even when the task requires detection and a location-based goal-directed action, the cost of dividing versus focusing attention is similar for retinotopic and spatiotopic targets.

Most previous studies that tested how attention allocation is modulated by different frames of reference, the spatial coordinates were altered as a result of saccade execution; that is, participants rapidly shifted their gaze, and attention was measured after this

shift. In the present study, and in that of Niebergall et al. (2010), the set of coordinates was updated by a slow motion of smooth pursuit. This distinction in experimental protocol is more than technical. Whereas it is believed that complex compensatory mechanisms are required for maintaining visual stability across saccades (e.g., Golomb et al., 2008; Golomb, Nguyen-Phuc, et al., 2010), it is reasonable to hypothesize that no such mechanisms are required for updating coordinates across the slow retinal changes produced during pursuit. It is therefore possible that, during pursuit, the attentional system is more flexible and capable of using both retinotopic and spatiotopic coordinate systems to the same extent.

Exogenous versus endogenous attention

In this study we examined the effects of the coordinate system on the allocation of endogenous attention, attention that is voluntarily allocated after a symbolic cue. A study by Souto and Kerzel (2009) examined a similar question but focusing on exogenous attention—the involuntary shifts of attention caused by the abrupt onset of a peripheral cue. It was found that the presentation of salient peripheral cues resulted in faster saccades toward retinotopic targets, but no such effect was found for spatiotopic targets. Similarly, they found effects of inhibition of return only for retinotopic, but not for spatiotopic, targets. Exogenous and endogenous attention are known to be based on separate mechanisms (Barbot et al., 2012). Specifically, it was previously shown that endogenous attention is more flexible and better able to adjust based on goals and task demands (Carrasco, 2011). The present findings, together with the finding by Niebergall et al. (2010), contribute to this claim by suggesting that endogenous attention is not hard-wired to a specific coordinate system.

Reduced perception for spatiotopic targets

In addition to the main finding of similar attentional facilitation for spatiotopic and retinotopic targets, we found differences in the baseline perception of these two types of targets across both attentional conditions. In Experiment 1 this was manifested by higher performance for retinotopic relative to spatiotopic targets. In Experiment 2, where performance level was equated across conditions, it was manifested by lower perceptual thresholds for retinotopic targets. This finding is consistent with the findings by Niebergall et al. (2010). This baseline effect could be interpreted as reflecting the difference between conditions in performing smooth-pursuit while attending to the non-pursued objects (Hutton & Tegally, 2005; Kerzel et al., 2008; Lipton, Frost, & Holzman, 1980). Previous findings provided evidence supporting attentional enhancement in the perception of retinotopic relative

to spatiotopic targets by showing that pursuit gain is reduced when attention was allocated to spatiotopic, relative to retinotopic objects (Kerzel et al., 2008). It may be the case that it took more attentional resources to perform the pursuit while attending to the spatiotopic relative to the retinotopic target, regardless of the dual versus focused attention manipulations. In our findings there was a small trend showing slightly higher pursuit gain for retinotopic relative to spatiotopic targets, but this trend was insignificant. Therefore, although attentional enhancement of perception in the retinotopic condition is possible, we find no evidence for attentional effect on the pursuit gain, as reported by previous studies.

An alternative possible explanation for the reduced perception of spatiotopic targets can be that these targets do not have a fixed retinal position. The retinal motion produced by the spatiotopic targets during pursuit may induce a blurred perception and make these targets more difficult to detect and discriminate. However, this explanation is not consistent with the finding in Experiment 1 of an interaction between the foveal distance of the target and its coordinate system. Retinal blur is expected to have a lower effect in the periphery, where receptive fields are larger. Therefore, if blur was the reason for the difference between the two targets, we would have anticipated finding a lower difference between the targets in the periphery. Instead we find the opposite: the differences between retinotopic and spatiotopic targets was larger in the far periphery (8°) than in the nearer periphery (6°).

Another explanation is that retinotopic targets are more easily attended because they are more easily grouped with the pursued objects than the spatiotopic targets. This hypothesis is supported by previous evidence suggesting a tight link between pursuit and attention. Findings show that perception accuracy is better for a pursued relative to non-pursued objects, suggesting that attentional resources are allocated to the pursued target (Kerzel et al., 2008; Khurana & Kowler, 1987). Since retinotopic targets move coherently with the pursuit targets, they may have also been easier to attend than spatiotopic targets. However, this view relies on a strong attentional link between the pursued stimulus retinotopic target. Our finding of no difference in pursuit gain between the conditions questions this interpretation. Previous findings showed that pursuit is improved when performing a task on the pursued object (Shagass, Roemer, & Amadeo, 1976; Sweeney, Clementz, Haas, Escobar, Drake, & Frances, 1994; Vangelder, Lebedev, Liu, & Tsui, 1995). Consistently, it could have been suggested that if there were a strong attentional link between the pursued stimulus and the retinotopic target, we would find enhanced pursuit gain when attending the retinotopic target, relative to the spatiotopic one. Importantly, regardless of the explanation for the difference in baseline performance between the retinotopic and the spatiotopic targets, this

difference could not provide an alternative explanation for the main finding of this study. In **Experiment 2** performance was equated for the two types of targets, and similar attentional effects were obtained.

Conclusion

In two separate experiments we show that during smooth pursuit, attention is proportionally divided between targets in the retinotopic and the spatiotopic frames of reference. This is the case not only when the response is manual but also when the response is a goal-directed oculomotor response. These findings demonstrate flexibility of the endogenous attention system. The endogenous attention system is not hard-wired to one frame of reference but is capable of adapting according to the changing circumstances and the requirements of a specific task.

Keywords: reference frame, goal-directed action, saccade preparation

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