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Elements of exogenous attentional cueing preserved during optokinetic motion of the visual scene

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Abstract

Navigating through our environment raises challenges for perception by generating salient background visual motion and eliciting prominent eye movements to stabilise the retinal image. It remains unclear if exogenous spatial attentional orienting is possible during background motion and the eye movements it causes and whether this compromises the underlying neural processing. To test this, we combined exogenous orienting, visual scene motion, and electroencephalography (EEG). A total of 26 participants viewed a background of moving black and grey bars (optokinetic stimulation). We tested for effects of non-spatially predictive peripheral cueing on visual motion discrimination of a target dot, presented either at the same (valid) or opposite (invalid) location as the preceding cue. Valid cueing decreased reaction times not only when participants kept their gaze fixed on a central point (fixation blocks) but also even when there was no fixation point, so that participants performed intensive, repetitive tracking eye movements (eye movement blocks). Overall, manual response reaction times were slower during eye movements. Cueing also produced reliable effects on neural activity on either block, including within the first 120 ms of neural processing of the target. The key pattern with larger event-related potential (ERP) amplitudes on invalid versus valid trials showed that the neural substrate of exogenous cueing was highly similar during eye movements or fixation. Exogenous peripheral cueing

Abbreviations: EEG, electroencephalogram; ERP, event-related potential; FEF, frontal eye field; ICA, independent component analysis; OKN, optokinetic nystagmus; OKS, optokinetic stimulation; QPs, quick phases; ROI, region of interest; RT, reaction time; SPV, slow phase velocity; TMS, transcranial magnetic stimulation.

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and its neural correlates are robust against distraction from the moving visual scene, important for perceptual cognition during navigation.

KEYWORDS

ERP, exogenous attention, optokinetic nystagmus, slow eye movements, visual perception

1 | INTRODUCTION

It can be crucial to react to unexpected events in our environment. One robust and common tool for exploring this in the lab uses an exogenous covert spatial cueing task. Centrally fixating participants are better at responding to a target stimulus at a given peripheral location if a salient enough cue stimulus is presented in the right place and with the right timing just beforehand (Carrasco, 2011; Jonides, 1981; Posner et al., 1980). This study addresses two sets of apparently wildly diverging findings within the field of exogenous cueing, regarding under which situations cues will trigger the focussing of cognitive resources to guide behaviour. These conflicting findings arise when studies go beyond using fixation on simple plain backgrounds for their experiments, instead using richer, or even moving visual scenes, such as what are seen during locomotion and navigation.

On the one hand are studies demonstrating either behavioural or neural signatures of attentional control during complex scenes. Attentional capture in some situations is strikingly unaffected by other visual stimuli or by eye movements (Spence, 2010). Complex information from scenes, and navigating through them, guide selection of perception and responses, and this is reflected in current psychological models (Wolfe, 2021) and neural frameworks (Peelen & Kastner, 2014) of visual search. Attentional networks are activated by complex computer-generated scenes in which stimuli such as people appear unexpectedly, with an activation pattern correlating with the extent to which participants would normally look directly at such salient cues (Nardo et al., 2011), and this can be extended to audiovisual environments (Nardo et al., 2014).

On the other hand is the evidence that cueing effects depend dramatically on what people are doing at the time. If attentional resources are called to the centre of the display, for example when participants monitor a rapidly changing central visual stimulus, then exogenous spatial cues no longer affect behaviour: even if the distracting stimuli are task irrelevant and require no response, do not comprise any sudden onsets (Kellie & Shapiro, 2004) and bear only low perceptual load (Santangelo et al., 2007, 2008). Distraction during visual

search has been the topic of a raging debate for decades (Luck et al., 2021).

We were prompted by these two different bodies of evidence to wonder whether exogenous cueing effects might still occur during a special case of salient background motion. Optokinetic stimulation (OKS) comprises moving scenes such as large high-contrast drifting gratings moving to one side. OKS is used experimentally to isolate one aspect of what the visual system is confronted with when either the agent moves linearly to the side in space or a large object passes by. We reasoned that it would be advantageous for an agent if exogenous cues could still guide behaviour even if the background environment was moving. Therefore, in one half of our experiment, participants were then presented with exogenous cues and subsequent targets while fixating on a point presented against an OKS background. In a previous study with OKS and dot targets (but without cueing), the pattern of findings could be explained if exogenous cueing were possible during OKS (Mastropasqua et al., 2020). Single pulses of transcranial magnetic stimulation (TMS) over the frontal eye field (FEF) presented just before target dots improved performance at visual discrimination of those dots, as if FEF TMS was acting as a peripheral cue.

To extend this further, in the other half of the experiment, identical stimuli were presented but without a fixation point. Under these conditions, OKS can trigger continuous, repetitive, slow tracking eye movements, in the direction of the moving visual scene. These are followed by fast resetting eye movements, in the opposite direction. This pattern of eye movements, the optokinetic nystagmus (OKN), eliminates the retinal slip that would distort the visual input (Angelaki & Hess, 2005; Ilg, 1997; Kowler, 2011; Watanabe, 2001). Here we then tested whether exogenous cueing can operate during OKN. The OKN could indirectly impair cueing effects as the eye movement leads to motion of the retinal image of cue and target. This could not only impair discrimination but also reduce the extent to which valid cues and targets are presented in the same retinal spatial location or raise demands on maintaining visual stability. Further, interference might conceivably come from the oculomotor aspect of OKN generation, which, although reflexive, does show some of the properties of voluntary eye

movements, such as modulating the curvature of saccades planned in parallel, or saccadic inhibition (Harrison et al., 2014), consistent with the premotor theory of attention (Rizzolatti et al., 1987) specifying the link between covert and overt orienting (Smith et al., 2012).

Attention can prioritise information processing at multiple stages (Luo & Maunsell, 2019; Nobre & Kastner, 2014) assigning limited resources according to the goal of the individual (Desimone & Duncan, 1995). Even if the behavioural effects of cueing were similar during OKS, or OKN, to that shown previously without either, they could be being supported neurally in fundamentally different ways, that is, at different stages of processing. Event-related potentials (ERPs) over posterior scalp sites suggest that the earliest reliable modulation by spatial cueing occurs at the time of the early P1 component (latency 90–130 ms, (see Hillyard & Anllo-Vento, 1998; Mangun, 1995; Martín-Arévalo et al., 2016 for reviews), and this component is particularly dominated by exogenous attention (e.g. Hopfinger & West, 2006). We exploited the extensively used tool, independent component analysis (ICA), for eye movement artefact removal (Makeig & Onton, 2012), extending it here to OKN, testing with electroencephalography (EEG) whether the neural processing of these cues and targets during OKS with or without OKN movements was completely different from that occurring in previous studies and to each other or whether they were characterised by a similar pattern.

In summary, it remains unknown whether the exogenous cueing effects on behaviour and the ERP, previously demonstrated during fixation, can occur during dynamic visual stimulation such as OKS or during performance of the OKN. We hypothesised the existence of an exogenous cueing effect during OKS, reflected in the modulation of behaviour and the P1 ERP component, as reported in previous studies during fixation. An alternative possibility would have been that is strikingly harder or even impossible to demonstrate exogenous cueing effects during OKS or OKN.

2 | MATERIALS AND METHODS

2.1 | Participant screening

Thirty healthy volunteers (mean age 28 ± 6 years, 19 female) were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971) and gave informed consent for a protocol approved by the LMU Munich Medical Faculty Ethics Committee. Participants had no prior history of neurological or psychiatric disorders, had normal or corrected-to-normal vision and were

compensated either with 9 euros per hour or course credit.

One participant was excluded due to performing below chance and 3 due to low quality EEG data (fewer than 30 trials per condition), leaving 26 participants.

2.2 | Exogenous attention during OKN

Stimuli were presented at 40 cm on an LCD monitor (1680 × 1050 pixel resolution, refresh rate 60 Hz). OKS background was 48° visual angle (VA) wide and 15° VA tall and composed of black (RGB: 0, 0, 0) and grey (RGB: 105, 105, 105) bars moving leftward at a constant speed of 33°/s (bar width 2.3 cm/3.3° VA). Targets, white dots (1.6-cm diameter, RGB: 255, 255, 255), were presented for 100 ms at 15° VA eccentricity in the upper or lower hemifield. Dots moved from the midline either leftward, rightward, or were still, with equal probability. Using moving rather than static dots as targets meant that some retinal motion was present in both fixation and eye movement blocks, reducing overall differences between them. Dot location (upper vs. lower), direction and speed (between 1°/s and 32°/s) were all randomized. On two thirds of trials, exogenous attentional cues were presented 200 ms before target onset for 33 ms on the vertical midline either in the upper or lower field. Importantly, these cues were presented equally likely (50%) at either the location of the upcoming target ('valid trial') or at the opposite location ('invalid trial') and therefore were non-informative as to trial type. Cues were only presented on two thirds of trials to maximise salience. The stimulus onset asynchrony (SOA) between cue and target was kept fixed at 200 ms (near to the peak facilitation for peripheral cued location, see Müller & Rabbitt, 1989) to maximise the chance of demonstrating attentional orienting. The task consisted of discriminating as quickly and accurately as possible whether the dots were leftward moving, still or rightward moving, responding with the right index, third or fourth finger, respectively. Targets were moving at different speeds and in different directions so that retinal motion was present on both fixation and eye movement blocks and allowing comparison with previous work (see Mastropasqua et al., 2020). In order to investigate the effect of exogenous attentional cues on the visual perceptual consequences of reflexive eye movements, perceptual judgements were recorded during visually driven eye movement and during fixation on a moving visual scene. This design allowed to test for effects of attention with and without eye movements under comparable visual stimulation. On eye movement blocks, participants were instructed to look passively at the middle of the screen. On fixation blocks, participants

fixated a central cross (superimposed on the moving background) consisting of a black cross drawn inside a grey circle (RGB: 128, 128, 128). The presentation order of the 15 eye movement and 15 fixation blocks was randomized; in each block, 36 targets were equally distributed across location and cue type (no cue, valid cue and invalid cue; see Figure 1). Eyetracking (see below) was calibrated (10 s) before each block. The effect of exogenous attentional cueing was tested on reaction time (RT), accuracy and EEG data using a three-way analysis of variance (ANOVA) with target direction (left vs. still vs. right), cue type (valid vs. invalid) and block (Fix vs. OKN) as within-subjects factors.

2.3 | EEG acquisition and pre-processing

EEG was recorded continuously at 1000 Hz (BrainAmp DC amplifier, Brain Products, Munich, Germany) from

59 scalp sites using active equidistant electrodes (M72 layout, EASYCAP, Herrsching, Germany). No online filters were applied. Additional electrodes were used for ground (between positions 31 and 1, respectively, approximating FPz and FCz in the 10-10 system); reference (ear lobes, active reference on the left) vEOG and hEOG were recorded from two electrodes placed below or lateral to each eye, respectively. Impedance was kept below 10 K Ω . EEG analysis used the EEGLAB Toolbox (Delorme & Makeig, 2004). EEG was re-referenced offline to the average of the left and right ear lobes and filtered (notch 50-Hz filter and a Butterworth zero phase filter, bandpass 0.1 to 40 Hz (12 dB/octave) (Luck, 2014). Bad channels (mean 6 per participant) were interpolated for figures using a topographic interpolation (spherical spline, order 4). Interpolated channels were not included in the later region of interest (ROI) analysis. EEG was segmented to 1000 ms before and 2000 ms after target onset. Baseline correction used 1000 ms before target onset. Fast-ICA

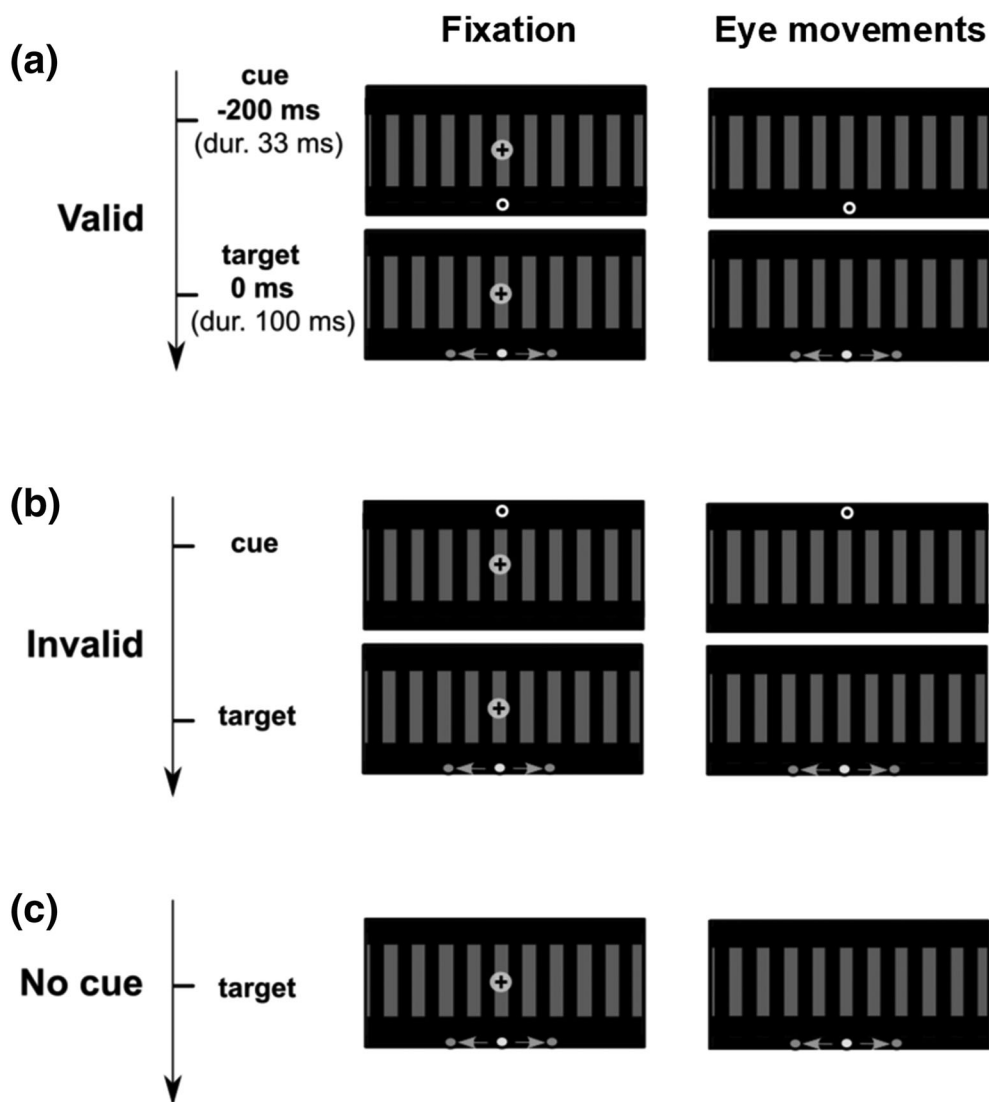


FIGURE 1 Exogenous cueing task during optokinetic stimulation. During both blocks, fixation (first column) and eye movements (second column), bars were moving to the left, and visual target stimuli (dots) were presented in either the upper or lower part of the screen. Targets moved at random speed (between 1°/s and 32°/s) left, right or were still. The inter trial interval (ITI) between target onsets ranged from 2000 to 5000 ms. Cues (hollow circles) were always presented 200 ms before targets (filled dots, see panels a and b). In the fixation block, an additional central fixation point allowed the participants to fixate and suppress the eye movements

(Hyvärinen & Oja, 2000) was performed to remove the eye movement component from the EEG signal. Eye movements components were identified by visual inspection of topographies: Due to the specific shape of those reflexive eye movements, a clear OKN component could be found in each participant (see Figure 2).

2.4 | Event-related potentials

Data were segmented from 100 ms before cue onset until 600 ms after (which was also 400 ms after target onset) and baseline corrected to 100 ms before cue onset. If the peak-to-peak EEG signal exceeded $\pm 100 \mu\text{V}$ in any channel or if the vertical and horizontal EOGs exceeded $\pm 80 \mu\text{V}$, epochs were rejected (Sawaki et al., 2015). A minimum number of 30 trials per condition was established as the criterion to maintain data quality. Upper and lower visual field stimuli were collapsed. The initial P1 in response to a visual stimulus is modulated by cognition: changes in the amount of attention to stimuli are reflected in the amplitude modulation of this early brain response (Coles & Rugg, 1995; Luck, 2014). To assess the brain response to valid trials during OKS, the recording sites and the time bin showing the largest P1

component amplitude were selected in the evoked response to still targets during OKS without eye movements. This was then used for two analyses. First, valid and invalid trials were compared during fixation. Note that, looking ahead, the P1 amplitude on invalid trials was even larger, and so the differences between valid and invalid trials cannot be attributed purely to selecting electrodes with large effects in forming the ROI on valid trials and subsequent regression to the mean. Second, the ROI on the fixation dataset was then used to test for effects on the fully orthogonal OKN data set. This approach minimises risks of finding false positives in large rich datasets such as can occur in EEG studies of visual cognition (Luck & Gaspelin, 2017). A group of channels showing the largest amplitude following the target onset on valid still trials, during the fixation block (80- to 120-ms post-target), was selected. In this way, the attentional cueing effect was first explored on the ERP waveforms elicited by the target without reflexive eye movements but during the same visual stimulation as in the eye movement condition. A central posterior-left ROI (positions 4, 11, 12, 13, 24, 25, 39) corresponding approximately to CPz, P2, Pz, P1, POz, PO3, PO7 was formed; two electrodes (13 and 24) were not included in the analysis because they had been interpolated previously.

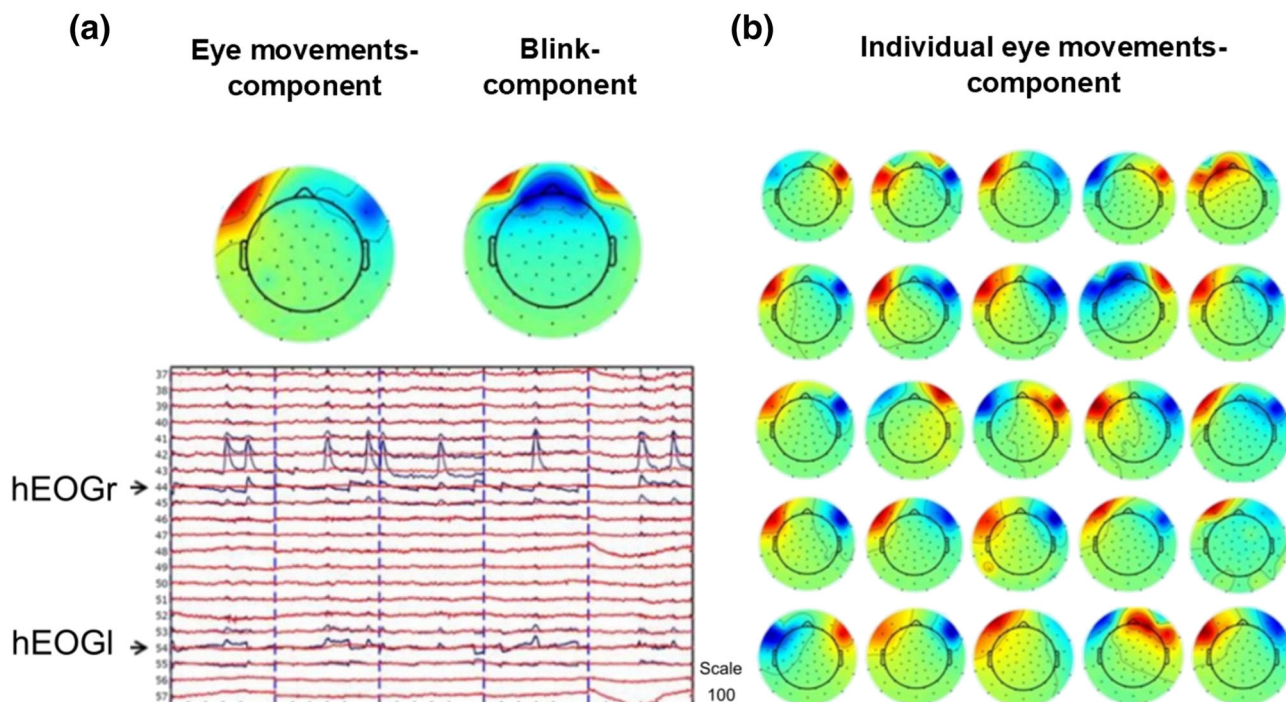


FIGURE 2 (a): Topographies of eye movement (upper left) and blink (upper right) components identified by independent component analysis (ICA), in one representative participant. Lower panel: examples of raw data showing the electroencephalogram (EEG) signal before (blue) and after (red) the components detected were removed. (b) Map of individual eye movement components in the other 25 participants showing the consistency of this component in the EEG signal

2.5 | Eye movement recording

Head-mounted video-oculography of the left eye sampled at 220 Hz (EyeSeeCam System, EyeSeeTec, Munich, Germany). Eye movements were recorded during eye movement blocks, and during fixation, only eye movement data during eye movement block was analysed. After blinks (when the signal is lost) were removed, quick phases (QPs) of the eye movements were defined as eye velocity greater than $10^\circ/\text{s}$ with absolute acceleration greater than $300^\circ/\text{s}^2$. QP start and end point were defined from the point where the eye velocity peaked, to the point where the eye velocity neared $0^\circ/\text{s}$. This allowed identifying the QPs in the direction of the OKS. The data were segmented from 300 ms before cue onset to 300 ms post-target onset in order to investigate whether the exogenous cue affected slow phase velocity (SPV). One participant was not included in the analysis due to a technical fault with eyetracking, leaving 25.

3 | RESULTS

3.1 | Behavioural results

3.1.1 | Reaction time

Figure 3 shows faster RTs on valid trials than invalid trials on both fixation and eye movement blocks, and this was supported by statistical testing. Attentional cueing modulated performance at the visual motion discrimination task, even during continuous eye movements (main effect of cue: $F(1,25) = 52.4$, $P < 0.0001$, $\eta^2p = 0.68$). This effect of exogenous attention on RTs was independent of target direction and block (lack of interactions between target and cue: $F(2,50) = 0.06$, $P = 0.89$, $\eta^2p = 0.002$; between cue and block: $F(1,50) = 1.02$, $P = 0.32$, $\eta^2p = 0.39$) and between all three factors: ($F(2,50) = 2.49$, $P = 0.1$, $\eta^2p = 0.91$). As the attentional cueing effect did not differ between dot motion directions, target directions (left, still, right) were collapsed. This attentional cueing effect was also found within either block separately during fixation ($t(25) = -6.05$, $P < 0.0001$) and during eye movements ($t(25) = -6.2$, $P < 0.0001$; Figure 3). Hence, cueing effects on motion discrimination RT were not found to differ between blocks where participants were moving their eyes or fixating on the moving visual scene. The mean benefit of valid attentional cueing was 24 and 28 ms for fixation and OKN, respectively. RTs during eye movements were generally slower (main effect of block ($F(1,25) = 57.92$, $P < 0.0001$, $\eta^2p = 0.7$)). The comparison of the proportion of change (valid/invalid) between fixation and eye movements showed no

significant difference ($t(25) = 0.409$, $P = 0.686$). There is decisive evidence in favour of the absence of this difference (scaled JZS BF = 4.47, Rouder et al., 2009), supporting the null hypothesis that despite the faster RT on fixation trials, the effect of cue is the same between the two blocks.

3.1.2 | Accuracy

Attention did not affect accuracy, nor were there any interactions between cue and block or target direction (all F s ≤ 2.3 , all P s > 0.1 , η^2p values ≤ 0.09), but a main effect of target direction ($F(2,50) = 51.6$, $P < 0.0001$, $\eta^2p = 0.67$) and block ($F(1,25) = 68.4$, $P < 0.0001$, $\eta^2p = 0.73$) were found and their interaction ($F(2,50) = 39.2$, $P < 0.0001$, $\eta^2p = 0.61$). The analysis on the data combined by target direction revealed no interaction between cue and block ($F(1,25) = 0.2$, $P = 0.67$, $\eta^2p = 0.08$). Performance was better during fixation compared with eye movements ($t(25) = 8.3$, $P < 0.0001$). More correct responses were recorded during valid fixation (84%) and invalid fixation (84%) than during valid eye movements (71%) and invalid eye movements trials (71%), with a similar level of accuracy registered following valid and invalid cues in both blocks (see Figure 3). These error rates (16% and 29%, respectively, for fixation and eye movements) are higher than found in many studies but similar to those from some exogenous cueing tasks using multisensory contexts or where the cue was made difficult to detect (e.g. Fuller et al., 2009; Ho et al., 2005; Rangelov et al., 2015; Santangelo et al., 2008).

An additional analysis included the no-cue condition. The 2 (blocks, 'fixation' vs. 'eye movements') \times 3 (cue type, 'no' vs. 'val' vs. 'inv') ANOVA did not reveal any interactions between the two factors ($F(2,50) = 1.184$, $P = 0.31$, $\eta^2p = 0.05$; $F(2,50) = 1.22$, $P = 0.31$, $\eta^2p = 0.05$, respectively, for RT and accuracy). Differences between the no cue and the other conditions (all P values < 0.02) are likely to reflect the alerting, arousal and temporal expectation arising from having any cue present at all.

3.2 | Event-related potentials

A target-locked ERP analysis investigated whether a similar attentional cueing effect, that is, on both fixation and eye movement blocks, was found on neural activity and if this was similar in the presence and absence of eye movements. Based on the ROI, showing a larger amplitude in the evoked response to valid still trials during fixation (see Figure 4), the signal was extracted from the

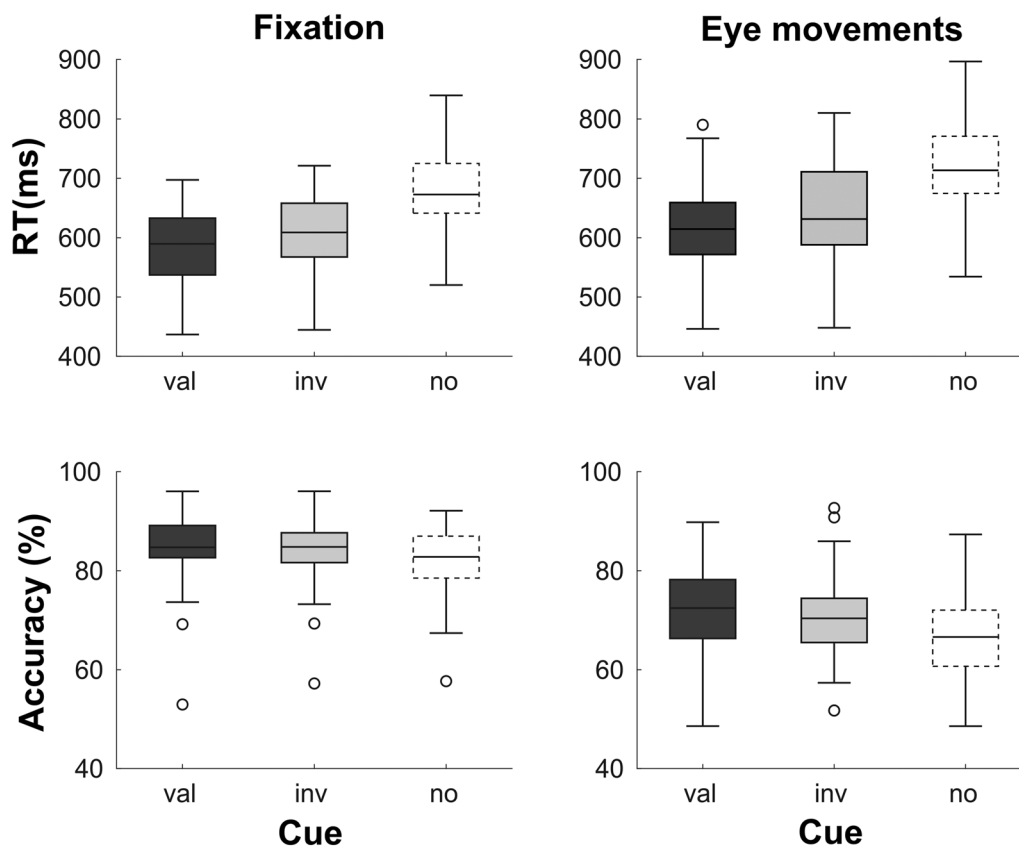


FIGURE 3 Boxplot of reaction time (RT) data (upper panel) and accuracy data (lower panel): on the left are displayed the behavioural results during fixation and on the right during eye movements. On the x-axis are plotted the data per cue condition, valid and invalid; in addition is showed with the dashed box plot the no-cue condition. Exogenous attentional cueing affects RTs during fixation and eye movements. No effect was found on accuracy data, for either block

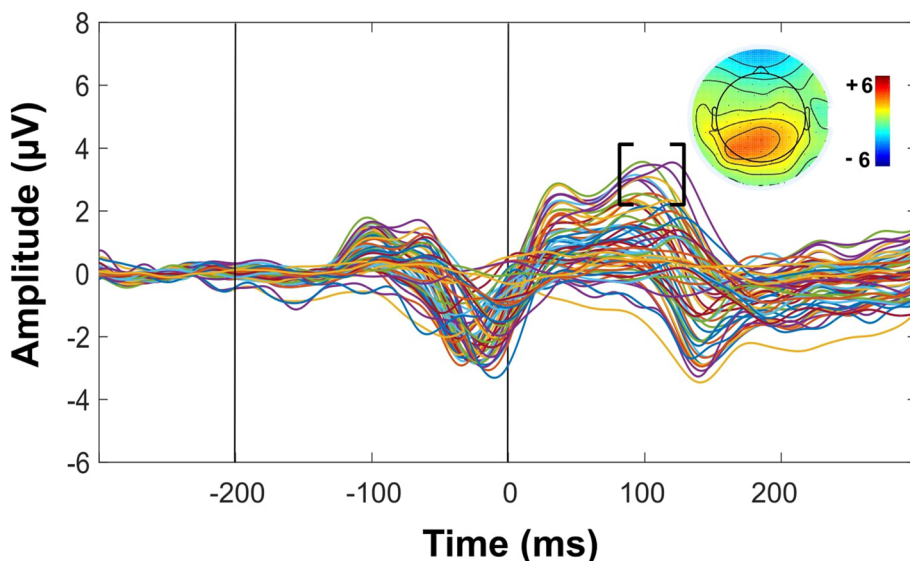


FIGURE 4 Butterfly plot of grand average event-related potentials (ERPs) from the central posterior-left ROI evoked on valid still fixation trials. Cue onset at -200 ms and target onset at 0 ms. Channels presenting the maximal amplitude are indicated with black brackets, 80- to 120-ms post-target. The insert shows the scalp distribution

same electrodes at the 80- to 120-ms time bin in each condition and block. The neural activity showed the same pattern as the behavioural results: no interaction between cue, block and target direction (all $F_s \leq 2.2$, all $P_s > 0.09$,

$\eta^2 p$ values ≤ 0.09). Once we verified that the exogenous cueing effect was not dependent on visual motion direction, we collapsed the target directions and tested in a two-way within-subjects ANOVA. A main effect of cue

was found ($F(1,25) = 9.73$, $P = 0.005$, $\eta^2p = 0.28$) and importantly no main effect of block ($F(1,25) = 1.08$, $P = 0.31$, $\eta^2p = 0.41$) nor the interaction between the two factors ($F(1,25) = 0.69$, $P = 0.8$, $\eta^2p = 0.003$). Significant differences between valid and invalid trials were found within each block ($t(25) = -2.74$, $P = 0.01$ and $t(25) = -2.81$, $P = 0.01$, respectively, for fixation and eye movements), where invalid targets elicited a larger amplitude than the validly cued targets. Highly similar waveforms and effects were observed for fixation and eye

movement blocks (see Figure 5). The difference waveform between valid and invalid trials in each block is shown in Figure 6.

3.3 | Eye movement SPV

Exogenous attentional cueing did not affect the oculomotor response during eye movements. The average SPV was calculated for valid and invalid trials in two

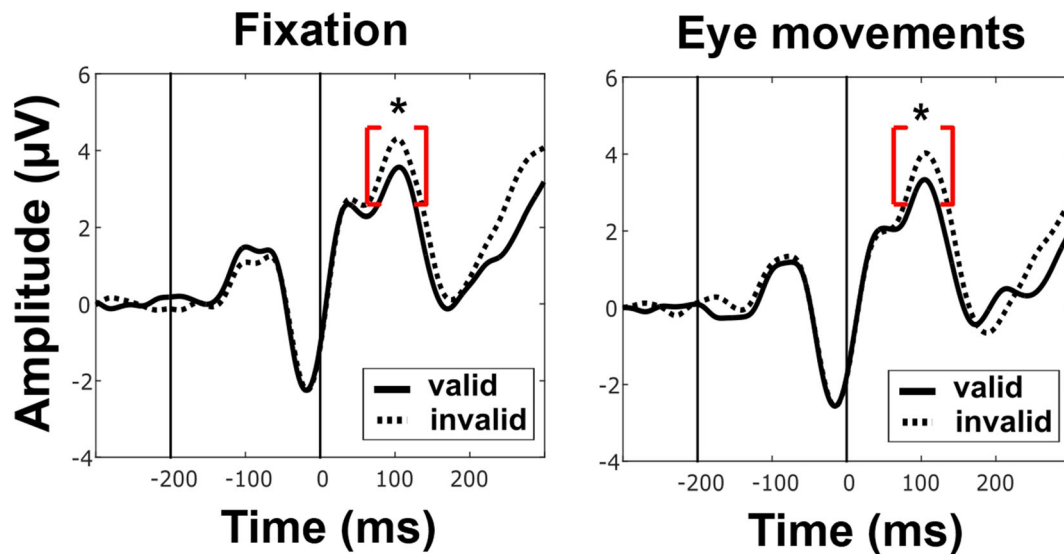


FIGURE 5 Event-related potentials (ERPs) from the central posterior-left ROI. Exogenous attention cueing affects the ERP during both fixation (left panel) and during eye movements (right panel). Targets were presented at time zero; valid and invalid targets were preceded by cues at 200 ms before target onset

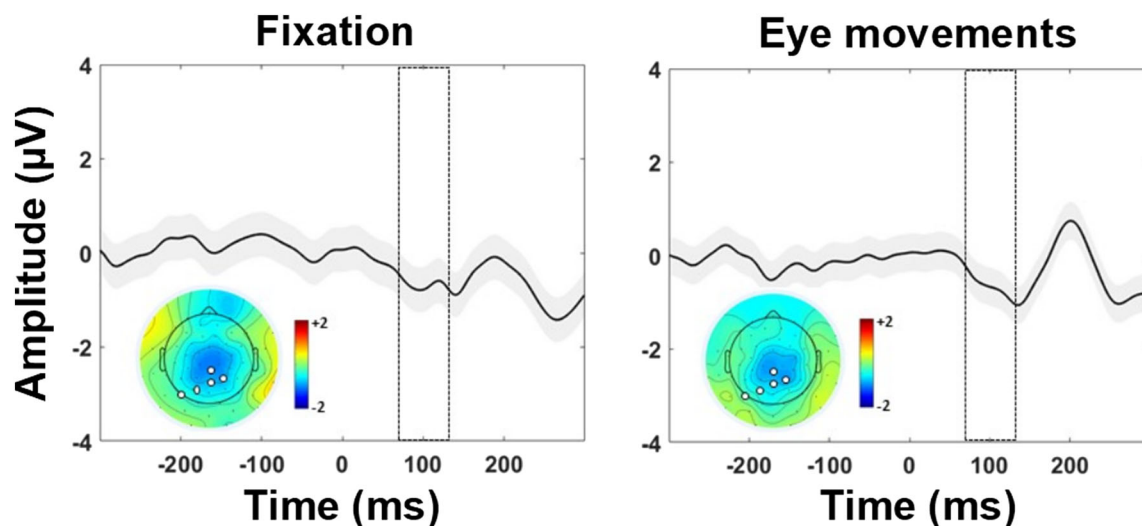


FIGURE 6 Valid versus invalid wave differences and SD (shadow) for fixation (left panel) and eye movements (right panel), in the central posterior-left region of interest (ROI). Targets were presented at time 0, and cues appeared 200 ms earlier. Time bin (80 to 120 ms) selected for the analysis is indicated with dashed-black rectangle; topographies show the distribution over the scalp of valid minus invalid differences. Small white circles indicate the electrodes included in the ROI

segments, one preceding the cue onset and one following the target onset; before cue onset, the same eye velocity, $8.5^\circ/\text{s}$, was registered in both attentional conditions (valid and invalid); after target onset the SPV remained similar, $8.1^\circ/\text{s}$ and $7.8^\circ/\text{s}$, respectively, for valid and invalid. Post-hoc paired comparisons did not find any significant difference between the SPV before cue and after target in each attentional condition ($t(24) = 0.91$, $P = 0.37$ and $t(24) = 2.05$, $P > 0.05$, for valid and trials). We derived the SPV differences between a 300-ms period after (post) target onset and a 300-ms period before (pre) cue onset. As observed at the behavioural and neural level, eye velocities did not differ between target directions ($F(2,48) = 0.81$, $P = 0.43$, $\eta^2 p = 0.03$). No interaction between target direction (left vs. still vs. right) and cue (valid vs. invalid) was found ($F[2,48] = 0.2$, $P = 0.81$, $\eta^2 p = 0.08$), and so as before target direction was collapsed. There was no effect on the ongoing eye movement velocity after either valid or invalid targets (all P s > 0.05). The effect of exogenous attentional cueing was not found in eye movement data; there was no significant difference between valid and invalid trials ($t(24) = -0.32$, $P = 0.75$).

4 | DISCUSSION

In this study, we tested whether exogenous cueing can occur during OKS. Peripheral flashed cues affected participants' performance even while they were viewing optokinetic stimuli. This cueing effect was evident as faster RTs, both when participants were following the moving visual scene with their eyes and when maintaining fixation. A highly similar pattern of neural modulation by the cues was present on both blocks, again independently of eye movements. These results demonstrate that exogenous cueing can occur during OKS, as has been reported in previous studies during fixation with blank backgrounds, and extend previous studies of exogenous attention during dynamic environments.

4.1 | Exogenous spatial cueing affected RTs

The facilitatory behavioural effect of valid exogenous cueing to peripheral stimuli has been widely reported, usually during fixation with a blank background (Carrasco, 2011; Müller & Rabbitt, 1989; Posner & Cohen, 1984). Exogenous attention affects performance although cues are usually uninformative, and its effect on performance does not scale with cue validity (Carrasco, 2018; Giordano et al., 2009; Kinchla, 1980;

Mangun & Hillyard, 1990; Sperling & Melchner, 1978; Yantis & Jonides, 1984).

The experimental design ensured that any spatial cueing effects reflect specifically exogenous and not endogenous orienting (Carrasco, 2011). Firstly, the SOA between cue and target does not give time for endogenous processes to occur (Müller & Rabbitt, 1989). Here we were manipulating involuntary or automatic processes that unlike voluntary attention have only a transient effect (Nakayama & Mackeben, 1989). Secondly, the spatial cues varied in a manner orthogonal to the task, that is, the location of the cue was not relevant to the task people performed (motion discrimination of the target). The cue was presented in either the upper or lower visual field, and this bore no information about whether the target was presented in the same visual field or how it was moving. Thirdly, cue validity was 50%: The probability of the dot target appearing at the valid or invalid location was the same.

Our data also showed that faster RTs followed 'cue' compared with 'no-cue' trials. We speculate that this may have been because the overall presence of a cue (whether valid or invalid) alerted or temporally oriented participants, leading them to engaging more with the optokinetic stimuli.

Exogenous peripheral cueing modulated RTs, but not accuracy, with faster RTs after valid versus invalid cues. Whether cueing effects are occurring at the level of the sensitivity of perceptual encoding processes on the one hand, or on more response-related processes such as affecting decision criteria and/or response bias, is still under debate (Nobre & Kastner, 2014; Souto & Kerzel, 2021). There is also heterogeneity as to whether cueing effects are only referred to as attentional if effects are unambiguously on perceptual encoding or if the term is extended to include response-related processes, and some even suggest abandoning the term 'attention' altogether (Hommel et al., 2019). Some papers synthesise the literature by suggesting that voluntary attention affects perceptual processes, but involuntary attention does not (Prinzmetal, McCool, & Park, 2005; Prinzmetal, Park, & Garrett, 2005). However, some approaches treat both visual selection and decision-making components as part of attentional control, focusing in some cases more on decisional aspects (Krauzlis et al., 2014) or framing these two components by asking whether attentional effects can be dissociated into enhanced sensory processing versus the later biasing of that information to guide decisions (Luo & Maunsell, 2019; Sridharan et al., 2017), including recent studies suggesting exogenous attentional cues operate by both mechanisms (Sagar et al., 2019). According to such an interpretation, attention can affect multiple

stages of processing all the way from perception to response (Nobre & Kastner, 2014).

4.2 | Slower RTs during eye movements

The fast resetting eye movements between slow phases, like saccades, are so fast that visual input during the eye movement is blurred beyond being useful and is even suppressed (Bridgeman, 2011; Bridgeman et al., 1975; Campbell & Wurtz, 1978) precluding attentional orienting. Therefore, the discussion here focusses on slower eye movements, in particular those triggered in previous experiments during optokinetic motion of the background visual scene or in studies where participants track foreground motion with the eyes against a blank background (smooth pursuit).

RTs were slower in eye movement blocks than fixation blocks. The additional retinal motion of the target during eye movement blocks may impair visual discrimination through increasing perceptual load (Lavie, 2010): additionally, acuity is reduced during experimentally or clinically observed nystagmus (e.g. Currie et al., 1993) and OKN disrupts target localisation (Kaminiaz et al., 2007; Tozzi et al., 2007). During OKN, retinal motion could arise after a QP when the eye has jumped to a different location or during the slow phase if the gain is imperfect. OKN is normally considered to be automatic, but given that OKN can in some respects resemble voluntary eye movements (Harrison et al., 2014), it may not yet be possible to entirely rule out that some costs may arise from OKN generation. That said, at the same time that RTs were overall longer in the eye movement blocks, the absolute size of the cueing effect was highly similar with or without eye movements, indicating some independence between the RT costs of the eye movement blocks and the RT effects of the exogenous cues.

4.3 | When do visual stimuli and attention affect eye movements?

In our study, cues did not affect the ongoing eye movements. Previous studies that have shown effects of other stimuli on eye movements, however, used very different designs, and so here we briefly outline the differences between studies which may be responsible.

We recently used a virtually identical task where TMS pulses were presented instead of the cues. In that study, pulses of TMS to the right FEF did slow down SPV (Mastropasqua et al., 2020). TMS also improved task performance and affected the EEG, and both of those effects

depended on the target dot direction. By contrast, in the current study, the cues did not affect eye velocity nor was the cueing effect dependent on target direction. A large network of areas implement visual exogenous cueing (Corbetta et al., 2008; Nobre, 2001) beyond the right FEF, and so the prior Mastropasqua et al. (2020) study may be selectively revealing the causal role of one part of one cortical area in one hemisphere.

Importantly, previous studies showing effects of other stimuli on eye movement speed have used a range of different attentional demands. Attention affects OKN in other experimental settings (Dubois & Collewijn, 1979; Gresty & Halmagyi, 1979; Kanari et al., 2017; Rubinstein & Abel, 2011; Williams et al., 2006). Endogenous covert attention reduces the ability to suppress OKN (Williams et al., 2006). The cueing in the current study was exogenous, not endogenous.

Given the relative lack of studies investigating how visual cues affect OKN SPV, we here expand our survey to smooth pursuit eye movements, which although very different from slow phase nystagmus in many ways are the nearest matching eye movement in times of spatiotemporal profile. Smooth pursuit can be perturbed by different visual backgrounds (Haarmeier & Kammer, 2010; Spering & Gegenfurtner, 2007; Spering & Montagnini, 2011), especially if unpredictable (Kerzel et al., 2010; Schwarz & Ilg, 1999; Suehiro et al., 1999). By contrast, the OKS comprises an extremely regular and predictable background. Studies of attention during smooth pursuit eye movements suggest that task parameters determine whether eye movements are affected (Barnes, 2008). Some early studies showed that it was very difficult to perform a smooth pursuit task while covertly searching for a pre-specified peripheral target (Khurana & Kowler, 1987). A dot field moving in the opposite direction to a target field does not disrupt eye movements (Kowler et al., 1984), and pursuit may (Souto & Kerzel, 2011) or may not (Souto & Kerzel, 2008) be affected by endogenous attentional orienting depending on the task. Endogenous cueing of motion direction shifts the direction of smooth pursuit eye movement when gratings moving in different directions are presented to different eyes (Spering & Carrasco, 2012). Timing is relevant, whereby previous studies designed to test different phases of eye movements dissociated between attentional orienting during initiation (Ferrera & Lisberger, 1995, 1997; Garbutt & Lisberger, 2006; Spering et al., 2006) versus maintenance of smooth pursuit (Kerzel et al., 2008, 2009; Khurana & Kowler, 1987; Lovejoy et al., 2009).

Hence, the absence of any effect on eye movements should be taken as specific to the task parameters used in this study.

4.4 | Effects of attentional cueing on brain activity

The millisecond temporal resolution of EEG provides additional evidence for whether the underlying processing differs between conditions (Coles, 2003), complementing behavioural responses' inherent limitation of necessarily only directly measuring the outcome of perceptual judgements. Accordingly, we also measured the effect of cueing on brain activity with ERPs and found that the key pattern emerging during fixation—larger ERP amplitudes with invalid versus valid cueing at around 100 ms—was also evident even when participants were constantly moving their eyes. We did not find evidence that the most prominent level at which cueing affected neural activity was drastically different when people performed optokinetic eye movements. These neural data are then both consistent with, and complementary to, behavioural evidence that performing eye movements in response to the OKS did not fundamentally abolish the orienting of attention.

Although accuracy differed between fixation and eye movement blocks, there was no neural correlate of this in P1 amplitude. It may be that this block effect (fixation versus eye movements) is independent of the cueing effect (valid versus invalid) and would be evident using a different ERP component, EEG or other measure, outside of the scope of the current study. Some neural dissociation between effects of block and cueing might indeed be expected given that there was also a behavioural dissociation, in that block affected accuracy whereas cueing affected RTs.

In our study, the P1 component was largest on invalid trials. However, the classical effect of peripheral cueing in the literature is quite the opposite—a larger P1 component on valid trials. As has been previously noted in the literature (e.g. Fu et al., 2009), whether peripheral cueing enhances or inhibits the P1 actually varies across studies, depending on SOA and precise stimulus properties. Notably, those earlier classical studies that found larger valid P1 components tended to use minimal backgrounds and simple stimuli, and critically, the cue-target SOA was jittered such that cue and target-related ERP components (such as CNV and P1) could be dissociated (Hillyard & Anllo-Vento, 1998; Mangun, 1995; Martín-Arévalo et al., 2016; Woldorff, 1993). By contrast, studies like the current one that reported larger invalid P1 components used the specific combination of fixed SOAs plus challenging perceptual stimuli that were either hard to detect (Chica et al., 2010) or presented under high perceptual load (e.g. Fu et al., 2009; Tan et al., 2015). Our design used a fixed SOA to reduce the variability in exogenous cueing strength that can arise with variable ISIs that

could have lead to missing any cueing effects (Müller & Rabbitt, 1989). We necessarily used a challenging visual environment for the scientific question at hand. There are at least two potential explanations for why peripheral cueing enhances the ERP on invalid trials if there is a fixed SOA and a perceptually challenging environment. Larger invalid P1s with peripheral cueing under perceptual load have been interpreted as representing feedback whereby visuospatial attention enhances the perceptual salience of unexpected stimuli processed in occipital areas (e.g. Tan et al., 2015). It would be consistent with this to speculate that the optokinetic grating present on all trials in our experiment also provided high perceptual load. In addition though it should be noted that the way that ERP components summate is highly non-linear and that the amplitude of an ERP component cannot be taken to index the simple amount of activation of an area (Luck, 2014). Future work could disentangle SOAs and perceptual load.

Independent component analysis (ICA) is used extensively to remove the artefacts in the signal that arise from movement of the eyes (Delorme et al., 2007; Delorme & Makeig, 2004; Makeig et al., 1996; Makeig & Onton, 2012; Nikolaev et al., 2016) and is used for example in studies of neural processing during eye movements (Chen et al., 2017). ICA is a heuristic algorithm which presents the user with an array of candidate components, from which the user selects one or some to remove from the signal. Single 'eye movement' components were immediately identifiable for each participant which were accountable for the entire artefact, shown here in full as we could not find previous reports of this in the literature (Figure 2). The eye movement component was differentiable from the blink component and was remarkably conserved across participants: One reason for this may be that in comparison with, say, free eye movements, those eye movement dynamics may be relatively regular and stereotyped.

4.5 | Attention and dynamic visual stimulation

The capacity of a stimulus to capture our attention can be massively reduced (Ruz & Lupianez, 2002; Santangelo et al., 2008), for example, by endogenously setting the spatial window of attention (Theeuwes, 1991) or adding load to the perceptual system (Lavie, 2010; Santangelo et al., 2007). This is relevant for applied research such as warning signals during driving (reviewed in Spence & Soto-Faraco, 2020). To increase the ecological validity of attentional research, studies have explored attentional orienting during more complex naturalistic

environments, using eye movements to index spatial attentional orienting, leading, for example, to computing saliency maps of complex images (Itti et al., 1998). The efficacy of events to attract eye movements in a computer-generated virtual environment predicts activation of the FEFs and intraparietal sulcus in the dorsal attentional network (Nardo et al., 2011). Our study relates to such work by showing that, despite highly salient background motion, exogenous spatial cueing effects can still occur on manual RTs and the EEG, as opposed to on eye movements and the BOLD signal, and it would be important to extend this to other measures. Expectation can modulate the effects that radially expanding optic flow has on postural sway and event-related desynchronization of the alpha band (Obereisenbuchner et al., 2021). Recent studies have found that behavioural and electrophysical markers of cognition are markedly different in dynamic and virtual environments compared with simpler lab set ups (Draschkow et al., 2021; Gramann et al., 2021).

4.6 | Limitations of the study and future work

Note that one limitation of this study was the absence of cue-target jittering or cue-only trials which could allow methods optimised for segregating out the ERP to cue and target (Woldorff, 1993). The pattern of cueing reducing P1 may then be related to the presence of the cue-related potential beforehand or to the ongoing background OKS, and future work will be necessary to relate this to previous effects. Independently of this, we were here able to show that the effect of cueing still occurred with or without eye movements. Also, given that it has been reported that attentional effects differ with cue salience (Fuller et al., 2009), it is also plausible that the salience of our cues did not allow dissociating between cue effects during the two blocks. Cue salience (together with SOAs) could be a factor determining the polarity of the P1 validity effect (Fu et al., 2009). Other studies could investigate whether the manipulation of cue contrast can dissociate between attentional cueing effects during fixation and eye movements induced by moving visual scenes.

Note also the inherent limitation of our ICA approach which is that we did not dissociate between effects of quick and slow phase eye movements on the EEG. Rather, only a single component was used to capture the variance from both the slow and QPs of the eye movement. Future work could optimise this further by comparing directly the effects of these eye movements on the EEG. In particular, that could test the possibility that the two types of eye movements

might produce similar ICA components given the extreme stereotypy and repetitiveness of the artefacts in question and the helpful ambiguities of the ICA such as its independence of the sign of the components (Tharwat, 2020). ICA is not selective to fast eye movements but can in principal also remove slowly changing artefacts. The striking similarity between the ERPs during OKN and fixation would suggest that the eye movement related artefacts were filtered out.

5 | CONCLUSION

We investigated the exogenous peripheral covert spatial cueing effect in a discrimination task during concurrent dynamic visual stimulation. We demonstrated that the exogenous cueing effect is measurable both during fixation on a moving background or during eye movements in response to that moving background. The findings are in favour of our hypothesis which predicted that cueing effects would be robust enough to affect performance and the early neural processing of visual stimuli, and furthermore, even when ongoing reflexive eye movements are induced by the moving visual scene. Our results extend prior work using other types of eye movements into the field of OKN. In the future, this line of research could inform our understanding of how spatial attention operates when we move through our environment.

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CONFLICT OF INTEREST

None.

AUTHOR CONTRIBUTION

A.M. and P.C.J.T. conceived and designed research; A.M. and G.V. performed experiments; A.M. and G.V. analysed the data; A.M. and P.C.J.T. interpreted results of experiments; A.M. prepared figures; A.M. and P.C.J.T. drafted, edited and revised manuscript; and A.M., G.V., and P.C.J.T. approved the final version of manuscript.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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