

Strategic distractor suppression improves
selective control in human vision

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ABSTRACT

Our visual environment is complicated and our cognitive capacity is limited. As a result, we must strategically ignore some stimuli in order to prioritize others. Common-sense suggests that foreknowledge of distractor characteristics, like location or color, might help us ignore these objects. But empirical studies have provided mixed evidence, often showing that knowing about a distractor before it appears counter-intuitively leads to its attentional selection. What has looked like strategic distractor suppression in the past is now commonly explained as a product of prior experience and implicit statistical learning, and the long-standing notion that distractor suppression is reflected in alpha-band oscillatory brain activity has been challenged by results appearing to link alpha to target resolution. Can we strategically, proactively suppress distractors? And, if so, does this involve alpha? Here, we use concurrent recording of human EEG and eye movements in optimized experimental designs to identify behaviour and brain activity associated with proactive distractor suppression. Results from 3 experiments show that knowing about distractors before they appear causes a reduction in electrophysiological indices of covert attentional selection of these objects and a reduction in the overt deployment of the eyes to their location. This control is established before the distractor appears and is predicted by the power of cue-elicited alpha activity over visual cortex. Foreknowledge of distractor characteristics therefore leads to improved selective control, and alpha oscillations in visual cortex reflect the implementation of this strategic, proactive mechanism.

SIGNIFICANCE STATEMENT

In order to behave adaptively and achieve goals we often need to ignore visual distraction. Is it easier to ignore distracting objects when we know more about them? We recorded eye movements and electrical brain activity to determine if foreknowledge of distractor characteristics can be used to limit processing of these objects. Results show that knowing the location or color of a distractor stops us from attentionally selecting it. A neural signature of this inhibition emerges in oscillatory alpha-band brain activity, and when this signal is strong, selective processing of the distractor decreases. Knowing about the characteristics of task-irrelevant distractors therefore increases our ability to focus on task-relevant information, in this way gating information processing in the brain.

INTRODUCTION

This paper addresses two linked and contentious issues in our understanding of visual attention. The first concerns our ability to strategically and proactively suppress distractors. Can we volitionally limit processing of stimuli that we know will be task irrelevant before they appear? The second issue regards the relationship between distractor suppression and alpha-band oscillatory brain activity. If proactive suppression is possible, is it reflected in alpha?

Extant evidence for strategic distractor suppression is mixed. Studies have shown that cues identifying distractor locations speed target responses (Munneke, van der Stigchel, & Theeuwes, 2008; Awh, Matsukura, & Serences, 2008; Chao, 2010), cause eye movements to deviate away from the inhibited location (van der Stigchel & Theeuwes, 2006), reduce the need for inhibitory processing when the distractor appears (Heuer & Schubö, 2019), and elicit anticipatory activity in retinotopic visual cortex (Ruff & Driver, 2006; Munneke, Heslenfeld, Usrey, et al., 2011). But other work shows that distractor cues lead to monitoring of the cued location (Wang & Theeuwes, 2018), such that information from stimuli at this location intrudes into visual perception (Chang, Cunningham, & Egeth, 2018), and that neural signatures of distractor inhibition fail to emerge when there is no target to select (Hilimire, Hickey, & Corballis, 2012).

Studies of feature cueing are no less confusing. Foreknowledge of distractor features, like color, can elicit preparatory activity in visual cortex (Reeder, Olivers, & Pollmann, 2017). This appears to benefit search for a target (Woodman & Luck, 2007; Arita, Carlisle, & Woodman, 2012) by facilitating suppression of the distractor after it appears (Carlisle & Woodman, 2011; de Vries, Savran, van Driel, et al., 2019). But this is not consistently observed (Becker, Hemsteger, & Peltier, 2015) and other work shows that maintaining mnemonic representations of distractors causes these stimuli to draw attention (Moher & Egeth, 2012; Cunningham & Egeth, 2016; Beck, Luck, & Hollingworth, 2018). Part of the confusion stems from the fact that distractor suppression can be created by implicit learning (Noonan, Adamian, Pike et al., 2016;

Cunningham & Egeth, 2016; Wang & Theeuwes, 2018; van Moorselaar & Slagter, 2019; Ferrante et al., 2018) and this is often confounded with strategy in experimental designs. Recent reviews unanimously conclude that proactive distractor inhibition emerges as a product of prior experience, expectations, and implicit learning, but that evidence for strategic distractor suppression is unconvincing (van Moorselaar & Slagter, 2020; Chelazzi, Marini, Pascucci et al., 2019; Noonan, Crittenden, Jensen, et al., 2017; Gaspelin & Luck, 2019; Luck, Gaspelin, Folk, et al., 2020).

A deep body of literature has linked distractor suppression with the emergence of alpha-band oscillatory brain activity, but as broad doubt has grown regarding proactive distractor suppression generally, questions regarding the relationship between alpha and suppression have also emerged. Alpha (~8 – 12 Hz) is clearly linked to neural inhibition: it predicts decreases in neural spiking (Haegens, Nácher, Luna, et al., 2011), gamma band activity (Spaak, Bonnefond, Maier, et al., 2012), and fMRI signal (Sheeringa, Petersson, Oostenveld, et al., 2009). Evocatively, a cue identifying the location of a forthcoming target causes alpha to increase in the ipsilateral hemisphere, which represents the physical area where no relevant stimulus will appear (Worden et al., 2000; Thut, Nietzel, Brandt et al., 2006). As alpha laterality increases, the representation of stimuli in the unattended field degrades (Händel, Haarmeier, & Jensen, 2011). This sort of finding has led to the influential proposal that alpha reflects a neural process – perhaps the phasic activation of inhibitory GABAergic interneurons – that stops the propagation of unattended visual information in retinotopic cortex (Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007; Foxe & Snyder, 2011). But neural inhibition as a basic mechanism may instantiate computational processes linked to target resolution rather than distractor suppression, and recent work has failed to find a relationship between alpha and behavioural indices of distractor suppression created through implicit learning (Noonan et al., 2016; van Moorselaar & Slagter, 2019). Prominent theoretical reviews suggest that the relationship between alpha and distractor suppression is unconvincing and that alpha is likely to reflect target processing (Foster & Awh, 2019; Noonan et al. 2019; van Moorselaar & Slagter, 2020).

Here, we use concurrent recording of EEG and eye-movements to test the notion of strategic, proactive distractor suppression and to identify alpha's role in this cognitive mechanism.

METHODS AND MATERIALS

Experiment 1 was designed to measure the impact of a spatial distractor cue on ERP evidence of selective processing, as reflected in the N2pc (Luck & Hillyard, 1994) and distractor positivity (P_D ; Hickey, Di Lollo, & McDonald, 2009). To foreshadow, Experiment 1 demonstrates that a spatial cue elicits alpha over posterior lateral cortex and reduces selective processing of the distractor. Experiment 2 builds from this finding to test if variance in distractor selection is predicted by the power of cue-elicited lateral alpha. Experiment 3 extends both earlier studies to investigate the impact of a semantic cue identifying the distractor color.

In Experiments 1 and 2, the target always appeared directly above or below fixation and the distractor always appeared at one of 4 lateral locations (to the left or right in the upper or lower hemifield; Figure 1). There are critical implications of this layout. First, it meant that the distractor cue in no way limited the scope of possible target locations, removing the possibility that the distractor cue provided information about the location of the target.

Second, this layout meant that targets were always on the vertical meridian and distractors were always lateral. Locations on the vertical meridian of the visual field are equally represented in the two visual cortices, so processing of these locations generates equal activity across the brain hemispheres. In contrast, lateral locations are initially represented in the contralateral hemisphere, so visual processing of these locations generates lateralized brain activity. By presenting targets at vertical positions and distractors at lateral positions, we were able to identify lateralized brain activity linked to distractor processing when it was not confounded with activity linked to target

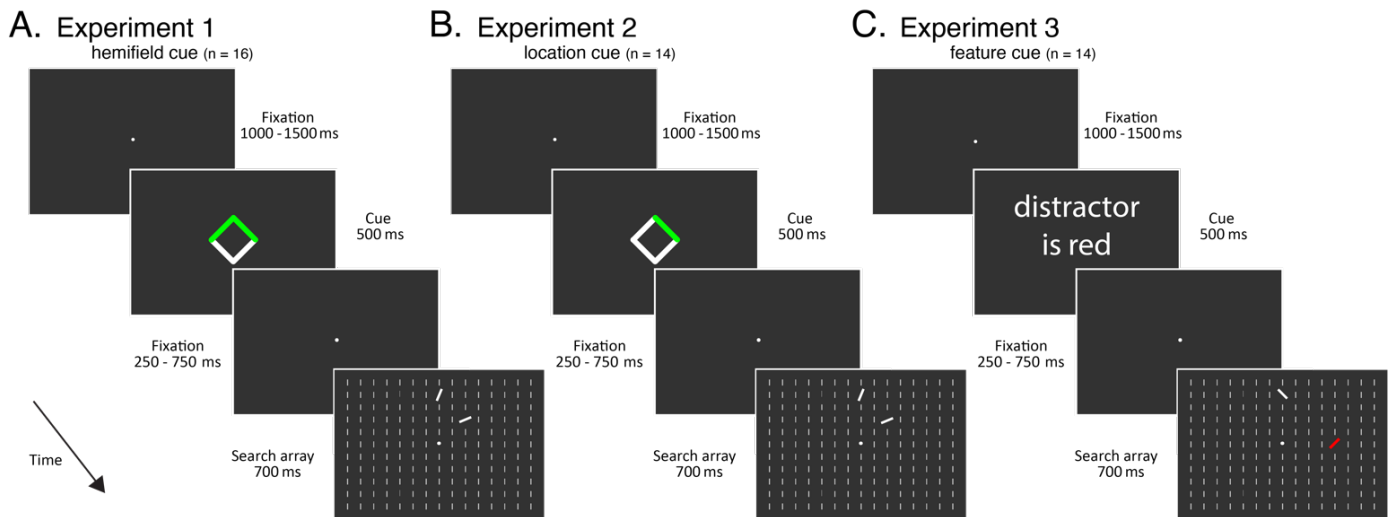


Figure 1 – Schematics of cue trials. A.) In Experiment 1, the green elements of the cue indicated that the distractor would appear at one of two lateral locations in the upper visual hemifield or at one of two lateral locations in the lower visual hemifield. B.) In Experiment 2, the green element identifies the specific location where the distractor would appear. C.) In Experiment 3, the cue indicated that a red distractor would appear. Within each experiment, these cue conditions were contrasted with conditions in which the cue was uninformative. Note that the size of the cues are not to scale, the semantic cue in Experiment 3 was actually a single word ('distractor' or 'ready'), and the salient target and the distractor in the search array were of the same size as background line elements in the actual experiment.

processing (Woodman & Luck, 2003; Hickey, McDonald, & Theeuwes, 2006; Hickey, Di Lollo, & McDonald, 2009).

Third, this layout meant that the target and distractor appear near to one another in the same upper or lower visual hemifield, or distant from one another in separate upper and lower hemifields. Distractor interference is known to scale as a function of the proximity of target and distractor stimuli (eg. Mounts, 2000; Hickey & Theeuwes, 2011; Mathôt, Hickey, & Theeuwes, 2010), and our expectation was that participants might be particularly motivated to employ proactive suppression when the experimental design contained conditions where target and distractor could activate a similar pool of retinotopic neurons. This circumstance is thought to create ambiguity in representation, competition for neural resources, and increased need for attentional mechanisms (Luck, Girelli, McDermott, et al., 1997; Desimone & Duncan, 1995).

Finally, this layout created a consistent relationship between location and distractor status. Recent results suggest that distractor suppression may develop through prior experience (eg. Ferrante et al., 2019; Wang & Theeuwes, 2018; van Moorselaar & Slagter, 2020). Our stimulus layout provided preconditions potentially required for the initial development of distractor suppression, which may be necessary for subsequent strategic recruitment of this mechanism. Similar logic applied in Experiment 3, where red color more often characterized the distractor than it did the target. This gave extended opportunity for participants to become familiar with the need to suppress red stimuli, allowing us to answer the question of whether, once established, distractor suppression could be proactively recruited.

Participants

Seventeen volunteers (4 male; 23.2 years \pm 2.7 SD; 2 left-handed) completed Experiment 1, 15 volunteers (3 male; 22.1 years \pm 2.2 SD; 2 left-handed) completed Experiment 2, and 14 volunteers completed Experiment 3 (4 male; 23.2 years, SD = 2.7 years; 2 left-handed). One participant from each of Experiments 1 and 2 was excluded from consideration due to low task accuracy resulting in too few trials for analysis (> 2 SD from group mean). All participants had normal or corrected-to-normal vision, none reported any neurological or psychiatric disorder, none took part in more than one of the experiments, and each was paid €10 per hour of participation. The study was approved by the local ethics committee and conducted in accordance with the Declaration of Helsinki.

Stimuli and procedure

As illustrated in Figure 1, the stimuli and procedure for each of the experiments was similar. Each trial began with a requirement for participants to fixate a central mark, which was verified via eye-tracking. Participants then initiated the stimuli sequence by pressing the space bar of a standard keyboard, which also triggered a drift-correction procedure in the eye-tracking software. The central fixation subsequently appeared

alone for a random duration of 1000 – 1500 ms (uniform distribution), followed by appearance of the cue for 500 ms, return of the fixation cross for 250 – 750 ms (uniform distribution), and appearance of the search array for 700 ms. The search array consisted of a 15 x 15 square array of white line elements surrounding the central fixation mark (see Fig. 1). The array subtended approximately $27^\circ \times 27^\circ$ visual angle and each element was $0.1^\circ \times 1^\circ$. Two elements in the array – the target and distractor – had off-vertical orientation. The participant's task was to make a saccadic eye movement to the target line element.

In Experiments 1 and 2, the target was defined both by degree of rotation and location. The target was rotated 22.5° to the right and appeared 7.7° (visual angle) directly above or below fixation, whereas the distractor was oriented 67.5° to the right and was located 5.4° (visual angle) from the fixation mark along a path tilted 45° from the vertical path between fixation and target (Figs 1A, 1B). A diamond-shaped cue ($1.5^\circ \times 1.5^\circ$ visual angle) identified where the distractor would appear in 50% of trials. In Experiment 1, the upper or lower half of the otherwise-white (RGB: 200, 200, 200) cue could have green color, indicating that the distractor would appear in one of two bilateral locations in the upper or lower visual hemifield. In the cue trials of Experiment 2, only one line segment of the diamond was green and this identified the precise distractor location. In remaining trials the distractor remained entirely white, providing no information about the distractor location. This is referred to as the no-cue condition below.

In Experiment 3 the target was defined by direction of rotation. Both the target and distractor line segments were 45° off-vertical, rotated in opposite directions, and half of the participants were instructed to make a saccade to the left tilted line element and the rest to the right tilted element. The target and distractor could appear at one of 4 equidistant locations 7.7° (visual angle) to the left / right of fixation or above / below fixation. When the target appeared at locations on the vertical meridian of the display, the distractor appeared to the left or right of fixation, whereas when the target appeared to the left or right of fixation, the distractor necessarily appeared on the vertical

meridian. In 66% of trials, the distractor had unique red color (RGB 250,0,0; Fig. 1C). In the remaining trials the target had unique red color. The semantic cue was either the word ‘ready’ (‘pronto’ for Italian-language participants) or ‘distractor’. The ‘ready’ cue appeared in 2/3 of trials and indicated that either the target or the distractor could have unique red color with equal probability. The ‘distractor’ cue appeared in 1/3 of trials and indicated that the distractor would be uniquely identified by red color. The cue appeared at fixation in 14 point font.

Experiments 1 and 2 consisted of 1 practice block of 64 trials followed by 12 experimental blocks of 64 trials. This took approximately 2 hours to complete, including 1 hour of EEG preparation. Experiment 3 was longer, consisting of 1 practice block of 32 trials followed by 18 blocks of 64 trials, and took approximately 2.5 hours, including 1 hour of EEG preparation. For all experiments, stimuli were presented on a 57 cm VIEWPixx LCD monitor (120 Hz) with a viewing distance of 1 m. The experiments were prepared using Psychtoolbox-3 (Brainard, 1997).

Eye-tracking and EEG recording

Eye movement and EEG data were simultaneously recorded in all experiments. A desk-mounted Eyelink 1000 (SR Research, Mississauga, Canada) recorded monocular eye position at 1 kHz. In most cases tracking was of the right eye, but occasionally the left eye was used when this generated better eye-tracker calibration.

EEG was recorded at 1 kHz from 62 cap-mounted Ag/AgCl electrodes in a 10/20 montage and 2 electrodes mounted over the left and right mastoids. Electrode impedances were kept below 10 k Ω during recording. EEG was amplified with a BrainAmp amplifier (BrainProducts GmbH, Munich, Germany) with right mastoid reference and subsequently re-referenced to the average of both mastoid signals. Analog anti-alias filters were applied during recording (0.016 – 250 Hz) and the data was subsequently digitally low-pass filtered using a 101-point zero-phase non-causal least-square FIR kernel (0 dB attenuation at 40 Hz; -6 dB at 45 Hz).

Data analysis

Analysis was conducted with custom scripts for MATLAB R2020a (Mathworks, Natick, USA) that employed the EEGLAB toolbox (Delorme & Makeig, 2004), the EYE-EEG toolbox (Dimigen, Sommer, Hohlfeld, Jacobs, & Kliegl, 2011), the Fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011), and the MATLAB statistics toolbox (v.11.7). Statistical analysis relied on parametric ANOVAs, permutation contrasts, and mixed linear modelling. In permutation contrasts the null distribution is based on 10^5 random samples of the effect of interest with replacement. In mixed linear modelling, maximum likelihood is employed for variance estimation, Akaike information criterion (AIC) is employed for model comparison, and ANOVA derivations employ Satterthwaite approximations of degrees of freedom.

Eye Movements

Eye movements with velocity exceeding $30^\circ/\text{s}$ or acceleration exceeding $8000^\circ/\text{s}^2$ were marked as saccades. Saccadic response times (SRTs) were calculated as the time between stimulus onset and the beginning of the first saccade larger than 3° (visual angle). The saccade was recorded as target-directed or distractor-directed when it landed within 2.7° (visual angle) of the center of these stimuli.

In Experiment 1, saccade trajectory deviations were quantified as the mean angular deviation from a straight-line path between the saccade starting point and the center of the targets for each eye-tracker sample (Van der Stigchel et al., 2006). The first five samples of the saccade were excluded from this calculation. Negative saccade deviation values reflect deviation away from the distractor location. In order to illustrate mean saccades, linear interpolation was employed to generate representations of each saccade with equal number of samples. Within each condition these interpolated saccades were mean averaged across trials, and subsequently across participants, to generate the saccade paths presented in Figure 3.

EEG

Infomax independent component analysis (ICA; Bell and Sejnowski, 1995) was conducted on combined EEG and eye position data. Artifactual independent components were identified based on their covariance with eye movement data using a saccade-to-fixation variance criterion of 1.1 (Plöchl et al, 2012) and variance associated with these components was removed from the EEG. Epochs were created in an interval beginning 1 s before stimulus onset and ending 1 s after. ERPs were calculated from mean signal in a cluster of lateral posterior electrode sites where the N2pc (Luck & Hillyard, 1994a, 1994b) and P_D (Hickey, Di Lollo, & McDonald, 2009) are maximal (PO3/4, PO7/8, P5/6, and P7/8) and baseline corrected on an interval beginning 100 ms before stimulus onset and ending 50 ms after. Only correct trials were included in ERP analysis.

Oscillatory analysis of pre-stimulus EEG was used to index the effect of the spatial cue prior to the onset of target and distractor stimuli. This relied on the application of Gabor transforms to data observed in correct trials. Kernel cycles increased linearly from 1 cycle at 4 Hz to 8 cycles at 40 Hz, such that kernels had a length of 221 ms at 8.3 Hz, 215 ms at 10 Hz, and 213 ms at 12.5 Hz. The conditional difference in oscillatory power was computed between cueing conditions (with no other baseline) before being mean averaged across a cluster of electrodes over lateral posterior cortex (see Figure 6). The electrode clusters corresponded to those employed for ERP analysis and are consistent with those used in earlier studies of lateral alpha and attention (eg. Worden, Foxe, Wang, & Simpson, 2000). In Experiment 2, lateral power was subsequently computed by subtracting ipsilateral values from contralateral values. In Experiments 1 and 3, bilateral power was calculated by averaging across the sets of lateral electrodes. Cluster-based permutation tests were employed to test the effect of the cue on oscillatory power. Clusters were defined across frequency and latency dimensions with a cluster-defining threshold of $p < 0.05$ and cluster significance at $p < 0.05$. In

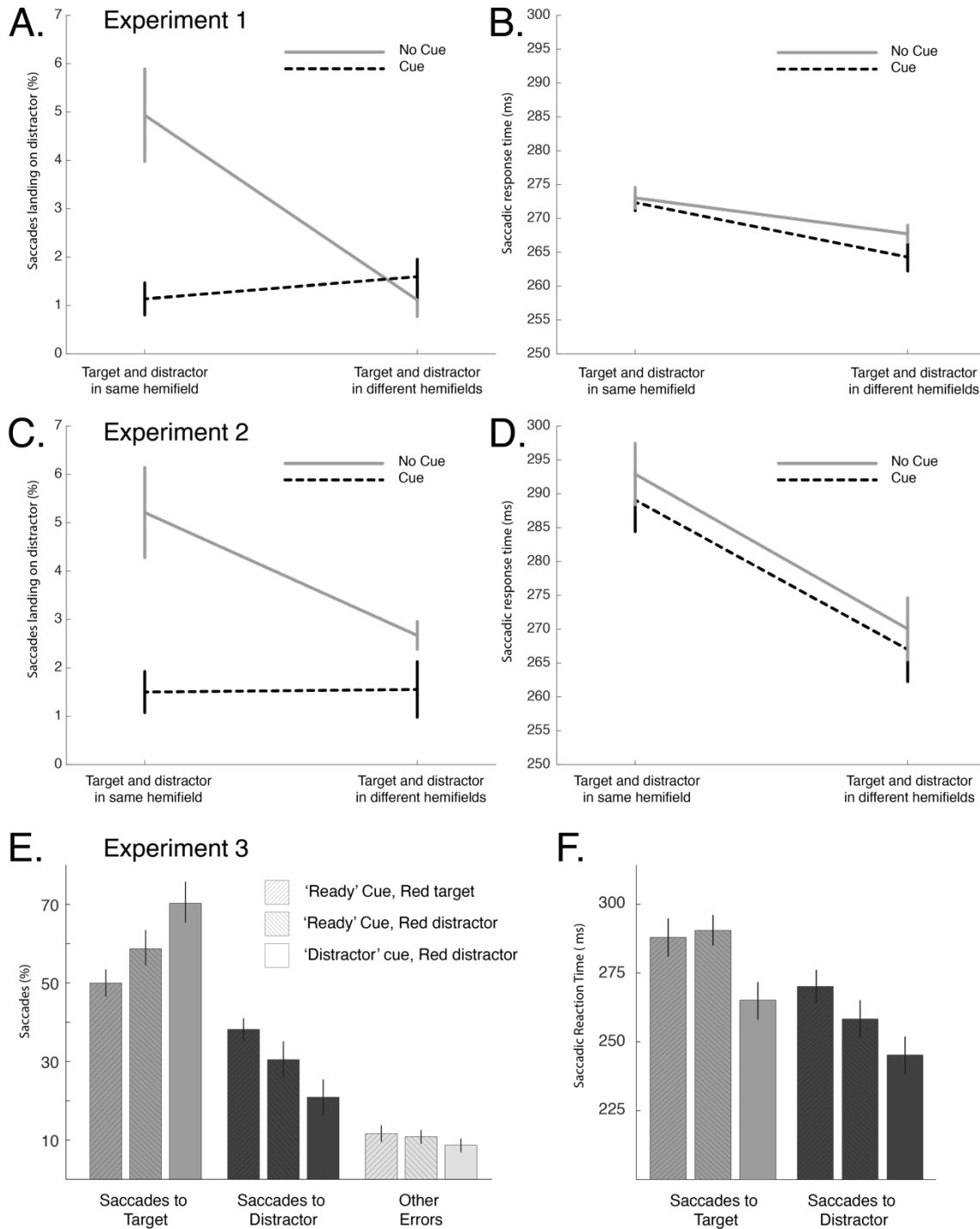


Figure 2 – Behavioural results. A.) Saccadic performance in Experiment 1. When the target and distractor appeared in the same visual hemifield, the spatial cue reduced the proportion of saccades landing on the distractor. B.) Saccadic response times in Experiment 1. C.) Saccadic performance in Experiment 2. Results from Experiment 1 are broadly reproduced. D.) Saccadic response times in Experiment 2. E.) Saccadic performance in Experiment 3. The 'distractor' cue reduced the proportion of saccades landing on the distractor. F.) Saccadic response times in Experiment 3. The 'distractor' cue reduces saccadic response times in accurate trials. All error bars reflect within-participant SEM (Cousineau, 2005).

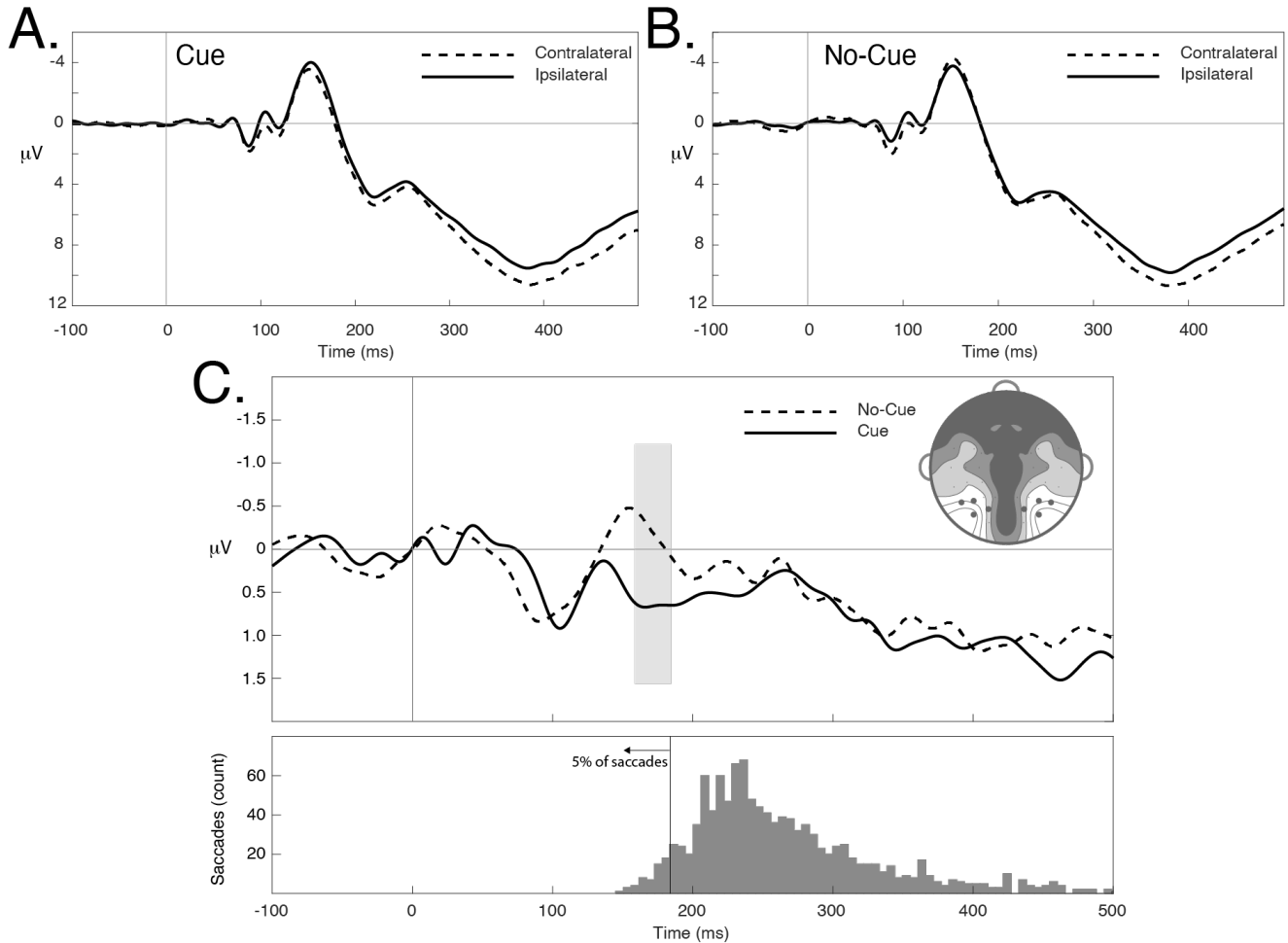


Figure 3 – ERPs from Experiment 1, time-locked to onset of the search array, when the array contained a target and distractor in the same upper or lower visual hemifield. A.) Posterior lateral ERPs elicited contralateral and ipsilateral to the location of a cued distractor. B.) Posterior lateral ERPs elicited contralateral and ipsilateral to the location of an uncued distractor. C.) Contralateral-minus-ipsilateral difference waves. Illustrated in the bottom panel is the distribution of saccadic response times. The cue caused a positive shift in the difference wave immediately before the onset of saccadic responses. Topography illustrates mean voltage difference from the interval identified by shading. Because the effect is a difference in contralateral-minus-ipsilateral waveforms, the lateral topography is represented in both hemispheres with midline electrodes set to zero value.

Experiments 2 and 3, generation of the null distribution relied on exhaustive relabelling of cue and no-cue conditions (2^{14} iterations), and in Experiment 1 relied on a random sample of 2^{14} relabellings of cue and no-cue conditions (of the 2^{16} combinations possible). Statistical analysis was conducted across a time range beginning 850 ms before stimulus onset and ending 850 ms after and across a frequency range beginning at 4 Hz and ending at 40 Hz.

RESULTS

Experiment 1

In Experiment 1, the distractor cue identified two bilateral locations in the upper or lower visual hemifield where the distractor could appear (Figure 1a). This hemispheric cue was employed to ensure that the cue did not elicit lateralized activity that could sustain into the post-target interval and complicate interpretation of activity evoked by the distractor itself.

Behaviour

Trials were removed from analysis if the eyes were not at fixation at trial start (3.8% of trials), if the saccade was anticipative (SRT of <60 ms; 0.3%), or if the eyes landed elsewhere than on the target or distractor ($>2.7^\circ$ visual angle from center of object; 1.5%).

As illustrated in Figure 2a, when the target and distractor appeared together in the upper or lower visual hemifield, the cue reduced the proportion of saccades that were deployed to the distractor. This effect did not emerge when the stimuli were presented in opposite visual hemifields. To test this, we conducted a 2-way repeated measures ANOVA (RANOVA) with factors for shared hemisphere (same hemisphere vs. different hemispheres) and cue (cue vs. no-cue). This identified main effects of cue ($F(1,15) = 6.32$, $p = 0.023$) and shared hemisphere ($F(1,15) = 6.29$, $p = 0.023$) and an interaction between the factors ($F(1,15) = 13.76$, $p = 0.002$).

Figure 2b illustrates SRTs as a function of the same factors. Analysis identified a main effect of shared hemisphere ($F(1,15) = 10.24$, $p = 0.006$), reflecting slower SRTs when the stimuli appeared in the same visual hemisphere. No other significant effects emerged (cue: $F(1,15) = 1.55$, $p = 0.232$; interaction $F < 1$).

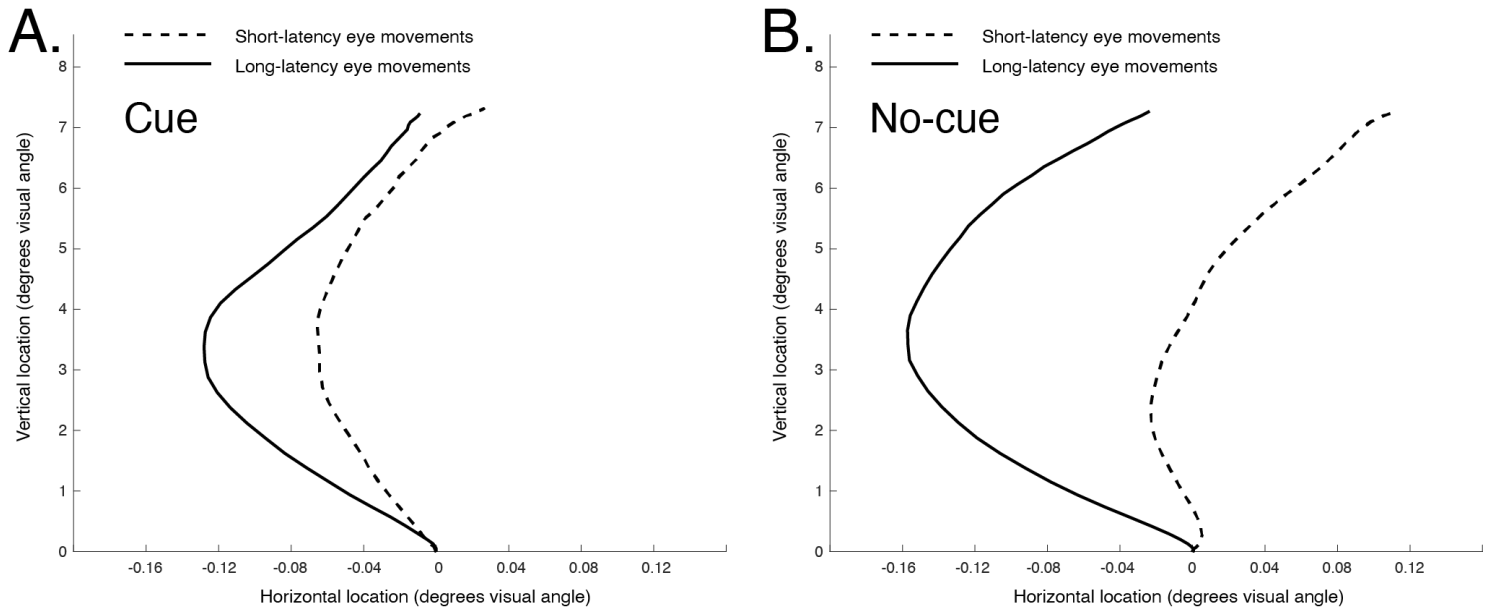


Figure 4 – Saccadic deviation results from Experiment 1. Note that while the target could appear above or below fixation, and the distractors to the left or right and above or below fixation, these images have been rectified so that the illustrative target location is above fixation (at origin) and the distractor is to the right. A.) Mean short-latency and long-latency saccades following a distractor cue. B.) Mean short-latency and long-latency saccades following a neutral cue.

ERPs

Our interest lay in lateral effects over occipital cortex in the time range of the N2pc (Luck & Hillyard, 1994a, 1994b) and distractor positivity (P_D ; Hickey, Di Lollo, & McDonald, 2009). These lateral ERP components track attentional selection and stimulus-triggered distractor suppression, respectively. Figure 3 presents the ERPs elicited over lateral occipital cortex ipsilateral and contralateral to the distractor when the distractor appeared in the same visual hemifield as the target. Results show that the cue impacts the laterality of the visual ERP in the range of the N2pc and P_D . When the distractor hemifield was cued, the contralateral waveform becomes more positive than the ipsilateral waveform from ~150 ms post-target (Figure 3a). In the no-cue condition, the contralateral waveform in the same interval is more negative than the ipsilateral waveform (Figure 3b). These lateral effects are small in magnitude compared to the bilateral morphology of the ERP and are therefore more clearly illustrated in the contralateral-minus-ipsilateral difference waves presented in Figure 3c. From ~150 to

~250 ms post-target, the difference wave elicited in the no-cue condition is more negative than is the difference wave elicited in the cue condition, reflecting stronger attentional selection of the distractor in the no-cue condition.

We focused statistical analysis on the interval immediately preceding the onset of saccadic responses. Following our earlier work, we operationally defined this as the 25 ms preceding the 5th percentile of the distribution of eye movements (165 – 190 ms, Figure 3c; Weaver, van Zoest, & Hickey, 2017). This ensured that the electrophysiological signal was not tainted by physiological artefacts of the eye movement that may have survived ICA correction and, more importantly, that the brain activity reflected in the signal preceded overt selective behaviour and thus had the opportunity to play a role in determining that behaviour.

Mean ERP voltage in this interval was assessed in a 4-way RANOVA with factors for electrode laterality (ipsilateral vs. contralateral), cue (cue vs. no-cue), and shared visual hemifield (same hemifield vs. opposite hemifield). An additional factor representing a median split of data based on saccadic response speed was included to equate these ERP analyses with analysis of saccade deviation described below (fast vs. slow). The critical result was an interaction of electrode laterality, hemisphere, and cue ($F(1,15) = 5.093$, $p = 0.039$; see Figure 3c), reflecting relative positivity of the contralateral-minus-ipsilateral difference wave in cued trials, relative to no-cue trials, when the target and distractor were presented in the same visual hemifield rather than different hemifields. To follow up on this interaction, we contrasted the mean voltage of the difference waves for cue and no-cue conditions when the target and distractor were in the same or opposite visual hemifields using separate permutation tests. When target and distractor were presented in the same hemifield, this difference was significant ($p = 0.004$; Fig 3c). When the target and distractor were presented in opposite hemifields, it was not ($p = 0.583$; not illustrated).

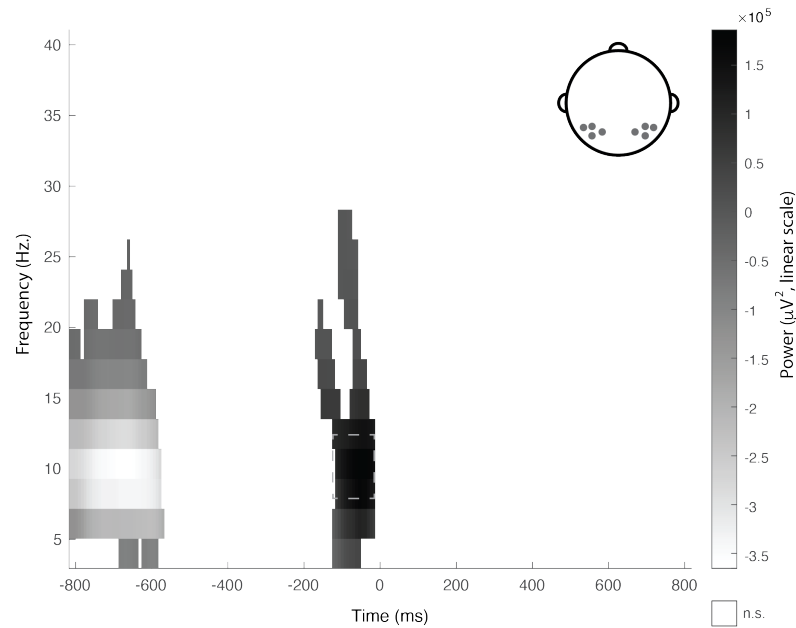


Figure 5 –Posterior oscillatory power in Experiment 1. Shaded areas reflect time-frequency combinations where oscillatory power significantly differed between cue conditions. The time-frequency interval identified by broken box was used in trial-wise analysis of the relationship between oscillatory power and EEG amplitude.

The RANOVA identified one other significant effect, an interaction of electrode laterality, shared hemisphere, and response speed ($F(1,15) = 8.885$, $p = 0.009$). Importantly, this effect did not involve the critical manipulation of cue. This appears to reflect a propensity for the lateral distractor-elicited response to be more positive when target and distractor were presented in the same hemifield and the response was slow rather than fast, but more negative when target and distractor were presented in opposite hemifields and the response was slow rather than fast. It may reflect a decrease in target-distractor interference and a propensity to broadly explore the environment when participants are relaxed about task completion. No other effect was significant (electrode laterality: $F(1,15) = 1.346$, $p = 0.264$; saccadic response speed: $F(1,15) = 4.255$, $p = 0.057$; cue: $F(1,15) = 1.129$, $p = 0.305$; electrode laterality X cue: $F(1,15) = 1.709$, $p = 0.211$; all other F s < 1).

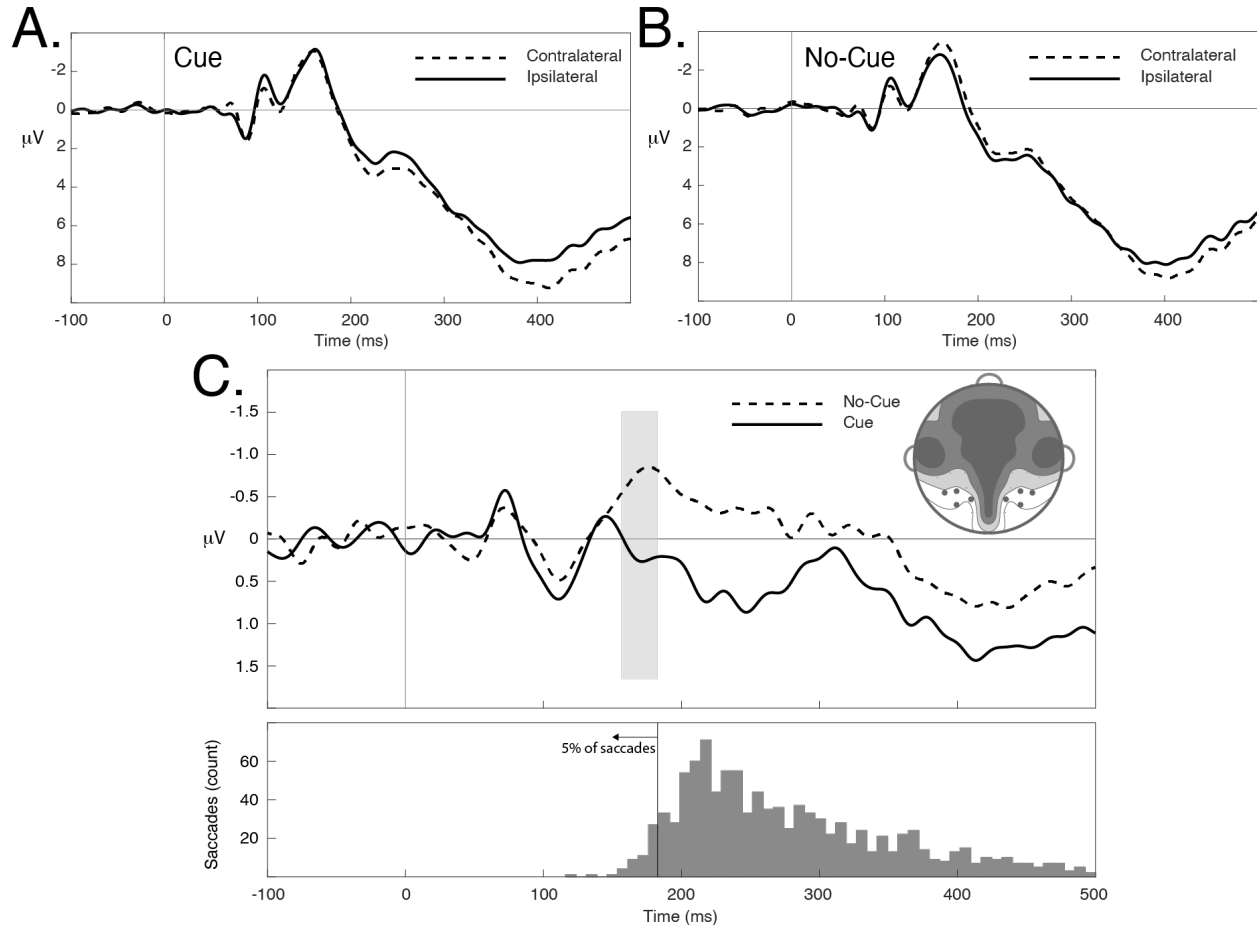


Figure 6 – ERPs from Experiment 2, time-locked to the onset of the search array, when the array contained target and distractor in the same upper or lower visual hemifield. A.) Posterior lateral ERPs elicited contralateral and ipsilateral to the location of a cued distractor. B.) Posterior lateral ERPs elicited contralateral and ipsilateral to the location of an uncued distractor. C.) Contralateral-minus-ipsilateral difference waves. Illustrated in the bottom panel is the distribution of saccadic response times. Topography is calculated as described in the caption to Figure 3.

The ERP and saccadic performance data from Experiment 1 suggest one of two interpretations. The cued location may be proactively suppressed, causing stimuli appearing at that location to be less salient. As a result, the cued distractor does not draw attention and does not elicit an N2pc. This has an important implication: because distractor suppression would be fully implemented before the target and distractor stimuli appeared, it should be temporally stable in the post-target interval and not develop over time.

The alternative is that the cue primes a mechanism of stimulus-triggered distractor suppression – reflected in P_D amplitude – that acts to negate distractor salience after the stimuli appear (Sawaki & Luck, 2010). By this interpretation, the cued distractor is actively suppressed in the post-target interval and elicits a P_D . The implication here is that distractor suppression develops within the post-target interval, and that distractor salience should accordingly be high soon after onset of the search array and reduce as the suppressive reaction builds.

Saccade deviation

We leveraged this distinction in time-course expectations to clarify our interpretation of the ERP results from Experiment 1. The developmental time-course of distractor suppression can be tracked in saccade deviation. Short-latency, target-directed eye movements show a tendency to deviate toward salient distractors during saccadic flight. But if the saccade is longer-latency – if more time has passed between stimulus onset and saccade onset – the saccade comes to deviate away from the distractor location (Godijn & Theeuwes, 2006; Mulckhuysen, Van der Stigchel, & Theeuwes, 2009; Hickey & van Zoest, 2012; Weaver, van Zoest, & Hickey, 2017). This pattern has been linked to the development of a spatial inhibitory tag in the oculomotor system to resolve competition in neural representation (McPeck, Han, & Keller, 2003; for review, Van der Stigchel, Meeter, & Theeuwes, 2006). Saccade deviation can therefore be used to determine if the proactive distractor suppression identified in Experiment 1 is triggered by stimulus onset, and therefore shows a time-course in the post-target interval, or if it is implemented prior to stimulus onset, and is therefore stable in the post-target interval.

Figures 4a-b present results from analysis of saccade deviation in Experiment 1. Note that while the target could appear in the upper or lower hemifield, and the distractor to the left or right of fixation and above or below fixation, these plots have been rectified so the illustrative target location is in the upper visual hemifield and the distractor appears to the right (see Figure 1a). In the no-cue condition, short-latency saccades (cross-participant mean of per-participant conditional medians: 240 ms \pm 31 ms S.D.) tended

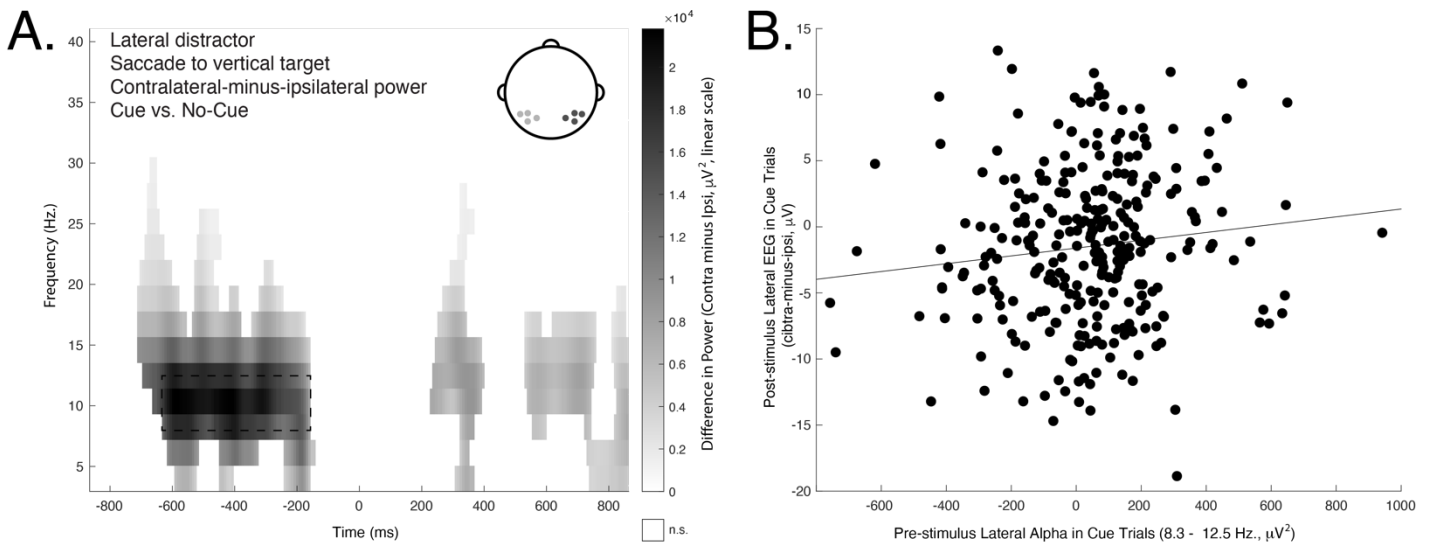


Figure 7 – Time-frequency results from Experiment 2. A.) Lateral posterior oscillatory power. Shaded areas reflect time-frequency combinations where contralateral-minus-ipsilateral difference in oscillatory power was greater in the cue condition than the no-cue condition. The time-frequency interval identified by broken box was used in trial-wise analysis of the relationship between oscillatory power and EEG amplitude. B.) Trial-wise relationship between pre-stimulus alpha and post-stimulus EEG amplitude for one illustrative participant. Note that while this illustration is of raw data, modelling was based on rank transformed values and included multiple predictive factors. Line reflects ordinary least-square linear fit.

to deviate toward the distractor location, whereas long-latency saccades (307 ms \pm 46 ms S.D.) deviated away from the distractor location. The cue reduced this pattern: short-latency saccades (240 ms \pm 33 ms S.D.) showed less deviation toward the distractor than is observed in the no-cue condition, whereas long-latency saccades (311 ms \pm 53 ms S.D.) showed less deviation away.

To test this pattern, mean deviation was entered into a RANOVA with factors for cue, saccadic response latency, and shared visual hemifield. This identified a critical interaction between cue and saccadic response latency ($F(1,15) = 6.116$, $p = 0.026$; hemisphere: $F(1,15) = 2.391$, $p = 0.143$; speed: $F(1,15) = 3.668$, $p = 0.075$; hemisphere \times speed: $F(1,15) = 3.754$, $p = 0.072$; all other $F_s < 1$). Follow-up permutation contrasts identified that in no-cue trials, short-latency saccades differed in saccade deviation from long-latency saccades ($p = 0.002$), but that in cue trials, there was no significant

difference ($p = 0.167$). Results from saccade deviation thus show that a.) the cue reduced the initial salience of the distractor, such that it did not draw eye movements initiated quickly, and b.) the cue removed the need for strong post-stimulus suppression, so that eye movements initiated after longer delay were not so strongly repelled away from the distractor. The cue attenuated the developmental time-course of stimulus-triggered distractor suppression, consistent with the idea that cue-elicited suppression was implemented prior to stimulus onset.

Time-frequency analysis

Time-frequency analysis focused on cue-elicited bilateral oscillatory power over posterior occipital cortex. Results are illustrated in Figure 5. In the interval between the cue and search array, the cue created an initial decrease in oscillatory power in the alpha band that was followed by an increase before onset of the search array. This is consistent with the idea that participants interpreted the informative cue, causing a decrease in alpha, before subsequently implementing strategic suppression that is reflected in alpha power (eg. Bonnefond & Jensen, 2012).

We approached results from Experiment 1 with the idea that variance in cue-elicited bilateral alpha might predict selective processing in the post-target EEG, but failed to find any evidence of this. Because we do find evidence of this relationship in Experiments 2 and 3, details of this analysis are provided here. To test the relationship between alpha and EEG, we isolated cue trials and extracted trial-wise pre-target alpha power (over the time-frequency interval identified by broken rectangle in Figure 5) and trial-wise post-target lateral EEG amplitude (over the time interval identified by grey rectangle in Figure 3c). We rank transformed these values to reduce the impact of outlier values (Iman & Conover, 1979; Conover & Iman, 1981) and used mixed linear modelling and model selection to assess the relationship between cue-elicited alpha and distractor-elicited N2pc (using `fitlme.m` from the MATLAB statistics toolbox). A simple initial model included a continuous fixed effect predictor for alpha power

(oscillatory_power) and a random effect for the intercept of each participant (participant; AIC: 47876; Equation 1).

(1) N2pc \sim oscillatory_power + (1 | participant)

We attempted to improve this model by adding all combinations of the following factors: random effects for the per-participant oscillatory power intercept and slope, a categorical fixed factor for the effect of distractor elevation in the visual field (top vs. bottom), a categorical fixed factor for target location (top vs. bottom), and a continuous fixed factor for SRT. The inclusion of distractor and target location was motivated by known variance in N2pc and P_D as a function of the elevation of the eliciting stimulus in the visual field (eg. Hickey, Di Lollo, & McDonald, 2009). None of these models performed better than the simple model described above. ANOVA analysis of this model failed to identify any relationship between bilateral alpha and distractor-elicited lateral EEG ($F(1,4125) = 0.302$, $p = 0.583$).

Experiment 1 was designed to elicit strategic, proactive suppression of the cued distractor locations. However, there is the possibility that participants may have responded to the cue by deploying spatial attention to the target location in the counter-cued field. This strategy is unlikely as it would have no net benefit to task performance: it would make for easier programming of target-directed saccades in the 50% of trials where the target appeared at the monitored location, but, equally, would make for more difficult target localization and saccade preparation in the 50% of trials where the target appeared on the other side of fixation. However, the results allow us to empirically assess the possibility. First, the deployment of spatial attention in response to a spatial cue is known to cause a broad and long-lasting decrease in bilateral alpha over occipital cortex (eg. Sauseng et al., 2005; Thut et al., 2006; Dombrowe & Hilgetag, 2014). If participants deploy spatial attention to the counter-cued upper or lower visual hemifield, we should see a decrease of cue-elicited bilateral alpha in the cue condition as compared to the no-cue condition. In fact, our results show the opposite, with cue-

elicited alpha increasing in this interval (Figure 5). Second, if participants strategically deployed spatial attention to the counter-cued visual field, this should be motivated by a behavioural benefit when the target appears at the monitored location. Results from Experiment 1 show no such spatial cueing effect on eye movements; when target and distractor appear in different hemifields, neither saccadic accuracy (Figure 1A) nor SRT (Figure 1B) differ between cue and no-cue conditions. Finally, while we have no clear expectations for how such a deployment of spatial attention would impact saccadic curvature, it is difficult to imagine how this could generate the pattern of saccade deviation we see in Experiment 1 (Figure 4). In contrast, the pattern of saccade deviation we observe is explicitly predicted by the notion of cue-elicited proactive inhibition.

Experiment 2

ERP results from Experiment 1 identified variance in selective processing of the distractor as a function of the spatial distractor cue, and saccade deviation results suggested that cue-elicited suppression was implemented prior to onset of the search array. Time-frequency results identify a cue-elicited increase in bilateral alpha power, but this does not robustly predict subsequent distractor processing in the ERP. Bilateral alpha may be unsuited for this type of analysis, as it can reflect neural mechanisms unrelated to spatial suppression of the cued location. Lateral alpha – the difference of alpha across ipsilateral and contralateral hemispheres – provides better insight on spatial processing, and with this in mind Experiment 2 employed a cue that identified the discrete lateral location where a distractor would appear (Figure 1B).

Behaviour

Trials that did not begin with fixation (1.5%), that were anticipative responses (0.2%), or that did not result in target or distractor selection (7.6%) were removed from analysis. As illustrated in Figures 2c and 2d, behavioural results replicated those observed in Experiment 1: when the target and distractor appeared together in the upper or lower visual hemifield, the cue reduced the proportion of saccades that were deployed to the

distractor. This emerged in statistical analysis of saccadic performance as an interaction of cue and shared hemisphere ($F(1,13) = 14.13$, $p = 0.002$). The main effect of cueing also emerged ($F(1,13) = 8.13$, $p = 0.014$; shared hemisphere: $F(1,13) = 2.54$, $p = 0.135$). Analysis of SRT identified main effects of shared hemisphere ($F(1,13) = 6.17$, $p = 0.027$) and cue ($F(1,13) = 8.45$, $p = 0.012$; interaction $F < 1$).

ERPs

As illustrated in Figures 6a-c, ERP results from Experiment 2 also replicate Experiment 1: in the 25 ms interval preceding the 5th percentile of saccade onsets (158 – 183 ms), the cue caused a reduction in distractor-elicited N2pc. Building from Experiment 1, statistical analysis took the form of a single planned permutation contrast of the mean difference in ipsilateral-minus-contralateral voltage between cue and no-cue conditions in the 158 – 183 ms interval, limited to conditions where the target and distractor appeared in the same visual hemifield ($p = 0.003$). This effect did not emerge when the target and distractor appeared in different hemifields ($p = 0.534$).

Time-frequency analysis

Results from time-frequency analysis are illustrated in Figure 7. In the interval between the cue and search array, the cue created a broad increase in oscillatory power in the cortical hemisphere contralateral to the cued location.

As in Experiment 1, we approached results from Experiment 2 with the idea that cue-elicited oscillatory activity might predict selective processing of the distractor. To test this, we isolated cue trials and extracted trial-wise pre-target lateral alpha power (by subtracting ipsilateral power from contralateral power over the time-frequency interval identified by dashed rectangle in Figure 7a) and trial-wise post-target lateral EEG amplitude (over the time period identified by grey rectangle in Figure 6c; N2pc). We again rank transformed these values and used mixed linear modelling and model selection to assess their relationship. A simple initial model included a continuous fixed effect predictor for alpha power (alpha) and a random effect for the intercept

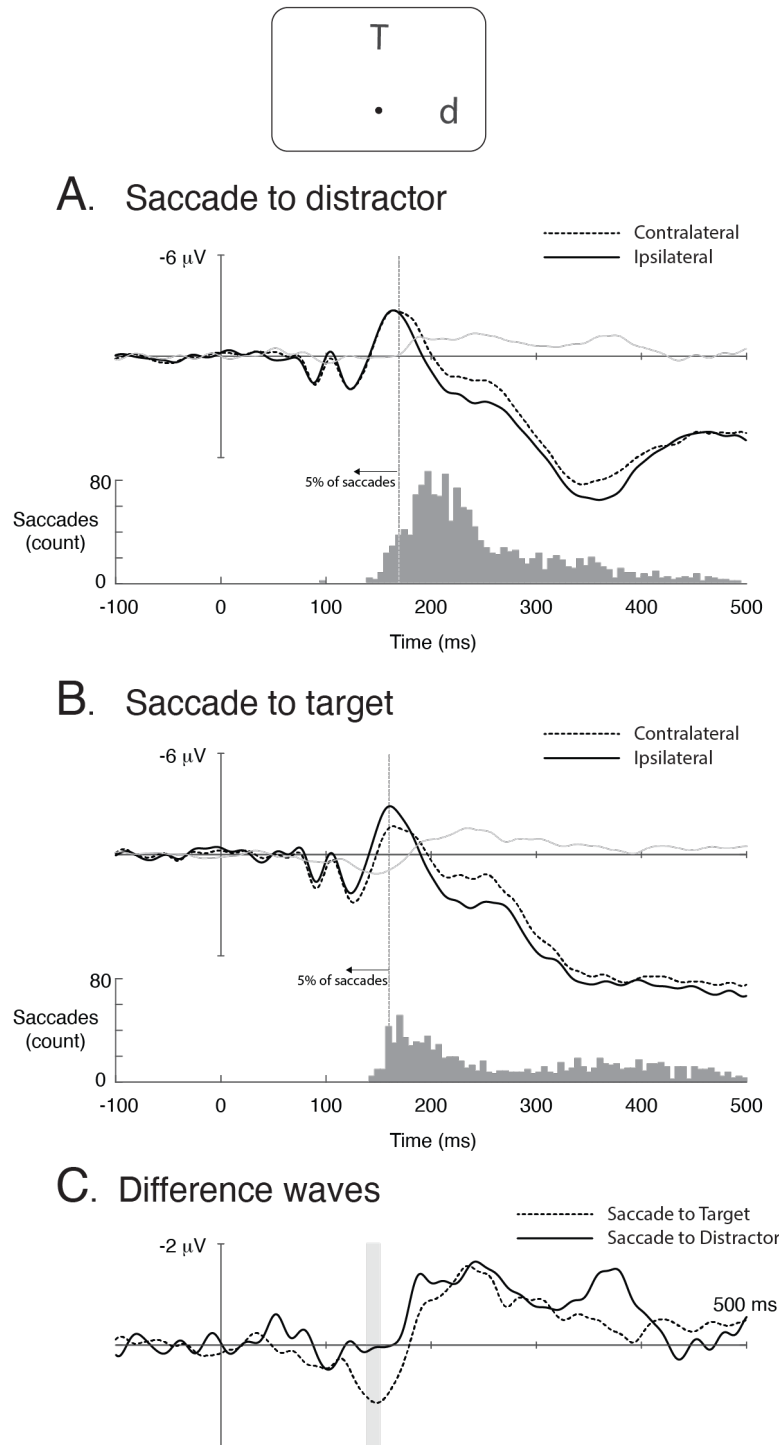
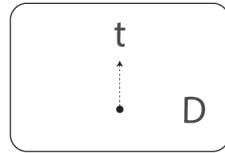
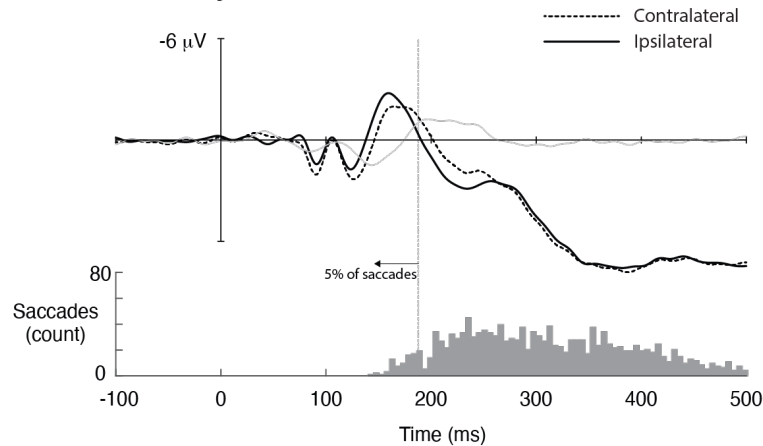


Figure 8 – ERPs from Experiment 3 following a 'Ready' cue, when the target was on the vertical meridian and the distractor at a lateral location, time-locked to the onset of the search array. The top panel is a stylized representation of the search array; the stimulus with red color is denoted by capital letter. Histograms reflect the distribution of SRTs in each condition. A.) Posterior lateral ERPs elicited contralateral and ipsilateral to the distractor in trials where the eyes were deployed to the distractor. B.) Posterior lateral ERPs elicited contralateral and ipsilateral to the distractor in trials where the eyes were deployed to the target.

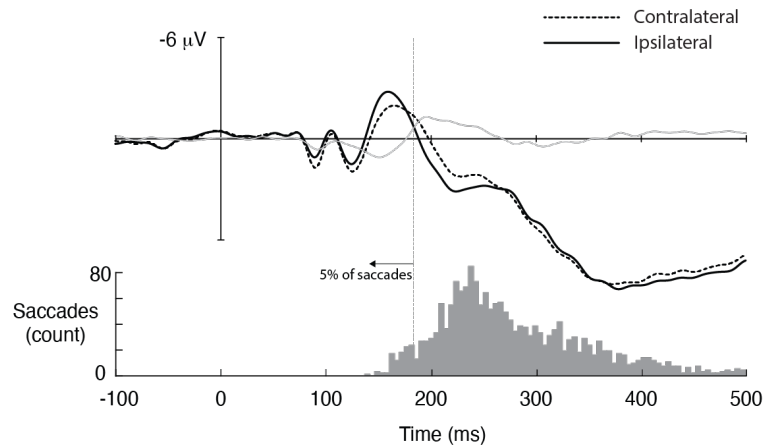
Lateral red distractor / Saccade to target



A. 'Ready' cue



B. 'Distractor' cue



C. Difference waves

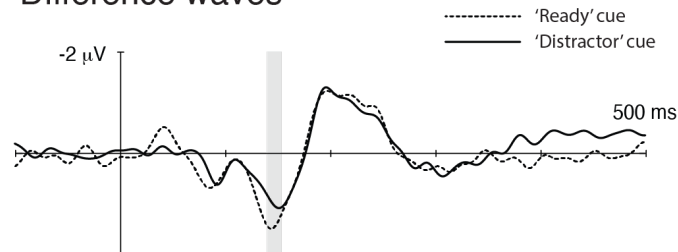


Figure 9 – ERPs from Experiment 3 when the eyes were deployed to a target on the vertical meridian, and a red distractor was successfully ignored. The top panel is a stylized representation of the search array; the stimulus with red color is denoted by capital letter. Histograms reflect the distribution of SRTs in each condition. A.) Posterior lateral ERPs elicited contralateral and ipsilateral to the distractor in trials following a 'Ready' cue. B.) Posterior lateral ERPs elicited contralateral and ipsilateral to the distractor in trials following a 'Distractor' cue.

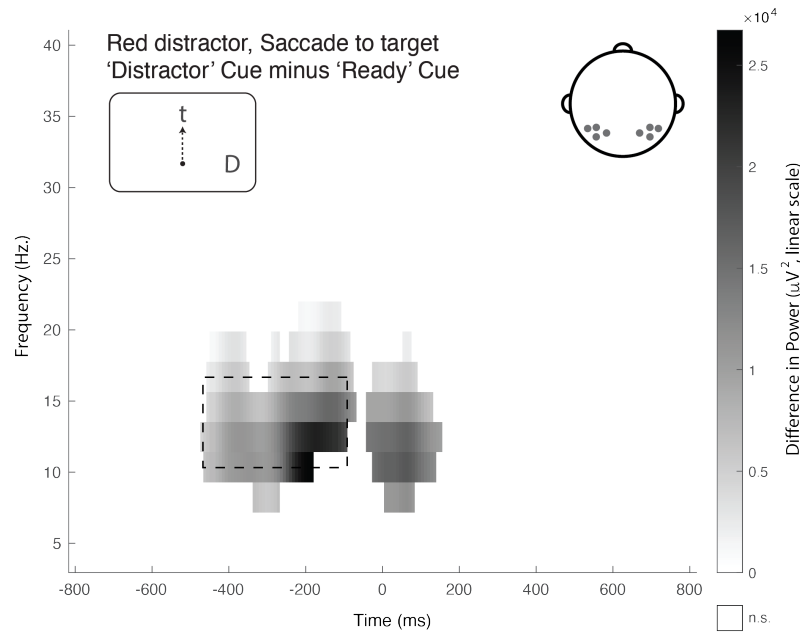


Figure 10 –Posterior bilateral oscillatory power in Experiment 3. Shaded areas reflect time-frequency combinations where oscillatory power was greater in the ‘Distractor’ rather than ‘Ready’ cue condition. The time-frequency interval identified by broken box was employed in trial-wise analysis of the relationship between oscillatory power and EEG amplitude.

of each participant (participant; AIC: 43526). This model was sequentially improved by adding a random effect for the per-participant alpha slope (AIC: 43499) and fixed factors for the additive effect of distractor elevation in the visual field and its interaction with alpha (distractor_elevation; AIC: 43498; see Equation 2). No model improvement resulted from the further inclusion of factors for the random effect of distractor elevation for each participant, the fixed effect of the target-distractor spatial proximity, the fixed effect of SRT, or the random slope of SRT for each participant.

$$(2) \text{ N2pc} \sim \text{oscillatory_power} * \text{distractor_elevation} + (1 + \text{oscillatory_power} | \text{participant})$$

ANOVA analysis identified a positive relationship between cue-elicited alpha and distractor-elicited lateral EEG ($F(1,3755) = 7.86$, $p = 0.005$), with lateral alpha predicting a decrease in the negative-polarity distractor-elicited N2pc (see Figure 7b). Distractor

elevation also had a significant effect on EEG ($F(1, 3755) = 3.88, p = 0.049$), with a distractor in the lower hemifield creating a larger N2pc. The effect of alpha interacted with distractor elevation ($F(1,3755) = 5.43, p = 0.020$), with cue-elicited alpha showing a stronger relationship with distractor-elicited N2pc when the distractor was in the lower hemifield. That the lateralized effect is more sensitive to pre-stimulus alpha when the eliciting stimulus is in the lower hemifield again suggests that variance in this brain activity reflects variance in N2pc, as the N2pc emerges more robustly for lower-field visual stimuli while the P_D emerges more robustly for upper-field visual stimuli (Hickey et al., 2009; Tay, Harms, Hillyard, & McDonald, 2019).

Experiment 3

Experiments 1 and 2 demonstrated that the spatial distractor cue elicited strategic and proactive distractor suppression that was indexed in cue-elicited lateral alpha power and reduced overt and covert selection of the distractor. Experiment 3 was designed to determine if a feature cue could have a similar impact on distractor processing. In the critical ‘distractor’ cue condition, participants were informed that the forthcoming distractor would be uniquely characterized by red color (Figure 1C). Our expectation was that the ‘distractor’ cue would elicit proactive suppression of the red distractor.

Behaviour

Trials that did not begin with fixation (4.0%), that were anticipative responses (0.7%), or that did not result in target or distractor selection (3.3%) were removed from analysis. Saccadic performance is illustrated in Figure 2e. Permutation contrasts demonstrated that in the ‘ready’ cue condition, the apparent increase in saccadic selection of the target when red color characterized the distractor rather than target was not statistically significant ($p = 0.095$). However, accuracy did improve when the red distractor was preceded by a ‘distractor’ cue rather than a ‘ready’ cue ($p < 0.001$). SRT is illustrated in Figure 2f. A RANOVA with a factor for saccade direction (target vs. distractor) and cue type (‘ready’ cue and red target; ‘ready’ cue and red distractor; ‘distractor’ cue) identified a main effect of saccade direction ($F(1,13) = 11.95, p = 0.004$), reflecting faster onset of

saccades to the distractor, and a main effect of cue ($F(2,13) = 17.15$, $p < 0.001$; interaction $F < 1$), reflecting a combination of a general speeding when the distractor was red and a specific speeding in the ‘distractor’ cue condition.

ERPs

As illustrated in Figures 8a-c, when participants made a saccade to a red target on the vertical meridian of the display after a ‘ready’ cue, the ERP elicited over contralateral visual cortex showed greater positive voltage in the interval preceding saccades, as compared to when participants deployed their eyes to the distractor. To test this difference we conducted a RANOVA with factors for electrode laterality (ipsilateral vs. contralateral) and saccadic behaviour (target-directed vs. distractor-directed) based on mean ERP voltage in a 10 ms interval centered on the cross-conditional peak of the early lateral positivity (illustrated by grey box in Figure 8c). This identified a critical interaction between electrode laterality and cue type ($F(1,13) = 7.47$, $p = 0.017$). A main effect of electrode laterality also emerged, reflecting the general reliability of the lateral positivity regardless of subsequent eye-movement behaviour ($F(1,13) = 6.99$, $p = 0.020$; cue: $F(1,13) = 2.50$, $p = 0.138$).

This finding reproduces results from Weaver, van Zoest, and Hickey (2017; Experiment 1), where this early positive component was also found to be larger when a lateral distractor was successfully ignored and the eyes were accurately deployed to a target on the vertical. This is important because early positive-polarity activity can emerge in the lateral ERP for a number of reasons, some of them possibly linked to sensory imbalances across the visual hemifields (ie. the PPC; Fortier-Gauthier, Dell’Acqua, & Jolicoeur, 2013; Jannati, Gaspar, & McDonald, 2013). The early P_D observed here, and in Weaver, van Zoest, and Hickey (2017), cannot be a product of sensory activity because, when elicited by the same stimulus display, it only emerges when the distractor is successfully ignored.

The results described above thus demonstrate the utility of the early P_D as an index of distractor suppression. In order to determine the impact of the cue on this index of distractor suppression, we focused on results observed when participants made a correct saccade to a target on the vertical meridian, ignoring a lateral red distractor (Figures 9a-c). Recent studies have found that when statistical learning (van Moorselaar & Slagter, 2019; van Moorselaar, Lampers, Cordesius, & Slagter, 2020) or spatial cues (Heuer & Schubö, 2019) support distractor suppression prior to stimulus onset, the distractor-elicited P_D reduces in amplitude. The idea here is that preemptive distractor suppression reduces the need for a suppressive response when the distractor actually appears. Results from Experiment 3 support this notion, showing that the early P_D is smaller in amplitude following a ‘distractor’ cue rather than a ‘ready’ cue.

To test the reduction in early P_D amplitude we conducted a RANOVA with factors for electrode laterality and cue type (ready cue vs. distractor cue) based on mean ERP voltage observed in a 10 ms interval centered on the cross-conditional peak of the early P_D (grey box in Figure 9c). This identified a critical interaction between electrode laterality and cue type ($F(1,13) = 6.28$, $p = 0.026$), reflecting the reliable decrease in early P_D amplitude in the ‘distractor’ cue condition. An additional main effect of electrode laterality was identified ($F(1,13) = 8.17$, $p = 0.013$), demonstrating the general reliability of the early P_D across cueing conditions (cue: $F(1,13) = 4.03$, $p = 0.066$).

Time-frequency analysis

As illustrated in Figure 10a, when trials were preceded by a ‘distractor’ cue rather than a ‘ready’ cue, and participants therefore knew with certainty that red color would characterize the distractor stimulus, bilateral oscillatory activity in the pre-target interval increased through the alpha (8 – 12.5 Hz) and low beta range (12.5 – 25 Hz).

As in Experiment 2, we approached results with the idea that this oscillatory activity might predict variance in distractor processing as indexed in the post-target ERP. Our specific expectation was that pre-stimulus suppression, as indexed in oscillatory power,

might reduce the need for post-stimulus distractor suppression, as indexed in early P_D . We tested for this by a.) extracting power across a frequency band (10.4 – 16.7 Hz.) and latency interval (-480 to -60 ms) where cue type had a significant impact on oscillatory power, and b.) extracting mean EEG amplitude in a 10 ms post-target latency period centered on the cross-conditional peak of the early P_D (grey box in Figure 9c).

As in earlier experiments, we rank transformed these values and used mixed linear modelling and model selection to identify the relationship between cue-elicited oscillatory power and the early P_D . An initial model contained a continuous fixed effect predictor for oscillatory power and a random effect for the intercept of each participant (AIC: 18217). This model was sequentially improved by adding a fixed effect for SRT and the interaction of oscillatory power with SRT (AIC: 18201), and random effects for the per-participant alpha intercept and slope (AIC:18199; see Equation 3). Inclusion of per-participant intercept and slope for SRT did not lead to model improvement.

$$(3) \text{ early_}P_D \sim \text{oscillatory_power} * \text{SRT} + (1 + \text{oscillatory_power} | \text{participant})$$

ANOVA analysis of this model identified a positive relationship between cue-elicited oscillatory power and EEG amplitude ($F(1,1759) = 7.21$, $p = 0.007$), with cue-elicited alpha / beta predicting an increase in amplitude of the early P_D . SRT also had a significant positive effect on EEG ($F(1,1759) = 22.71$, $p < 0.001$), with larger amplitude early P_D associated to slower saccade onset. Critically, these effects interacted ($F(1,1759) = 13.30$, $p < 0.001$).

To gain further insight on this interaction we conducted a median split based on SRT and fitted each of the resulting datasets with a simple model containing a fixed effect for oscillatory power and a random effect for the per-participant intercept (see Equation 4).

(4) $\text{early_P}_D \sim \text{oscillatory_power} + (1 \mid \text{participant})$

In analysis of short-latency SRT data, the relationship between oscillatory power and early P_D amplitude was negative, such that oscillatory power predicted a smaller P_D (parameter estimate: -0.0277), whereas in analysis of long-latency SRT data, the relationship between oscillatory power and early P_D was positive, such that oscillatory power predicted a larger P_D (parameter estimate: 0.0245). Bilateral alpha thus predicted a reduction in early P_D when participants responded quickly, but an increase in early P_D when participants responded at longer latency.

DISCUSSION

We demonstrate that foreknowledge of distractor characteristics leads to strategic, proactive distractor suppression. Experiments 1 and 2 employed a spatial cue, showing that the eyes were less likely to be deployed to a cued distractor when the target and distractor appeared in close spatial proximity. In both experiments, this change in overt behaviour was preceded by a reduction of the distractor-elicited N2pc, reflecting a decrease in attentional selection of the distractor. In Experiment 1, analysis of saccade deviation suggested that cue-elicited distractor suppression was implemented prior to onset of the search array. In Experiment 2, this proactive suppression was linked to the emergence of cue-elicited lateral alpha. As the target only ever appeared on the vertical meridian of the display, but the alpha effect was lateralized, the effect cannot be easily linked to monitoring of target location or other target-related processes. Analysis showed that the trial-wise magnitude of pre-target lateral alpha predicted trial-wise reduction of post-target distractor-elicited N2pc. Participants therefore appear able to strategically and proactively suppress distractors at a cued location, eliciting lateral alpha, and this reduces the propensity to covertly and overtly select the distractor when it appears.

Experiment 3 investigated the impact of a cue identifying a unique distractor feature. The 'distractor' cue identified with 100% validity that the distractor would be red,

whereas the ‘ready’ cue indicated that there was a 50% chance the distractor would be red and a 50% chance that the target would be red. The distractor cue led to a decrease in the proportion of saccades to the distractor. When the eyes were deployed to the target, post-target ERPs showed emergence of an early distractor-elicited P_D , reflecting online, stimulus-triggered suppression of the lateral distractor. The cue reduced the size of this early P_D , suggesting that cue-elicited suppression in the pre-target interval limited the need for stimulus-triggered suppression when the distractor appeared.

The semantic cue employed in Experiment 3 created an increase in bilateral alpha / low beta power – conceptually reproducing earlier results (Payne et al., 2013) – and trial-wise variance in this signal predicted post-target distractor-elicited early P_D . Bilateral alpha over posterior cortex has been interpreted as a general down-weighting of perceptual input (Bonnefond & Jensen, 2012; de Vries, Savran, van Driel, & Olivers, 2019), and this is consistent with results showing that it predicts a decrease in the need for stimulus-triggered distractor suppression – as indexed in early P_D – when participants make quick saccadic response to the target. However, the cue also improves target-directed saccadic accuracy and speed, which is hard to reconcile with the idea that all stimuli representations have been degraded. One alternative is that bilateral alpha contributes to perceptual down-weighting of the cued distractor specifically, leaving the target unaffected (Folk & Remington, 1998). This suppression could act to reduce the salience of a discrete feature – ‘redness’ in our experiment – or could suppress the entire feature dimension, so that discontinuities along this dimension do not ‘pop out’ (Liesefeld & Müller, 2019).

Why do we see unambiguous evidence of strategic, proactive distractor suppression, where prominent recent studies have not? A critical determinant appears to be that the target and distractor are defined within the same featural dimension. That is, the target and distractor in our experiments were rendered salient by orientation, and direction or magnitude of orientation played a role in defining which stimulus was the target. Studies showing an effect of proactive distractor suppression tend to define target and distractor

within the same dimension (Munneke, van der Stigchel, and Theeuwes, 2008; Munneke, Heslenfeld, Usrey, Theeuwes, and Mangun, 2011; Ruff & Driver, 2006). In contrast, Wang and Theeuwes (2018) recently failed to find an effect of a distractor cue when the target was consistently defined by unique form and the salient distractor by unique color. Visual processing is segregated such that retinotopic brain areas respond preferentially to discrete stimuli features like color, orientation, and motion (eg. Zeki & Shipp, 1988), and the definition of targets and distractors within the same featural dimension increases distractor interference (Liesefeld & Müller, 2019). One possibility is therefore that proactive distractor suppression is employed only when target-distractor similarity is high (van Zoest & Donk, 2008; Conci, Deichsel, Müller, & Töllner, 2019) and distractor representations intrude on target representations within the same dimension-specific cortical areas.

Competition created by physical proximity also appears to play an important role in determining how proactive distractor suppression impacts behaviour and brain activity. Experiments 1 and 2 show that proactive distractor suppression of a cued location impacts covert and overt selection of the distractor only when the target and distractor appear in close spatial proximity. This is consistent with what we know of distractor suppression more broadly. While the existence of strategic, proactive distractor suppression has been debated, distractor suppression during target selection is widely accepted as a core mechanism in the resolution of target information (eg. Moran & Desimone, 1985; Chelazzi, Miller, Duncan, & Desimone, 1993; Luck, Chelazzi, Hillyard, & Desimone, 1997). This ‘secondary’ distractor suppression (Noonan et al., 2019) occurs during target resolution and increases as the distance between target and distractor reduces (Mounts, 2000; Hickey & Theeuwes, 2011; Hilimire, Mounts, Parks, & Corballis, 2009; Hopf, Boehler, Luck, Tsotsos, Heinze, & Schoenfeld, 2006), reflecting an increasing need for the resolution of neural ambiguity as the stimuli come to stimulate an overlapping set of retinotopic neurons (Luck, Girelli, McDermott, & Ford, 1997; Desimone & Duncan, 1995; Tsotsos, Culhane, Wai, et al., 1995). The relationship between spatial competition and distractor suppression identified in our data is

important to the interpretation of extant results. A prominent recent failure to find an effect of a spatial distractor cue from Noonan et al. (2016) employed a design with targets and distractors presented either to separate upper and lower visual hemifields or separate left and right hemifields. The design was therefore similar to that employed in conditions of Experiments 1 and 2 where the target and distractor appeared distant from one another, and where we found no impact of the distractor cue on behaviour or post-target brain activity.

A final possibility is that strategic, proactive distractor suppression might develop from a basis of implicit learning. In extant studies targets and distractors tend to appear with equal frequency at the same locations. In contrast, in Experiments 1 and 2, distractors appeared at lateral locations where targets never appeared, and participants were never required to select stimuli at these locations. Over the course of ~800 trials, participants had the opportunity to learn how to ignore stimuli at these locations. Similarly, in Experiment 3, red color more commonly characterized the distractor than it did the target, giving participants the opportunity to learn how to effectively suppress red objects. This prior experience may be required in order for volitional control of suppression to emerge. That is, suppression of specific features or locations may become strategically accessible only once this cognitive operation is familiar, unambiguous, and well-practiced, and when characteristics of distractors do not commonly overlap with characteristics of targets.

Cue-elicited alpha emerged in all three experiments and, on the face of it, this conflicts with a developing literature looking at the impact of prediction and statistical learning on distractor suppression (Ferrante et al., 2017; Wang & Theeuwes, 2018; Won & Geng, 2020). Distractor suppression fostered by statistical learning does not appear to be associated with alpha (Noonan et al., 2016; van Moorselaar & Slagter, 2019, 2020; but see Wang, van Driel, Ort, & Theeuwes, 2019) and this has contributed to a wholesale discounting of the relationship between alpha and distractor suppression (Foster & Awh, 2019; Noonan et al. 2019; van Moorselaar & Slagter, 2020). This may be premature. It

seems possible that the distractor suppression created by statistical learning may be qualitatively different from that created by strategy. Statistical learning of distractor status over repeated experience could rely on slow mechanisms, like synaptic plasticity, and involve long-range neuromodulatory architecture (eg. Roelfsema & van Ooyen, 2005). This kind of latent distractor suppression, instantiated in synaptic weighting between idle cells, would not necessarily be associated with brain signal in the cue-target interval. In contrast, strategic, cue-elicited distractor suppression must be implemented in the cue-target interval and is therefore more likely to elicit discernible brain activity in this time.

One particular challenge to the relationship between alpha and distractor suppression has come from studies employing frequency-tagged visual stimuli. In frequency-tagging experiments, stimuli are presented with oscillating contrast at a specific frequency, generating a neural response with corresponding frequency. When stimuli are attended, this brain signal increases in power (eg. Müller, Teder-Sälejärvi, & Hillyard, 1998; but see Adam, Chang, Rangan, & Serences, 2020), which leads to the reasonable expectation that when stimuli are suppressed – generating lateral alpha – the tagged brain signal should decrease in power. But this is not what is observed (Antonov, Chakravarthi, & Andersen, 2020; Zhigalov & Jensen, 2020). Results from the current study provide some insight on this null relationship. We find that distractor suppression predicts variance in lateralized brain responses associated with relatively high-level visual cortex (Hopf, Luck, Girelli, Hagner, Mangun, Scheich, & Heinze, 2000). In contrast, the oscillatory signal induced by frequency-tagging tends to emerge over the occipital pole (eg. Müller et al., 1997), suggesting that it originates from early visual cortex (Di Russo et al., 2007). This raises the possibility that distractor suppression indexed in lateral alpha impacts stimuli representations in visual areas that simply do not express the frequency-tagging signal (Zhigalov & Jensen, 2020).

In summary, we present unambiguous evidence that strategic, proactive suppression of visual distractors leads to attenuated attentive and oculomotor responses to these

stimuli, and that this suppression is linked to the power of pre-stimulus alpha. Knowing the characteristics of visual distractors helps you ignore them.

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