



OPEN Attentional tracking reduces cortical alpha oscillations

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The premotor theory of attention suggests that both overt and covert attentional orienting are governed by similar mechanisms and neural structures, a concept extensively investigated in paradigms involving shifts in attention and gaze towards peripheral targets. Previous studies have found a strong link between cortical alpha oscillations and overt smooth pursuit of a target. However, the relationship between alpha oscillations and covert tracking of peripheral moving stimuli remains unclear. To address this, we asked 16 observers to maintain fixation while covertly attending to a visual stimulus moving along the horizontal meridian at varying speeds (2, 6, or 12 °/s), within either the left or right hemifield. We simultaneously recorded both eye movements and EEG data. Our results revealed that alpha power was significantly reduced when observers tracked a target that moved further in the periphery, independent of its speed. These findings confirm that the distribution of alpha power is sensitive to the allocation of covert attention during tracking. This suggests a tight link between the attentional processes involved in covert tracking and overt pursuit of a moving target, supporting the premotor theory of attention.

Keywords Attention, Covert tracking, Alpha oscillation, EEG

The idea that overt and covert orienting of attention (i.e., with and without the orienting of gaze towards the attended location) are largely based on the same principles, mechanisms, and neural structures is one of the main tenets of the premotor theory of attention¹. Most commonly, this has been studied in the context of paradigms where observers shifted covert attention to peripheral locations or shifted gaze to peripheral targets by executing saccadic eye movements^{2–6}.

There is, however, further considerable evidence regarding a tight link between smooth pursuit eye movements and attention (see⁷ for a recent review). Diverting attention from the pursuit target towards a peripheral flashed stimulus can reduce the gain of pursuit⁸, i.e., the ratio of eye speed to target speed. Furthermore, multiple studies have shown that the allocation of attention is linked to the pursuit target during steady-state pursuit. Van Donkelaar⁹ found that reaction times in the detection of stimuli flashed ahead of the pursuit target were faster compared to stimuli that were flashed behind it. Moreover, the location at which the best performance was observed moved further in the direction of pursuit as the speed of pursuit increased¹⁰. This latter finding was not replicated by Seya and Mori¹¹, who found the attentional bias in the direction of pursuit to be unaffected by pursuit speed. Khan and colleagues¹² also found attention to be unbalanced during pursuit, with faster manual reaction times to stimuli flashed ahead of the pursuit target compared to flashes that trailed the pursuit target. In this case, however, the advantage was rather broadly to the whole hemifield in the direction of pursuit, at least within the sampled window of 10°×10° centered on the pursuit target. The same study¹² also included an experiment where attention was probed by asking observers to saccade to a flashed stimulus during pursuit. Saccadic reaction times were also generally faster for flashed stimuli presented in the hemifield ahead of the pursuit target^{13,14}, although saccades generated towards targets immediately (up to approximately 3°) ahead of the target showed larger latencies, likely because of the interference between the oculomotor systems responsible for smooth pursuit and small catch-up saccades. Studies that probed the allocation of attention through the discrimination of small transient changes in an array of stimuli that moved along with the pursuit target did not report asymmetries with regard to the space ahead or behind the gaze point^{15,16}. This has been interpreted as indicating that pursuing a target does not imply a generalized tendency to attend ahead of its location but specifically a facilitation of attentional capture by transient stimuli and possibly a facilitation of voluntary orienting towards the space in front of the pursuit target¹⁵.

Generally speaking, investigating the allocation of attention during smooth pursuit using a dual task, whether detection or discrimination, bears the risk that the probing task itself modifies the way attention is allocated. For instance, observers might be led to use less focalized attention, expecting peripheral targets to be presented. This motivated Chen and colleagues¹⁷ to conduct a study where attentional modulation was probed using Steady-

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State Visual Evoked Potentials (SSVEPs) in response to a task-irrelevant stimulus, thus avoiding the need for an additional task on top of target pursuit. By using a combination of wedge-shaped checkerboards surrounding the pursuit target that flickered at different frequencies, they were able to tag the responses elicited in different sectors of the visual field during pursuit. The results confirmed an attentional bias favoring the locations directly ahead of the target (up to about 1.5°).

One additional finding in the study by Chen and colleagues¹⁷ was that, in addition to the modulation of visually evoked steady-state potentials, pursuing a target also led to a generalized reduction of endogenous alpha activity, as compared to simply attending to the flickering stimuli while fixating. It is noteworthy that this implied a potentially opposite effect of attention on steady-state responses and spontaneous oscillations, although both occurred in the alpha range¹⁸.

The study of cortical alpha activity during oculomotor pursuit has a long history, with the key question from the outset being the relationship between attention, oculomotor control, and alpha activity. Mulholland and Peper¹⁹ observed a substantial reduction, i.e., blockage, of alpha activity during pursuit. However, they considered this effect to be a result of oculomotor activity and unrelated to visual attention. Wertheim^{20,21} also noted the reduction of alpha activity associated with pursuit but attributed it specifically to the attentional control of pursuit, i.e., to the use of visual input for oculomotor control. In Wertheim's model, intentional control of pursuit, e.g., pursuing a stimulus that is so predictable in its motion as to require minimal adjustment based on visual input, is rather associated with an increase in occipital alpha power, also see^{22,23}.

More recently, the question of the association between smooth pursuit eye movements and occipital alpha activity has been addressed using MEG. In a combined MEG and fMRI study, Dunkley and colleagues²⁴ investigated the activation of the extrastriate visual cortex (MT+, as confirmed by the fMRI data) as observers executed smooth pursuit over a static background (thus producing a retinal motion signal) or over a background that moved along with the target (excluding the retinal motion signal). The results showed a generalized suppression of alpha and beta activity during overt pursuit, supporting a role of both extraretinal oculomotor signals and pursuit-related retinal motion signals in driving MT+ activity. The authors also found that the suppression of oscillatory activity in each hemisphere correlated with the position of gaze along the left-right sinusoidal pursuit trace. In a subsequent study²⁵, by having the target move sinusoidally in different hemifields, they demonstrated that eye position did not affect the lateralized suppression of alpha activity, and using linear motion, they demonstrated that pursuit direction and pursuit speed per se did not affect lateralized alpha activity. On the contrary, eye speed modulated the suppression of oscillations in the beta range.

These observations suggest a further opportunity to test the strictness of the connection between overt and covert attentional orienting. If pursuit-related reduction in alpha amplitude arises from the sensorimotor processes involved in overtly pursuing a target, i.e., in the use of target position and/or speed signals for the purpose of aligning gaze with the moving target, there should be no lateralized alpha reduction observed when covertly attending to a moving target. Conversely, if covert and overt tracking of a moving target involves similar neural mechanisms, the former should also be associated with lateralized alpha reduction.

In the present study, we had observers fixate either left or right of the screen midline while covertly attending to a visual stimulus that moved along the horizontal meridian at varying speeds. To anticipate the main result, our EEG recordings showed that alpha reduction was related to the eccentricity at which the covertly attended target travelled, and was also stronger contralateral to the hemifield where the target moved.

Method

Participants

Sixteen observers (7 females and 9 males, average age = 22.8, ranging from 18 to 27 years) participated in the experiment. All participants had normal or corrected-to-normal vision and were right-handed. Prior to participating, they signed written informed consent forms in line with the Declaration of Helsinki. All methods were carried out with the Declaration of Helsinki. The experiment procedure was approved by the Institutional Ethics Committee of the Shanghai University of Sport (No.102772023RT096). All observers were paid for their participation after the experiment.

Stimulus and procedure

The stimuli were displayed on an LED monitor (Lenovo, China), which had a spatial resolution of 1440 (H) × 900 (V) pixels (41 cm × 25.6 cm) and a refresh rate of 60 Hz. At a viewing distance of 65 cm, the screen extended 35° horizontally and 22° vertically in visual angle. Stimuli were programmed using the Psychophysics Toolbox^{26,27} in MATLAB (Mathworks, Natick, Massachusetts, USA). The experiment was conducted in a dimly lit room.

Stimuli were displayed against a black background (0.4 cd/m^2). The target for fixation and for attentional tracking was a filled red circle (radius = 0.25° , luminance = 21.1 cd/m^2). Figure 1 shows the sequence of events in a single trial. Before each trial, a blue circle was displayed at the target's starting position (either in the left or right hemifield). The observer was instructed to press the spacebar to initiate the trial when ready. After the key press, the blue circle changed to red, and the target remained stationary at the starting position for 500 ms. Observers were required to fixate on the starting position during this 500 ms period. Subsequently, the target moved horizontally across the screen, traveling back and forth for 5 s. The motion trajectory of the target was symmetric, centered on the middle line of the screen. For example, if the target's starting position was in the left hemifield, it moved horizontally to the right after the 500 ms fixation period, reaching a position symmetric to the starting point relative to the central vertical axis, and then returned. Throughout this movement, the observer was required to maintain fixation on the starting position while tracking the moving target with attention. Eye position was recorded for later analysis, and no feedback was provided to participants during the experiment. To make sure that the observer paid attention to the moving target, we included a counting task. In the time window of [0.5 4.5] seconds, the moving target could disappear briefly for 100 ms once or twice at random time points.

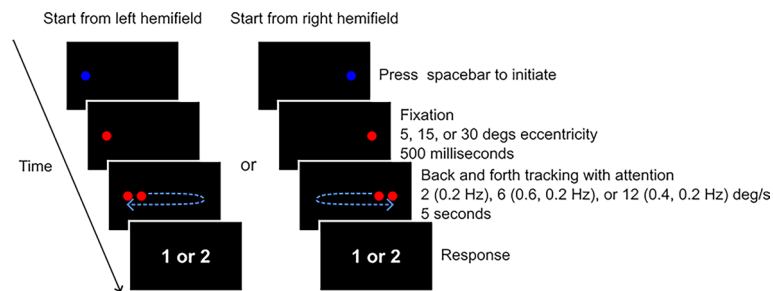


Fig. 1. Sequence of events in a trial. Participants were instructed to maintain fixation while attentively tracking a target that moved back and forth for 5 s. The target started moving from either the left or right hemifield at speeds of 2, 6, or 12 °/s. At a speed of 2 °/s, the travel eccentricity was 5°. At 6 °/s, the travel eccentricities were either 5 or 15°. At 12 °/s, the travel eccentricities were either 15 or 30°. While tracking the target with attention, observers were required to count the number of gaps in the stimulus (when the target disappeared briefly for 100 ms) and report the number at the end of each trial.

Gap onsets were generally equally likely to occur when the target was close to and far from fixation (Figure S1). For each participant and each condition, the probability of the target disappearing once or twice in each trial was 50%. As a result, approximately 47.6% of trials had one gap, while 52.4% had two gaps on average. In trials with two gaps, the two gaps were separated for at least 583 ms. There were no trials without a gap. The observer was required to count the number of gaps when tracking the target with attention, and report it by pressing the number key 1 or 2 at the end of each trial.

To disentangle the effect of speed and eccentricity (i.e., the travel distance between the target's starting position and its symmetric counterpart), we manipulated the speed and travel eccentricity of the target. The following 5 conditions were tested: the target moved at a speed of 2 °/s and traversed an eccentricity of 5° (S2-E5, the target started moving from a position of 2.5° to the left or right of the screen center and moved back and forth for 1 round, 0.2 Hz), a speed of 6 °/s and an eccentricity of 5° (S6-E5, the target started moving from a position of 2.5° to the left or right of the screen center and moved back and forth for 3 rounds, 0.6 Hz), a speed of 6 °/s and an eccentricity of 15° (S6-E15, the target started moving from a position of 7.5° to the left or right of the screen center and moved back and forth for 1 round, 0.2 Hz), a speed of 12 °/s and an eccentricity of 15° (S12-E15, the target started moving from a position of 7.5° to the left or right of the screen center and moved back and forth for 2 rounds, 0.4 Hz), a speed of 12 °/s and an eccentricity of 30° (S12-E30, the target started moving from a position of 15° to the left or right of the screen center and moved back and forth for 1 round, 0.2 Hz). There were 15 trials in each condition, which resulted in a total number of 75 trials. For each participant and each condition, the probability of the tracking target moving either from the left or right hemisphere in each trial was 50%. On average, approximately 50.9% of trials involved movement from the left hemisphere, while 49.1% involved movement from the right hemisphere. All trials were presented in a randomized order.

Target speed and eccentricity effect analyses

The main purpose of this study was to examine the effect of target speed and eccentricity on responses, especially on the alpha responses. As mentioned above, we set five tracking conditions, including S2-E5, S6-E5, S6-E15, S12-E15, and S12-E30. Based on this setup, we could assess the effect of target speed by comparing responses across different speed conditions—categorized as *slower* (e.g., S2-E5 or S6-E15) and *faster* (e.g., S6-E5 or S12-E15)—while keeping target eccentricity constant. For example, when the target eccentricity was 5°, the speed of 2 °/s was regarded as the slower condition compared to 6 °/s. The effect of target speed could therefore be assessed by comparing the responses in the slower speed conditions (calculated as the average of S2-E5 and S6-E15) with those in the faster speed conditions (calculated as the average of S6-E5 and S12-E15). Similarly, we could assess the effect of target eccentricity by comparing responses across different eccentricity conditions—categorized as *smaller* (e.g., S6-E5 or S12-E15) and *larger* (e.g., S6-E15 or S12-E30)—while holding target speed constant. For example, when the target speed was 6 °/s, the eccentricity of 5° was regarded as the smaller condition compared to 15°. The effect of target eccentricity could be assessed by comparing the responses in the smaller eccentricity conditions (calculated as the average of S6-E5 and S12-E15) with those in the larger eccentricity conditions (calculated as the average of S6-E15 and S12-E30). Importantly, for each participant, responses were first averaged across trials within each speed-eccentricity combination. Target speed and eccentricity effects were then analyzed based on these aggregated values.

Eye movement recordings and analyses

Eye movements from the right eye were recorded at 1000 Hz using an Eyelink Portable Duo eye tracker (SR Research, Mississauga, ON, Canada). A chin rest was adjusted so that the participant's head was in a natural position, ensuring that their gaze was directed at the center of the screen without any head movement. Before the formal experiment, a 9-point calibration procedure was used to ensure precise recording of participants' eye movements. Calibration accuracy was measured in terms of visual angle error between gaze points and screen coordinates, which ideally should be less than 0.5°. Additionally, a drift check was conducted before each trial, displaying a double circle at the starting position of the target and measuring the deviation between the computed

fixation position and the circle. Despite the fact that the observers were required to maintain stable fixation during attention tracking, they occasionally moved their eyes towards the moving target. In order to exclude data where the observer failed to maintain stable fixation, a two-step process of data exclusion was implemented. In the initial step, trials were manually inspected and excluded if participants' smooth pursuit exceeded 5°. In the second step, in individual trials, any eye position data deviated more than 1° from the required fixation position were excluded. Additionally, blinks in each trial were detected based on a sharp drop in pupil size using the built-in program of the eye tracker, and these data were excluded. The final mean exclusion rate was 6.8%. Afterwards, we analyzed eye movement data to check whether there were fixational biases towards the moving target (e.g.²⁸). The horizontal eye positions of each participant were analyzed separately for each condition, and baseline-corrected by subtracting the average position in the [-500 0] ms time window before motion onset. This baseline correction served as an offline calibration method to eliminate artifacts arising from initial eye position variability and head movements. A positive value indicated an eye position close to the target motion direction, while a negative value indicated a position far from the target motion direction. For example, if the target moved to the right and the eye position was 2° to the right of the baseline mean, the horizontal relative eye position was +2°.

EEG recordings and analyses

EEGs were recorded from 32 scalp sites according to the international 10–20 standard electrode positioning system. Signals were amplified and sampled at 1000 Hz (Brain Products, Munich, Germany). Ag/AgCl recording electrodes were securely attached to a 32-electrode cap, with the grounding electrode set at AFz, and the reference electrode set at Cz. The impedance between the scalp and each electrode was maintained below 10 kΩ.

Analyses were conducted using functions from the EEGLab toolbox²⁹ along with custom scripts in MATLAB. The EEG signals were re-referenced to a common average reference. Only trials with correct counting responses were included in the EEG analysis (93.5% of total trials). Subsequently, the corresponding EEG data were systematically excluded based on the specified eye movement data exclusion criteria described above. Specifically, EEGs from trials where participants failed to maintain fixation but smoothly tracked the stimuli were excluded. Then, each 5-second trial was segmented into five successive 1-second epochs. Any 1-second epoch characterized by unstable fixation (i.e., containing any position deviated more than 1° from the required fixation position) was systematically excluded from further EEG analysis. The average exclusion rate was 21.3% across all participants and conditions, with the individual rates ranging from 2.6 to 53.0%. Despite one participant having an exclusion rate as high as 53.0%, this participant still had at least 26 valid 1-second epochs in each condition. So his data was retained for the study. Exclusion rates also varied across different experimental conditions: S2-E5, Mean = 20.891%, 95% CI [13.619, 28.164]; S6-E5, 16.139%, 95% CI [8.470, 23.808]; S6-E15, 21.911%, 95% CI [14.669, 29.154]; S12-E15, 18.697%, 95% CI [12.815, 24.578]; S12-E30, 28.616%, 95% CI [20.940, 36.292]. A Friedman's test revealed a significant main effect of tracking condition on exclusion rates, $\chi^2(4) = 19.849$, $p < 0.001$. Post-hoc pairwise comparisons were performed using the Wilcoxon signed-rank test with Bonferroni correction for multiple comparisons. The results showed that the exclusion rate for S12-E30 was significantly higher than that for S6-E15, $z = 2.948$, p_{adj} (adjusted p -value for multiple comparison) = 0.032, and S12-E15, $z = 3.408$, $p_{\text{adj}} = 0.007$. These results indicate that the condition with higher target speed and larger eccentricity (i.e., S12-E30) was associated with higher exclusion rates, which could reflect the increased difficulty of maintaining stable fixation under this condition. Each 1-second epoch of every trial from individual participants was detrended by removing a linear trend fitted using least squares to eliminate low-frequency drift³⁰ and then subjected to a fast Fourier transform (fft.m in MATLAB). The EEG amplitude in the alpha range (8–12 Hz) was then averaged across the same condition. Based on the difference topographic maps (Fig. 4c), the averaged response at the Pz electrode was used for further analysis.

Statistical analyses

All statistical analyses were conducted using IBM SPSS software. Effects were tested using repeated measures ANOVAs and t-tests. For repeated measures ANOVAs, if the sphericity assumption was met, the analysis assuming sphericity was used; otherwise, the Greenhouse-Geisser correction was applied. Bonferroni corrections were applied by adjusting the p -values for post-hoc comparisons and for multiple t-tests, in order to control the increased probability of Type I errors due to multiple comparisons. All p -values reported as p_{adj} were corrected using the Bonferroni method. An alpha level of 0.05 was used to determine statistical significance for both uncorrected and corrected p -values, based on two-sided tests.

Results

Behavioral results

In the current experiment, observers were asked to use attention to track a target while completing a counting task. We calculated the accuracy of observers' behavioral responses under different conditions characterized by varying speeds and eccentricities of the target motion. These conditions included S2-E5, S6-E5, S6-E15, S12-E5, and S12-E30. Given that observers were instructed to report one or two gaps at the end of each trial, we examined the effect of the gap number on the detection accuracy (Figure S2a). Although we found a significant main effect of gap number, indicating that the accuracy was generally lower when the target disappeared twice, no significant interaction effect between gap number and conditions was observed. Therefore, the averaged accuracies from the one-gap and two-gap conditions were used in subsequent analyses. Figure 2 illustrates the accuracy percentages across five conditions. On average, observers showed an accuracy of 90.8%. The highest accuracy was observed for S2-E5 (96.3%) and the lowest for S6-E5 (83.3%). A one-way (tracking condition: S2-E5, S6-E5, S6-E15, S12-E15, vs. S12-E30, within-subjects) ANOVA was conducted to analyze the effect of target motion condition on response accuracy. The results revealed a significant main effect of condition on accuracy,

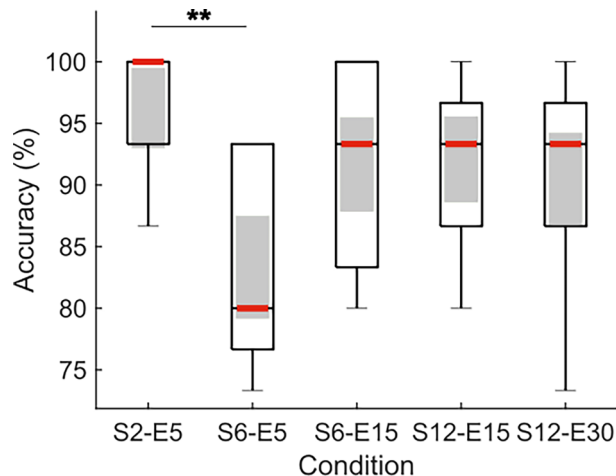


Fig. 2. Average accuracies of the counting task during attention tracking across different target motion conditions. Overall, accuracy was high across conditions; however, the S6-E5 condition demonstrated comparatively lower accuracy. The edges of each box represent the 25th and 75th percentiles, and the whiskers extend to the most extreme data points that are not considered outliers. The red horizontal lines indicate the median values. The height of the gray rectangles represents within-participant 95% confidence intervals³¹. Sx-Ey: S refers to target speed (°/s), and E refers to target eccentricity (°). For example, S2-E5 indicates a target speed of 2 °/s and a target eccentricity of 5°. The same pattern applies to other labels. ** $p < 0.01$.

$F(4, 60) = 5.743$, $p = 0.001$, $\eta^2 = 0.277$. Specifically, Bonferroni-corrected post-hoc comparisons indicated that the accuracy in the S2-E5 condition (95% CI [93.081, 99.419]) was significantly higher compared to the S6-E5 condition (95% CI [79.031, 87.636]), $t(60) = 4.939$, $p_{\text{adj}} = 0.002$. There were no significant differences in accuracy between the other conditions (all $p_{\text{adj}} > 0.08$).

Why did the S6-E5 condition have such a low accuracy? To gain a better understanding, we conducted two further analyses on the effect of gap position on detection accuracy. First, we checked accuracies for trials where the gap was close to fixation (defined as being within half of the condition's eccentricity from fixation) and trials where the gap was far from fixation (defined as being beyond half of the condition's eccentricity from fixation; Figure S3a). We found that the accuracy was particularly low in the S6-E5 condition when the gap appeared close to fixation. Second, we plotted the distribution of gap positions for error trials in the S6-E5 condition (Figure S4). We observed that most error trials occurred when one of the gaps was located at turning points close to fixation. Therefore, the low accuracy in the S6-E5 condition was primarily caused by the gaps overlapping with the fixation spot.

Next, we further examined the effects of target speed and eccentricity on behavioral accuracy. The effect of speed was examined by comparing the responses from slower speed conditions (calculated as the average of S2-E5 and S6-E15) with those from faster speed conditions (calculated as the average of S6-E5 and S12-E15), while keeping target eccentricity constant (i.e., 5° or 15°). A paired-sample *t*-test (one-sided, to assess the direction of difference) revealed that the accuracy in the slower speed condition (95% CI [91.428, 96.489]) was significantly higher than that in the faster speed condition (95% CI [85.306, 90.111]), $t(15) = 3.382$, $p = 0.002$, Cohen's $d = 0.873$. However, given the low accuracy of the S6-E5 condition, this significant effect of target speed on accuracy was most likely driven by this particular condition.

The effect of eccentricity was examined by comparing the responses from smaller eccentricity conditions (calculated as the average of S6-E5 and S12-E15) with those from larger eccentricity conditions (calculated as the average of S6-E15 and S12-E30), while keeping target speed constant (i.e., 6 °/s or 12 °/s). A paired-sample *t*-test (two-sided) showed no significant difference in accuracy between smaller (95% CI [85.306, 90.111]) and larger eccentricity (95% CI [87.950, 94.133]) conditions, $t(15) = -1.732$, $p = 0.104$, Cohen's $d = -0.447$.

Overall, we did not find consistent effects of target speed or eccentricity on behavioral accuracy, suggesting that these factors may not significantly influence behavioral accuracy in this task.

Eye position biases towards target motion direction

Previous research has found that the direction of fixational eye position shifts is influenced by the target motion direction during covert attention tracking²⁸. To verify this effect in our experiment, we analyzed the average horizontal eye position relative to the average of baseline eye position before each trial started in each tracking condition across all participants. To identify trends in eye position changes over time more easily, we divided the 5-second eye movement data into five 1-second intervals, averaging the horizontal relative eye position for each second. Note that this analysis was done after excluding data with unstable fixation ($> 1^\circ$) and blinks. First, we examined the effect of gap position on fixational eye position (Figure S3b–f). Specifically, we compared trials where the gap was close to fixation (defined as being within half of the target eccentricity from fixation) and trials where the gap was far from fixation (defined as being beyond half of the target eccentricity from fixation). Although we found a significant main effect of gap position on the fixational eye position (the shift of

eye position was, in general, larger when the gap was far from fixation compared to when it was close to fixation), no significant interaction effect between gap position and tracking conditions was observed. Consequently, the averaged fixation eye position from different gap positions was used in the subsequent analyses. Next, Fig. 3 illustrates the horizontal relative position as a function of time from motion onset across different target motion conditions. Positive values indicate that the horizontal eye position is close to the direction of target motion, while negative values indicate that it is far from the target motion direction. In general, there was a bias towards the direction of target motion in each condition, and this bias increased over time. A 5 (time window: 0–1 s, 1–2 s, 2–3 s, 3–4 s, vs. 4–5 s, within-subjects) \times 5 (tracking condition: S2-E5, S6-E5, S6-E15, S12-E15, vs. S12-E30, within-subjects) repeated measures ANOVA was conducted to analyze the temporal evolution of the horizontal relative eye position. The results revealed a significant main effect of time window, $F(4, 60) = 17.094$, $p < 0.001$, $\eta^2 = 0.533$. Polynomial comparisons of the time-window factor showed a significant linear trend in the fixational eye positions, $F(1, 15) = 33.904$, $p < 0.001$, $\eta^2 = 0.693$, and a significant quadratic trend, $F(1, 15) = 7.060$, $p = 0.018$, $\eta^2 = 0.320$. Additionally, there was no significant main effect of motion condition, $F(4, 60) = 0.409$, $p = 0.801$, $\eta^2 = 0.027$, and no significant interaction effect between time window and motion condition, $F(16, 240) = 1.483$, $p = 0.107$, $\eta^2 = 0.090$. Bonferroni-corrected post-hoc comparisons for the time window main effect showed that relative the 4–5 s time window (95% CI [0.020, 0.114]), the average horizontal relative eye positions for the other time windows were significantly further from target motion direction: 0–1 s (95% CI [−0.031, 0.020]), $t(60) = -5.214$, $p_{\text{adj}} = 0.001$; 1–2 s (95% CI [−0.045, 0.040]), $t(60) = -6.900$, $p_{\text{adj}} < 0.001$; 2–3 s (95% CI [−0.036, 0.056]), $t(60) = -5.700$, $p_{\text{adj}} = 0.001$; and 3–4 s (95% CI [−0.016, 0.075]), $t(60) = -4.625$, $p_{\text{adj}} = 0.003$. Compared to the 3–4 s time window, the average horizontal relative eye position for the 1–2 s time window was significantly further from the target motion direction, $t(60) = -4.000$, $p_{\text{adj}} = 0.007$. To further illustrate the eye position bias, we conducted one-sample t-tests (one-sided) to examine whether the fixational eye position was biased toward the target motion direction by comparing the average horizontal relative eye position to zero in each time window. Bonferroni-corrected multiple tests showed that for the S12-E15 condition, during the 4–5 s time window (95% CI [0.044, 0.126]), the horizontal relative eye position significantly larger than 0, $t(15) = 4.411$, $p_{\text{adj}} = 0.006$, Cohens' $d = 1.103$, indicating a bias of the fixational eye position toward the target motion direction. However, no significant differences were found in the other conditions (all $p_{\text{adj}} > 0.3$).

Additionally, we examined whether target speed and eccentricity had any effect on eye position biases. The effect of speed was examined by comparing the responses from the slower speed conditions (calculated as the average of S2-E5 and S6-E15) with those from the faster speed conditions (calculated as the average of S6-E5 and S12-E15), while keeping target eccentricity constant (i.e., 5° or 15°). A 2 (target speed: slower vs. faster, within-subjects) \times 5 (time: 0 to 5 s from target motion onset, within-subjects) repeated-measures ANOVA showed a

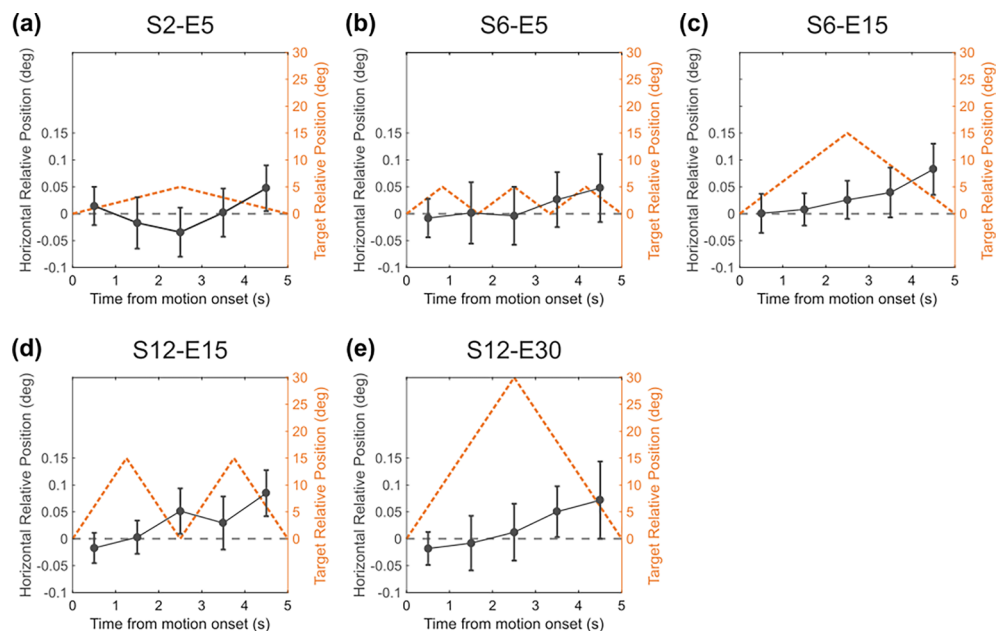


Fig. 3. Eye position analysis. Left axis: The horizontal eye position relative to the initial fixation position as a function of time from motion onset. The horizontal relative eye positions shifted overall toward the direction of target motion over time. A value of “0” indicates the initial fixation eye position. Positive values indicate a shift of eye position toward the direction of target motion, and negative values indicate a shift away from the target motion direction. Error bars denote within-participant 95% confidence intervals³¹. Right axis: The target’s moving position relative to its initial position as a function of time. A value of “0” indicates the initial position of the target. Each panel represents a specific condition. (a) S2-E5: Target speed of 2 °/s and target eccentricity of 5°. (b) S6-E5: Target speed of 6 °/s and target eccentricity of 5°. (c) S6-E15: Target speed of 6 °/s and target eccentricity of 15°. (d) S12-E15: Target speed of 12 °/s and target eccentricity of 15°. (e) S12-E30: Target speed of 12 °/s and target eccentricity of 30°.

significant main effect of time, $F(4, 60) = 15.607$, $p < 0.001$, $\eta^2 = 0.510$. However, there was no significant main effect of speed, $F(1, 15) = 0.048$, $p = 0.829$, $\eta^2 = 0.003$, and no significant interaction effect between target speed and time, $F(4, 60) = 1.781$, $p = 0.144$, $\eta^2 = 0.106$. The effect of eccentricity was examined by comparing the responses from the smaller eccentricity conditions (calculated as the average of S6-E5 and S12-E15) with those from the larger eccentricity conditions (calculated as the average of S6-E15 and S12-E30), while keeping target speed constant (i.e., 6 °/s or 12 °/s). A 2 (target eccentricity: smaller vs. larger, within-subjects) \times 5 (time: 0 to 5 s from target motion onset, within-subjects) repeated-measures ANOVA showed a significant main effect of time, $F(4, 60) = 14.470$, $p < 0.001$, $\eta^2 = 0.491$. However, there was no significant main effect of eccentricity, $F(1, 15) = 0.048$, $p = 0.829$, $\eta^2 = 0.003$, and no significant interaction effect between target eccentricity and time, $F(4, 60) = 0.381$, $p = 0.821$, $\eta^2 = 0.025$. Therefore, there was no significant effect of target speed or eccentricity on eye position biases.

Target-eccentricity-dependent alpha reduction

The main purpose of the current study was to compare the alpha response across different tracking conditions under the same target eccentricities or speeds. Figure 4a depicts the grand-averaged amplitude spectra for each tracking condition (S2-E5, S6-E5, S6-E15, S12-E15, and S12-E30) at the Pz electrode. The alpha-band (8–12 Hz) was consistently observed across participants for each condition, showing clear spectral peaks. Figure 4b presents the topographic distributions of alpha amplitude (averaged from 8 to 12 Hz) for different target motion conditions. The subtraction topographic maps of S2-E5 versus S6-E5, and S6-E15 versus S12-E15 illustrated the variation in alpha activity as a function of target speed (Fig. 4c, left). Similarly, the subtraction topographic maps of S6-E5 versus S6-E15, and S12-E15 versus S12-E30 illustrated the variation in alpha activity as a function of target eccentricity (Fig. 4c, right). Subsequent analyses focused on the response at the Pz, based on the difference topographic maps (as shown in Fig. 4c). We first checked the effect of gap number (one vs. two gaps) on the alpha amplitude in different tracking conditions (Figure S2b). We found a significant main effect of the number of gaps on the alpha amplitude, indicating that alpha amplitude was generally lower when the target disappeared twice, but no significant interaction effect between gap number and tracking conditions was observed. Therefore, the averaged responses from the one-gap and two-gap conditions were used in subsequent analyses.

Next, we statistically compared the alpha response at the Pz electrode across different tracking conditions. Figure 5 displays the average alpha amplitude at the Pz electrode for each tracking condition across all participants. A one-way (tracking condition: S2-E5, S6-E5, S6-E15, S12-E15, vs. S12-E30, within-subjects) repeated measure ANOVA revealed a significant main effect of tracking condition, $F(2.222, 33.329) = 6.015$, $p = 0.005$, $\eta^2 = 0.286$.

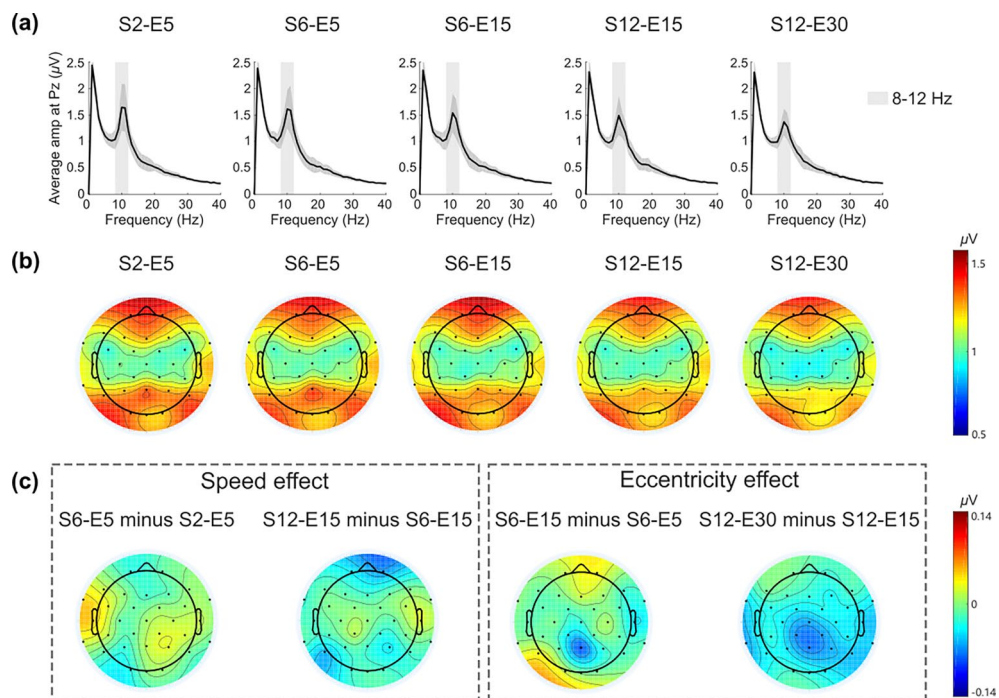


Fig. 4. Topographic maps for the experiment. **(a)** Grand-averaged ($N = 16$) amplitude spectrum for each tracking condition (S2-E5, S6-E5, S6-E15, S12-E15, and S12-E30) at the Pz electrode. The light-gray-shaded area indicates the 8–12 Hz frequency range. The dark-gray-shaded area represents the within-participant 95% confidence intervals³¹. **(b)** Topographic maps of the grand-averaged alpha amplitude for each condition. **(c)** Subtraction maps illustrating the speed and eccentricity effects. Left panel (Speed effect): S6-E5 minus S2-E5 and S12-E15 minus S6-E15. Right panel (Eccentricity effect): S6-E15 minus S6-E5 and S12-E30 minus S12-E15. Sx-Ey: S refers to target speed (°/s), and E refers to target eccentricity (°). The color bar represents the amplitude of the EEG signal in microvolts (μV).

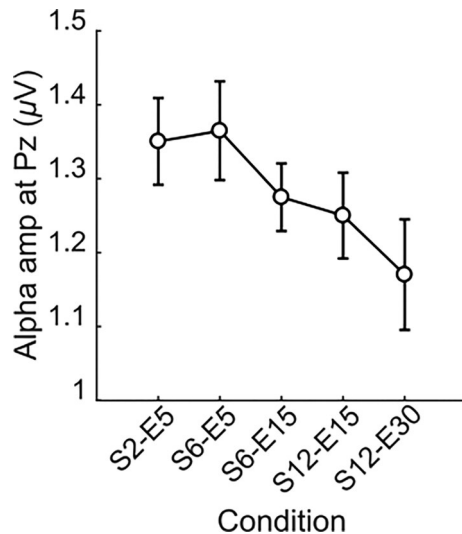


Fig. 5. Average alpha amplitude at the Pz electrode as a function of different conditions. Sx-Ey: S refers to target speed (°/s), and E refers to target eccentricity (°). Error bars indicate within-participant 95% confidence intervals³¹.

(with the Greenhouse–Geisser correction). Bonferroni-corrected post-hoc comparisons showed that the alpha amplitude at the Pz electrode for S6-E5 (95% CI [1.122, 1.607]) was marginally significantly higher than that for S12-E30 (95% CI [1.021, 1.319]), $t(60) = 3.25$, $p_{\text{adj}} = 0.052$. Other paired comparisons were not significant (all $p_{\text{adj}} > 0.09$).

We further examined the target speed and target eccentricity effect on alpha amplitude at the Pz electrode. To test the effect of target speed, we compared the average alpha amplitude at the Pz electrode from the slower speed conditions (calculated as the average of S2-E5 and S6-E15) and the faster speed conditions (calculated as the average of S6-E5 and S12-E15) across all participants, while keeping target eccentricity constant (i.e., 5° or 15°). A paired-sample t-test (two-sided) revealed no significant difference between the slower speeds (95% CI [1.078, 1.548]) and faster speeds (95% CI [1.102, 1.513]), $t(15) = 0.189$, $p = 0.853$, Cohen's $d = 0.013$. To test the effect of target eccentricity, we compared the average alpha amplitude at the Pz electrode from the smaller eccentricity conditions (calculated as the average of S6-E5 and S12-E15) and the larger eccentricity conditions (calculated as the average of S6-E15 and S12-E30) across all participants, while keeping target speed constant (i.e., 6°/s or 12°/s). A paired-sample t-test (one-sided, to assess the direction of difference) revealed that the alpha amplitude at the Pz electrode from the larger eccentricities (95% CI [1.043, 1.403]) was significantly lower than that from the smaller eccentricities (95% CI [1.102, 1.513]), $t(15) = -2.678$, $p = 0.009$, Cohen's $d = 0.234$. These results suggest that alpha reduction is dependent on target eccentricity, but not on target speed.

The lateralization effect

Our results indicate that target speed per se does not affect alpha reduction. However, it is possible that tracking a stimulus left or right in the visual field leads to a lateralization of alpha reduction. In order to investigate this aspect, we analyzed alpha responses at three electrode sites – P3, Pz, and P4 – under different tracking eccentricities and direction conditions while keeping target speed constant. Specifically, P3 and P4 electrodes represent the left and right hemispheres, respectively, while Pz serves as a central reference point. As depicted in Fig. 6, a pronounced lateralization effect is evident regardless of the target speed (i.e., 6° or 12°/s). When tracking stimuli in the left visual field (i.e., VF), the right hemisphere (P4) exhibits deactivation in alpha activity; conversely, when tracking stimuli in the right VF, the left hemisphere (P3) displays alpha activity reduction.

When the target moved at 6°/s (Fig. 6a), a 2 (target eccentricity: S6-E5 vs. S6-E15, within-subjects) \times 2 (tracking visual field [VF]: left vs. right, within-subjects) \times 3 (electrode: P3, Pz vs. P4, within-subjects) repeated measure ANOVA revealed an interaction between electrode and VF, $F(1.119, 16.792) = 15.339$, $p = 0.001$, $\eta^2 = 0.506$ (with the Greenhouse–Geisser correction). Other effects were not significant (all $ps > 0.07$). Subsequently, we examined the lateralization effect separately in each eccentricity condition under 6°/s. For S6-E5 (Fig. 6a, left), a 2 (VF: left vs. right, within-subjects) \times 3 (electrode: P3, Pz vs. P4, within-subjects) repeated measure ANOVA revealed a significant interaction effect between VF and electrode, $F(1.378, 20.677) = 8.043$, $p = 0.006$, $\eta^2 = 0.349$ (with the Greenhouse–Geisser correction). Other effects were not significant (all $ps > 0.1$). Bonferroni-corrected paired comparison revealed that at the P3 electrode, a significantly lower alpha response amplitude was found when tracking stimuli in the right VF (95% CI [0.984, 1.341]) compared to the left VF (95% CI [1.093, 1.506]), $t(30) = -3.044$, $p_{\text{adj}} = 0.008$. At the P4 electrode, there was a trend that the alpha response when tracking in the left VF (95% CI [0.998, 1.412]) was lower than when tracking in the right VF (95% CI [1.084, 1.627]), but this difference was not significant, $t(30) = -2.027$, $p_{\text{adj}} = 0.060$. For S6-E15 (Fig. 6a, right), a 2 (VF: left vs. right, within-subjects) \times 3 (electrode: P3, Pz vs. P4, within-subjects) repeated measure ANOVA revealed that there was a significant interaction between VF and electrode, $F(1.161, 17.417) = 14.171$, $p = 0.001$, $\eta^2 = 0.486$.

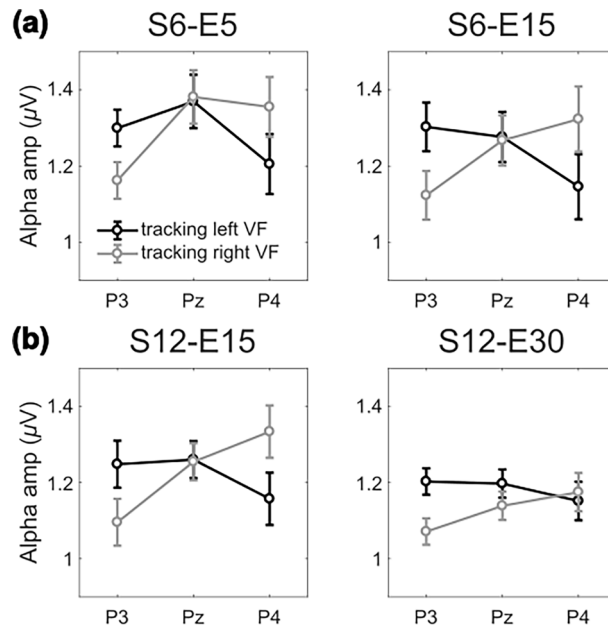


Fig. 6. Lateralization effect of alpha amplitude across different eccentricity conditions under the same speeds, i.e., 6 °/s (**a**) or 12 °/s (**b**). The black line and gray line represent the alpha response amplitude when tracking stimuli in the left visual field (VF) and in the right VF, respectively. Error bars denote within-participant 95% confidence intervals³¹. Sx-Ey: S refers to target speed (°/s), and E refers to target eccentricity (°).

(with the Greenhouse–Geisser correction). Other effects were not significant (all $ps > 0.4$). Bonferroni-corrected paired comparison revealed that at the P3 electrode, a significantly lower alpha response amplitude was found when tracking stimuli in the right VF (95% CI [0.952, 1.295]) compared to the left VF (95% CI [1.052, 1.554]), $t(30) = -2.983$, $p_{\text{adj}} = 0.009$. At the P4 electrode, the alpha response amplitude during tracking stimuli in the left VF (95% CI [0.939, 1.353]) was significantly lower than that observed during tracking in the right VF (95% CI [1.100, 1.547]), $t(30) = -2.213$, $p_{\text{adj}} = 0.043$.

When the target moved at 12 °/s (Fig. 6b), a 2 (target eccentricity: S12-E15 vs. S12-E30) \times 2 (VF: left vs. right) \times 3 (electrode: P3, Pz vs. P4) repeated measure ANOVA revealed a significant main effect of eccentricity, $F(1,15) = 6.673$, $p = 0.021$, $\eta^2 = 0.308$, a significant interaction effect between VF and electrode, $F(2,30) = 28.368$, $p < 0.001$, $\eta^2 = 0.654$, and a significant interaction effect among eccentricity, VF and electrode, $F(1.294, 19.403) = 6.076$, $p = 0.017$, $\eta^2 = 0.288$ (with the Greenhouse–Geisser correction). Other effects were not significant (all $ps > 0.07$). Subsequently, we examined the lateralization effect separately in each eccentricity condition under 12 °/s. For S12-E15 (Fig. 6b, left), a 2 (VF: left vs. right, within-subjects) \times 3 (electrode: P3, Pz vs. P4, within-subjects) repeated measure ANOVA revealed a significant interaction effect between VF and electrode, $F(1.424, 21.354) = 25.742$, $p < 0.001$, $\eta^2 = 0.632$ (with the Greenhouse–Geisser correction). Other effects were not significant (all $ps > 0.2$). Bonferroni-corrected paired comparison revealed that at the P3 electrode, a significantly lower alpha response amplitude was found when tracking stimuli in the right VF (95% CI [0.963, 1.229]) compared to the left VF (95% CI [1.026, 1.470]), $t(30) = -2.621$, $p_{\text{adj}} = 0.019$. At the P4 electrode, the alpha response amplitude during tracking stimuli in the left VF (95% CI [0.983, 1.331]) was significantly lower than that observed during tracking in the right VF (95% CI [1.128, 1.539]), $t(30) = -2.750$, $p_{\text{adj}} = 0.015$.

For S12-E30 (Fig. 6b, right), a 2 (VF: left vs. right, within-subjects) \times 3 (electrode: P3, Pz vs. P4, within-subjects) repeated measure ANOVA revealed that there was a significant interaction effect between VF and electrode, $F(2, 30) = 9.866$, $p = 0.001$, $\eta^2 = 0.397$. Other effects were not significant (all $ps > 0.1$). Bonferroni-corrected paired comparison revealed that at the P3 electrode, a significantly lower alpha response amplitude was found when tracking stimuli in the right VF (95% CI [0.924, 1.219]) compared to the left VF (95% CI [1.022, 1.383]), $t(30) = -3.970$, $p_{\text{adj}} = 0.001$. Other comparisons were not significant (all $ps > 0.1$).

Discussion

Our main observation was a target-eccentricity-dependent reduction in occipital alpha oscillations elicited by the covert tracking of a stimulus moving in the periphery, and no dependence of alpha reduction on target speed. This result is consistent with the observations that have reported a tight link between the attentional processes involved in covertly tracking and overtly pursuing a moving target (see⁷).

As anticipated in the Introduction, part of the evidence relating pursuit and attention comes from dual-task studies that found processing advantages for the spatial hemifield or the portion of space directly ahead of the target^{9–12}. However, this dual-task advantage might not extend to nonsalient stimuli that move along with the pursuit target^{15,16}. Additionally, evidence from the SSVEP study reported an enhancement of SSVEPs elicited by a flickering stimulus ahead of the pursuit target¹⁷.

Strong evidence for a functional analogy of overt and covert tracking comes from the study by Gregori Grgič and colleagues³², who had observers pursue or covertly track the motion of a target that moved sinusoidally on the horizontal meridian, and subsequently extrapolate the motion of the stimulus after its disappearance. As expected, by tagging the left and right hemifields with stimuli flickering at different frequencies, they were able to dynamically decode the position of gaze as observers overtly pursued the target. Crucially, they were also able to decode the position of the focus of attention during covert tracking and the position of the imagined target during motion extrapolation.

Our results are in line with those of Gregori Grgič and colleagues³², in that they confirm that covertly tracking a stimulus that moves on one side of the peripheral visual field is associated with an imbalance of neural activity in visual areas, in their case revealed by the modulation of oscillations evoked by the external flickering stimulus, in the present study revealed by the modulation of endogenous brain oscillations. In particular, we found that the alpha activity was reduced when the observers covertly pursued a stimulus moving further in the periphery, and more so in the hemisphere contralateral to the hemifield where the stimulus was moving.

Generally speaking, if covertly tracking a moving target, like overtly pursuing it, requires the involvement of attention, it is expected that this should be mirrored by a suppression of occipital alpha activity, particularly in the hemisphere contralateral to the hemifield where the attended stimulus is located. The exact nature of the relationship between attentional orienting and occipital alpha activity is still debated, especially regarding the extent to which alpha reduction represents a neural correlate of perceptual enhancement at the focus of attention and to what extent increased alpha oscillations represent a correlate of suppression for the portions of space that are ignored³³. It is indeed possible that both target enhancement and distractor suppression are mirrored in localized alpha activity independently and with different temporal dynamics, at least in the case of attention directed to stimuli represented in working memory³⁴. Furthermore, it is not clear whether alpha oscillations directly represent a correlate of the neural mechanism responsible for sensory gating in visual areas. In fact, dissociable effects of attention on Steady State Visual Evoked Potentials (SSVEPs) and alpha EEG oscillations seem to suggest that the latter is rather related to post-perceptual processes³⁵. There is evidence that when attention is allocated to one hemifield as a consequence of both endogenous and exogenous cues, and in the absence of distractors, alpha activity is reduced over the contralateral occipital cortex³⁶. It is also possible to recover the location that is being attended to by observers based on the topography of alpha oscillations (e.g.^{37–42}). In particular, Bahramisharif and colleagues⁴³ demonstrated that alpha could be used to continuously decode the position of the focus of attention as observers covertly tracked a moving (rotating) stimulus.

Dunkley and colleagues²⁵ also reported no effect of stimulus speed and stimulus eccentricity on alpha power during smooth pursuit. It should be noted that since the retinotopic position of the target during smooth pursuit is on average not lateralized and foveal, one would not necessarily expect eccentricity to have a major effect on the amplitude and lateralization of alpha reduction, as is the case during covert tracking. Note that caution is required when comparing our results with previous studies, because we did not perform a baseline-corrected analysis of alpha responses due to the limited 500 ms fixation period.

Our data did not show a specific effect of target speed on alpha reduction. This might appear inconsistent with the results of studies suggesting stronger involvement of attention in the pursuit of targets moving at higher speeds. In particular, Van Donkelaar & Drew¹⁰ reported an increase in detection response times as pursuit speed increased, a result replicated by Seya and Mori¹¹, whose data showed a marked worsening of performance between 5 and 10 °/s. Increased pursuit speeds are also associated with the level of activation in different areas within the oculomotor network, some of which might be involved in the attentional control of smooth pursuit^{44,45}. However, this may be less pronounced in steady-state pursuit of a continuously moving target, where speed-dependent activations are concentrated in the visual cortex^{46,47}. In any case, overt and covert tracking face the visual system with a partially different challenge. One possibility is related to the fact that overt pursuit tasks explicitly stress the need to precisely direct gaze on the moving target, especially when it is a relatively small moving spot⁴⁸. Although steady-state pursuit gain is close to one and largely independent of target speed in the range below 20 °/s^{49–51}, higher target speed will produce larger fixation errors, and thus require closer oculomotor control for foveating the target. On the other side, especially in a task like ours that required detecting a temporal gap in the moving target, very precise allocation of covert spatial attention to the target might be less relevant, meaning that target-speed-dependent attentional requirements might be reduced. It is an open question whether a task that would entail higher spatial resolution, for instance detecting misalignment in a stimulus flashed at the moving target location, would cause the attentional requirements and possibly a reduction in alpha amplitude to be dependent on target speed for covert tracking. It should be noted again that pursuit speed did not affect alpha suppression in the study by Dunkley and colleagues²⁵, meaning that the link between the attentional requirements of the task and alpha amplitude is not straightforward.

Dunkley and colleagues²⁵ did observe an effect of pursuit speed on beta activities in the middle temporal cortex using MEG recordings. To allow comparability, we analyzed the beta activities in our EEGs within the 15–25 Hz range, as used by Dunkley and colleagues²⁵. However, we did not observe clear peak responses within this beta range (Figure S5a). Furthermore, no target speed-dependent reduction of beta amplitude was evident (Figure S5). This lack of beta reduction could potentially stem from the different neural mechanisms engaged by smooth pursuit and covert tracking tasks, especially in areas like MT+^{52,53}. It is also important to consider the limitations of EEG, which, compared to MEG as used by Dunkley and colleagues²⁵, has lower spatial resolution and may not be sensitive enough to detect oscillatory activity in specific regions like MT+⁵⁴.

Notice that the behavioral data from our study are inconclusive with regard to the attentional requirements of the task in the different conditions. First of all, there was no unequivocal evidence of a dependence of detection accuracy on either target speed or eccentricity. Performance was selectively worse when the stimulus moved at 6°/s up to a 5° eccentricity, not when the stimulus was in general slow or fast, and not in general when it moved at short eccentricity. The only peculiar aspect of that particular condition is that it was the condition where the

stimulus changed direction most often. It is thus possible that the ability to detect the gaps in the stimulus was affected mainly by direction changes, rather than speed or eccentricity. What can, however, be inferred from our results is that the gap detection task forced observers to track the target covertly and that processing the detected gap required cognitive effort, as evidenced by alpha power being reduced when two gaps were presented.

Although detection accuracy was not affected by stimulus eccentricity, we did find a larger reduction of alpha power when the stimulus moved further in the periphery. This might indicate that the attentional requirements of the task increased because the sensory input was degraded in the periphery. However, we must be cautious when interpreting our result solely as an index of covert attentional orienting. Note that our paradigm involved observers fixating either left or right of the screen in trials where the target moved in the right or left hemifield, respectively. This means that the direction in which attention is covertly allocated is confounded with the direction in which gaze is overtly directed, in other words, there was a misalignment between the axis of the gaze vector and the craniotopic axis. It is hard to predict the effects of this misalignment independently of the lateralized allocation of attention. In principle, if at least a subset of attentional resources is attached to head orientation, this could have enhanced the imbalance produced by attentional tracking in our experiment, given that the head axis was congruent with the hemifield where the target moved. However, attention has so far been linked to the preparation of head movements^{55,56}, and it is not clear whether a link between attention and head direction would exist when the eyes and head are tonically misaligned. Moreover, since our experiment was not performed in darkness, it is possible that the change in the overall retinal stimulation based on the fixated location might have driven a hemispheric imbalance in alpha activity in a purely bottom-up fashion.

One consequence of having observers fixate at different locations in the case of targets moving in the left and right hemifield is that it prevented us from evaluating the slow ERPs described as a correlate of covert tracking^{28,57}. In our data, eye-position-related signals would be confounded with signals related to the focus of attention. This is not a major limitation, as the challenge of handling eye-dipole related artifacts from brain activity is even more pronounced when the eyes actually move during smooth pursuit. Therefore, slow ERPs are not the ideal testbed for comparing the attentional processes involved in smooth pursuit and covert tracking.

There is a final limitation in our paradigm that needs to be taken into account. Having stimuli move further in the periphery means that possibly more attention is needed to extract visual information, thus explaining the need for additional alpha reduction. On the other side, it is possible that allocating attention to different parts of the visual field modulates alpha activity in different parts of the visual cortex (e.g.⁴⁰), which could be transmitted more or less efficiently to the scalp sites that we used for assessing alpha activity.

Finally, our results revealed an additional correlate of the increased attentional requirements of covertly pursuing a peripheral target in the form of fixational eye movements. Starting from the seminal studies in the early 2000s^{58,59}, growing evidence has linked covert shifting of spatial attention to the preferential direction of microsaccades (see⁶⁰ for a recent review). There is also evidence that, at least in the case of orienting towards representations stored in working memory, spatial attention correlates with both microsaccade direction and alpha activity lateralization. The link between microsaccades and alpha activity, however, is not a necessary one, given that alpha modulation is present in trials without microsaccades as well⁶¹. Microsaccades are, however, probably not the most reliable index of covert attention orienting in a paradigm like ours, where observers had to track a peripheral stimulus over longer time periods. Recent findings seem to indicate that when observers repeatedly focus attention on a given peripheral location, the link between attention and microsaccade direction ceases to exist⁶², and it has been suggested that this result links microsaccades specifically to shifts of spatial attention, rather than to sustained attention⁶³. Instead, we concentrated on gaze position bias, which has been recognized before as a fixational index of attention orienting during covert tracking²⁸. At least in the case where observers were fixating on the left and attending to the right, there appeared to be a tendency to fixate towards the side where the stimulus was located. It must be noted however that our paradigm differs from the one of Makin and colleagues²⁸, in that we had stimuli moving only within one hemifield during each trial, and, perhaps more importantly, we had observers divert their gaze to the opposite side of the moving stimulus, meaning that any tendency against eccentric fixation would have produced a fixational bias correlated with the horizontal position of the target.

Our findings open new possibilities for testing the ability of observers to dynamically allocate attention, particularly considering possible individual differences. A study highly relevant in this context is the work by Kwon and colleagues⁶⁴, which focused on resource allocation and individual differences in working memory capacity. In their study, observers performed a dual task involving smooth pursuit of a target that moved predictively or randomly, combined with a demanding cognitive task (word recall). The main result indicated a reduction in parietal alpha activity only for individuals with low working memory capacity, and this reduction occurred selectively in the case of predictive smooth pursuit. In principle, one might have expected that pursuing a predictable target should have required less attention, resulting in less alpha desynchronization. However, in a dual-task context, alpha activity can be influenced by both tasks. In this specific case, the reduced demands of the oculomotor task might have freed up resources that low-WM observers could then allocate to the word recall task, potentially being the main reason for alpha desynchronization. It remains an open question whether the target-eccentricity-dependent alpha desynchronization observed in our study is a universal phenomenon. That is, it remains to be seen whether it would also occur if the covert tracking task were coupled with a different cognitive task and whether this effect would apply to all observers, regardless of individual differences in working memory capacity.

Data availability

Data supporting these findings are available at <https://osf.io/bejt6/>.

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Author contributions

X.X. conducted the experiments. Q.S. analyzed the data and prepared the figures with the support from J.C. and M.V. Q.S., J.C. and M.V. co-wrote the manuscript and reviewed the final version of the manuscript.

Declarations

Competing interests

The authors declare no competing interests.

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