A Temporal Dependency Account of Attentional Inhibition in Oculomotor Control

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Running Title: Temporal dependency

Number of Figures: 11

Number of Pages: 46

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Abstract

We used concurrent electroencephalogram (EEG) and eye tracking to investigate the role of covert attentional mechanisms in the control of oculomotor behavior. Human participants made speeded saccades to targets that were presented alongside salient distractors. By subsequently sorting trials based on whether the distractor was strongly represented or suppressed by the visual system – as evident in the accuracy (Exp. 1) or quality of the saccade (Exp. 2) – we could characterize and contrast pre-saccadic neural activity as a function of whether oculomotor control was established. Results show that saccadic behavior is strongly linked to the operation of attentional mechanisms in visual cortex. In Experiment 1, accurate saccades were preceded by attentional selection of the target – indexed by a target-elicited N2pc component – and by attentional suppression of the distractor – indexed by early and late distractor-elicited distractor positivity (Pd) components. In Experiment 2, the strength of distractor suppression predicted the degree to which the path of slower saccades would deviate away from the distractor en route to the target. However, results also demonstrated clear dissociations of covert and overt selective control, with saccadic latency in particular showing no relationship to the latency of covert selective mechanisms. Eye movements could thus be initiated prior to the onset of attentional ERP components, resulting in stimulus-driven behaviour. Taken together, the results indicate that attentional mechanisms play a role in determining saccadic behavior, but that saccade timing is not contingent on the deployment of attention. This creates a temporal dependency, whereby attention fosters oculomotor control only when attentional mechanisms are given sufficient opportunity to impact stimuli representations before an eye movement is executed.

Keywords: Vision, Attention, Oculomotor Control, Eye Movements, Electroencephalography

1. Introduction

Adaptive selective behavior relies on the ability to minimize reflexive eye movements to salient but task-irrelevant environmental stimuli. In humans and other primates, oculomotor control of this nature is thought to be supported by a network of frontal brain areas that suppress responses to salient distractors in the motor association cortex and midbrain (e.g., Munoz & Everling, 2004; Lennert & Martinez-Trujillo, 2011). Lesion and inactivation studies in humans (e.g., Guitton, Buchtel, & Douglas, 1985) and monkeys (e.g., Pierrot-Deseilligny, Rivaud, Gaymard, & Agid, 1991; Koval, Lomber, & Everling, 2011) demonstrate that the dorsolateral prefrontal cortex (DLPFC) plays a particularly crucial role in this function, with a dominant model proposing that this brain area acts to directly quash distractor-directed saccadic representations in the superior colliculus (SC; Munoz & Everling, 2004; though see Gazzaley & Nobre, 2012; Johnston, Koval, Lomber, & Everling, 2014).

It is less clear to what degree oculomotor control involves the inhibition of representations in the visual system. Electrophysiological work with primate models has largely been unable to address this question because of a focus on structures such as the frontal eye fields (FEF), lateral intraparietal area (LIP), and SC, which are strongly integrated with the saccade execution system (Everling, Dorris, & Munoz, 1998; Gottlieb, Kusunoki, & Goldberg, 1998; Gottlieb & Goldberg, 1999; Everling & Munoz, 2000; Suzuki & Gottlieb, 2013). Effects at this level may indirectly reflect suppression of premotor eye-movement sequencing rather than perceptual representations. In contrast, studies of micro-stimulation and infusion in monkey FEF show unambiguous effects on target detection (Moore & Fallah, 2001) and neural responses in early visual cortex (e.g., Moore & Armstrong, 2003; Ekstrom, Roelfsema, Arsenault, Bonmassar, & Vanduffel, 2008; Noudoost & Moore, 2011), but to date these invasive techniques have not been used to investigate representations of distractors.

The control of overt saccadic performance is closely linked to the control of covert attention (Corbetta et al., 1998; Moore, Armstrong & Fallah, 2003) and distractor inhibition in attentional selection has been the subject of more extended investigation. Inhibition plays a clear role in

attentional resolution of target features (Moran & Desimone, 1985; Chelazzi, Miller, Duncan, & Desimone, 1993), but this effect tends to emerge only when targets and nontargets are physically close and neural coding is accordingly ambiguous (Desimone & Duncan, 1995). Evidence of distractor inhibition in animal electrophysiology is uncommon when stimuli are separated by large distances (e.g., McAdams & Maunsell, 1999; Treue & Martinez-Trujillo, 1999). Nevertheless, long-distance inhibition has been inferred from human event-related potential (ERP) work, where two lateralized components – the N2pc (Luck & Hillyard, 1994a, 1994b) and distractor positivity (Pd; Hickey, Di Lollo, & McDonald, 2009) – emerge over occipital cortex under circumstances where distractor inhibition might be expected. The N2pc appears contralateral to the location of an attended stimulus and reflects target-centered cortical activity involved in attentional selection, possibly through the sheltering of target information via suppression of input to cells representing this stimulus (Luck, Girelli, McDermott, & Ford, 1997), whereas the Pd is elicited in visual cortex contralateral to ignored stimuli, suggesting that it reflects more direct action on distractor representations (Hickey et al., 2009). However, the relationship between these ERP indices of attentional selection and oculomotor control is not obvious and has not yet been the subject of research focus.

Here we use concurrent recording of eye movements and electroencephalogram (EEG) to investigate the relationship between attentional mechanisms of distractor suppression and oculomotor control. We approached experimentation with the broad idea that electrophysiological indices of attentional processing should be evident prior to saccade onset if visual suppression determines eye movement programming. Moreover, examination of this brain activity should predict the accuracy and quality of subsequent eye movements. To test these ideas we had participants make speeded saccades to targets presented alongside salient distractors. By subsequently sorting trials based on the accuracy (Exp. 1) or quality (Exp. 2) of the saccadic response we were able to isolate the N2pc and Pd components when oculomotor control was established and

when it was not, and thus to track the mechanisms of attention underlying these components during the programming of saccadic eye movements.

2. Materials and Methods

In our general paradigm participants were presented with visual search arrays composed of line elements (see Fig. 1). Each array contained a target and distractor defined by unique orientation, and participants were instructed to make an eye movement to one element while ignoring the other. Critically, the salience of these objects could be manipulated by increasing the angular difference of the target and distractor line elements from background elements (van Zoest & Donk, 2006).

In Experiment 1, the target was defined by orientation tilt in a specific direction, left- or right-tilted. Participants completed two blocked conditions, one in which the target was of greater salience than the distractor, and the other where this mapping was reversed. In both cases the location of target and distractor elements was randomly determined in each trial (see Fig. 1A). Our expectation was that when the target was salient, the distractor would be easily ignored and the eyes would be rapidly and accurately deployed to the target. However, when the distractor was salient, we expected that participants would commonly make erroneous saccades to this stimulus. Under these circumstances we would be able to compare electrophysiological signals elicited by identical displays as a function of subsequent saccadic performance.

Our core hypothesis was that accurate performance would be predicted by the post-stimulus emergence of N2pc and Pd components in the ERP. Thus a.) correct deployment of the eyes would be preceded by suppression of the distractor, as indexed by a distractor-elicited Pd, alongside target processing, as reflected in a target-elicited N2pc, but b.) misdeployment of the eyes would be preceded by a distractor-elicited N2pc and a target-elicited Pd.

We approached our results with additional interest in the possibility that pre-stimulus oscillatory activity might constitute an additional predictor of overt oculomotor performance. Occipital alpha (6-12 Hz.) in particular has been linked to mechanisms involved in the suppression of visual signals (Worden, Foxe, Wang, & Simpson, 2000; Kelly, Lalor, Reilly, & Foxe, 2006), and we accordingly approached experimentation with the idea that increased alpha might predict saccadic accuracy by modulating the speed of visual processing.

As detailed and discussed below, saccadic accuracy in Experiment 1 followed a time-course consistent with that observed in earlier eye-tracking studies: fast saccades were directed to the distractor whereas slow saccades were directed to the target (cf. van Zoest, Donk, & Theeuwes, 2004). A goal of Experiment 2 was to tease apart this confound of latency and accuracy. To this end, the target stimulus in Experiment 2 was always presented either directly above or below fixation, with the distractor presented at one of two locations slightly lateral to the straight-line path between fixation and target (see Fig. 1B). Our expectation was that accuracy in this task would be very high. Accordingly, analysis of eye movement results from Experiment 2 did not focus on saccadic accuracy, but rather on distractor-evoked deviation in the saccadic path. Saccades are known to curve away from distractors when these objects have been suppressed in the oculomotor system (Sheliga, Riggio, & Rizzolatti, 1994; Doyle & Walker, 2001) and these saccade trajectory deviations can be used as a continuous measure of the strength of distractor suppression at the onset of a saccadic response (Van der Stigchel, Meeter, & Theeuwes, 2006; Hickey & van Zoest, 2012). Experiment 2 was designed to test the hypothesis that this overt expression of distractor suppression would be related to the covert expression of distractor suppression indexed in the Pd.

2.1 Participants

Twenty-three participants were randomly selected from the University of Trento participant pool to take part in Experiment 1 and 20 participants were randomly selected to take part in Experiment 2.

All gave informed consent before participating in exchange for payment or course credit, had normal or corrected-to-normal vision, and no participant completed both experiments. All procedures were approved by the University of Trento Ethics Committee.

Three participants in Experiment 1 were excluded from primary analyses due to a high rate of incorrect saccades when the distractor was salient (>75%), and two were excluded from Experiment 2 due to a high rate of rejected trials across all task conditions (>30%; cf. trial rejection criteria below). The remaining 20 participants in Experiment 1 (19 right-handed, 22.6 years mean age) and the remaining 18 in Experiment 2 (15 right-handed, 23.9 years mean age) all happened to be female. The age and sex of our participants reflects the demographics of our participant pool, which is largely composed of Psychology undergraduates.

2.2 Stimulus Presentation

Both experiments were programmed using Matlab (version 8.0.0.783, The MathWorks, Inc., Natick, MA). Experiment 1 was presented on a Dell® 1907FPT 19" LCD Monitor (1024 × 768 pixel resolution; 60 Hz refresh rate) and Experiment 2 was presented on an Asus VG236H 23" LCD Monitor (1980 × 1080 pixel resolution; 120 Hz refresh rate).

Stimuli consisted of a 15 × 15 square array of white line elements presented on a black (Exp. 1) or grey (Exp. 2) background surrounding a central fixation point (see Fig. 1). The array subtended approximately 27° × 27° of visual angle (each element ~0.1° × 1°). Each array contained both a target and distractor line element, defined by their off-vertical orientation, embedded among vertically oriented nontargets.

In Experiment 1, the target and distractor were 20° or 70° to the left or right of vertical, were always of opposing orientation, and were presented at one of four possible equidistant locations 7.72° above, below, left, or right of fixation (see Fig. 1A). To allow for the association of lateralized ERP responses to discrete stimuli, if the target was presented on the vertical midline, the distractor

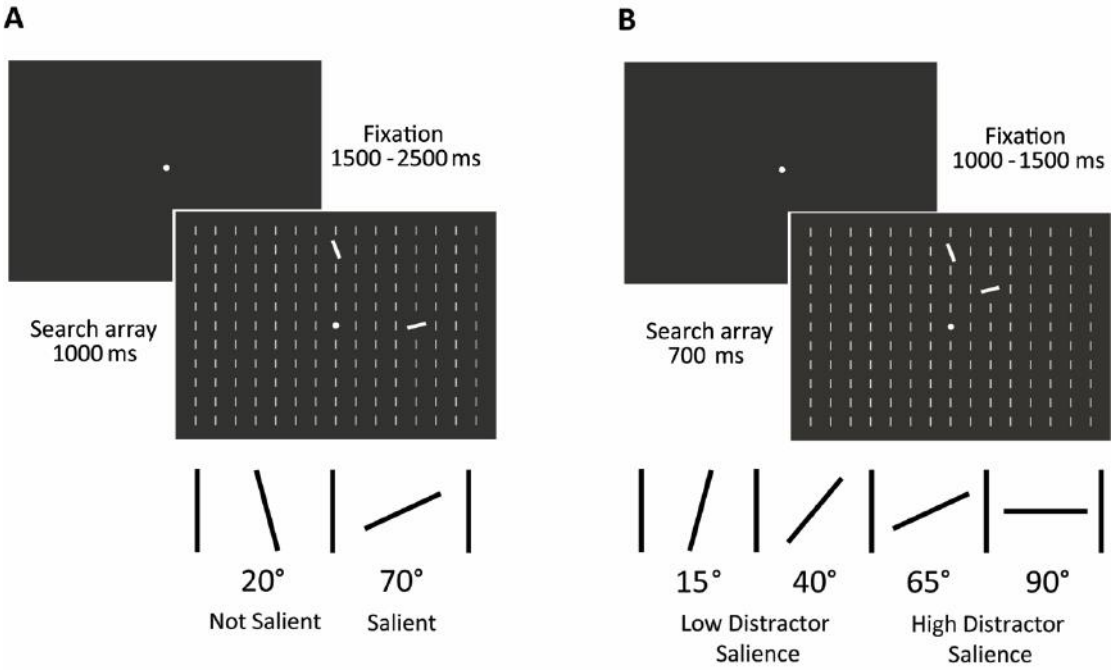

Figure 1. Trial sequence for Experiments 1 & 2. Participants made a rapid saccade to a uniquely oriented target line element while attempting to ignore a uniquely oriented distractor line element. Oblique line elements are rendered larger in the figure to facilitate identification; in the actual experiment all line elements were of the same size. (A) Experiment 1. The target was the relatively more salient element for half the experiment and the less salient element for the other half. Unique elements were defined by their opposing orientations (left vs. right-tilted) and could appear in one of four equidistant locations. (B) Experiment 2. Unique elements were defined by location, with the target either above (pictured) or below fixation on the vertical midline, and the distractor either to the right (pictured) or left in the same (upper or lower) visual field as the target. Distractors were either of low (15° or 40° orientation offset) or high salience (65° or 90° offset). The target was always offset at 15°.

was presented laterally along the horizontal meridian and vice versa (Woodman & Luck, 2003; Hickey et al., 2006). With this design, stimuli presented on the vertical meridian will impact each of the waveforms ipsilateral and contralateral to the lateralized stimulus equally, and thus cannot produce lateralized activity in the resulting ERP.

In Experiment 2, the target was 15° off vertical, with the distractor tilted 15°, 40°, 65°, or 90° (see Fig. 1B). Tilt direction was random for both target and distractor, with the target defined by its location directly above or below fixation (9.56° from fixation). Distractors were presented 5.41° from fixation on a patch that was 45° left or right from the straight-line path between fixation and target.

2.3 Procedure and Design

Participants initiated each trial by pressing a button while fixating on a central point, which also initiated a correction for eye-tracker drift. The fixation point subsequently remained onscreen for 1500–2500 ms (1000–1500 ms in Exp. 2) before the stimuli array appeared for 1000 ms (700 ms in Exp. 2). Participants were instructed to maintain fixation until the array appeared and to then make a speeded saccade toward the target element. Feedback tones indicated when saccades were too fast (<80 ms) or slow (>600 ms) and, in Experiment 2, when gaze was within 1.5° of the distractor. Participants were informed of average saccade reaction times (Exp. 1) or accuracy (Exp. 2) at the end of each trial block and completed 24 practice trials (20 in Exp. 2) followed by 12 blocks of 64 trials (14 blocks in Exp. 2).

In Experiment 1, one of the unique elements had a greater degree of orientation offset from the surrounding homogenous vertical nontargets, rendering it more salient (see Fig. 1A). The more-salient item acted as target for half of the experiment, with roles reversed for the other half of the session. The order of salience conditions was counterbalanced across participants, as was the specific orientation (left- vs. right-tilted) that characterized the target. Target and distractor location were counterbalanced within participants and presented in a random order.

In Experiment 2, the target was defined by location rather than orientation. Target and distractor positions and orientations (both degree and direction of offset) were counterbalanced within participants.

2.4 Data Recording

Eye movement and EEG data were simultaneously recorded. A desk-mounted EyeLink® 1000 (SR Research, Ltd., Mississauga, Canada) recorded the position of the right eye at 1000 Hz. EEG was recorded from the scalp using 62 Ag/AgCl electrodes arranged according to the 10/20 system

(Jasper, 1958). Two further electrodes were placed on the left and right mastoids and impedance was kept below 20 KΩ for all electrodes. EEG was amplified online using a BrainAmp amplifier (Brain Products GmbH, Munich, Germany), digitized at a sampling rate of 1000 Hz, referenced online to the right mastoid, and re-referenced offline to the algebraic average of both mastoids. During recording, an anti-aliasing filter with bandpass of 0.016–250 Hz was applied and data were subsequently digitally low-pass filtered at 35 Hz (zero-phase non-causal 84-point least-square FIR filter; -1 dB at 32.5 Hz; -6 dB at 37.5 Hz; -36 dB per octave).

2.5 Analysis

Data was analyzed using Matlab (Mathworks, Natick MA), the EEGLAB toolbox (v13.1.1; Delorme & Makeig, 2004), and the EYE-EEG extension to EEGLAB (v0.41; Dimigen, Sommer, Hohlfeld, Jacobs, & Kliegl, 2011).

2.5.1 Eye movement behaviour. Saccades were defined when eye movement velocity exceeded 30°/s or acceleration exceeded 8000°/s². The saccadic response time (SRT) was defined as the time between stimulus onset and the beginning of the first saccade larger than 3°. A saccade was considered to be directed to the target or distractor if it landed within 4° of that stimulus.

In Experiment 2 saccade trajectory deviations were defined as mean angular deviation between a straight line from saccade starting point to target center and straight lines from the saccade starting point to each 1-ms samples constituting the saccade path (see Van der Stigchel et al., 2006, for a detailed description of saccade deviation analysis). The first five samples of the saccade (5 ms) were excluded from this measure to reduce noise. Negative deviations index saccadic deviations away from the distractor location.

2.5.2 ERPs. EEG was segmented into epochs beginning 1000 ms before stimulus onset and ending 1500 ms (Exp. 1) or 700 ms (Exp.2) post-stimulus. Independent components (Bell & Sejnowski, 1995) were extracted from combined EEG and eye position data, and artifactual

components stemming from eye movements were rejected based on their covariance with eye movement data (using saccade-to-fixation variance ratio criterion of 1.1; Plöchl, Ossandon, & König, 2012). An interval beginning 100 ms before stimulus onset and ending 50 ms after was used to baseline correct the ERP.

In Experiment 1, ERPs were computed for each of eight conditions defined by factors of saliency (Salient Target vs. Salient Distractor), laterality (Lateral Target vs. Lateral Distractor) and saccade outcome (target-directed vs. distractor-directed). No analysis was conducted on the Lateral Target / Salient Target condition due to participants making too few distractor-directed saccades required to generate a reliable ERP for comparison across saccade outcome (*M* = 18.65 trials). The mean number of trials in each of the six remaining conditions was 90.23 +/- 22.41 SD. In Experiment 2, ERPs were computed for each level of distractor salience (high vs. low) and saccade latency (fast vs. slow). The mean number of trials in these conditions was 191.47 +/- 5.52 SD. Ipsilateral and contralateral ERPs were calculated in reference to the single salient stimulus presented at a lateral location in each display.

In both experiments, component peaks were identified within preselected intervals (150–300 ms for N2pc, Luck & Hillyard, 1994a, 1994b; 100–400 ms for Pd, Sawaki & Luck, 2013) and the size of the latency window varied as a function of the component length in time (10 ms window for Exp 1 Pd; 50 ms for N2pc and Exp 2 Pd components). When conditions are being compared in which a component clearly emerged in only one of the two conditions, the latency of this effect is used to extract amplitude in the contrasting condition.

Our study is designed to examine ERP activity elicited in close temporal proximity to eye movement behaviour, but eye movements create artefacts in the electrophysiological data. To ensure that our data accurately reflected brain activity we adopted two approaches to the data. First, as described above, we conducted an eye-tracker informed independent component analysis (ICA) to identify sources of artifactual variance, which were subsequently removed from the data.

This ICA importantly relied on temporally-fused EEG and tracker eye position data. Unlike electroculogram, eye tracker data is independent of EEG, and this approach accordingly allows for highly accurate identification of the electrical activity stemming from eye movements (Dimigen et al., 2011). Second, and more importantly, we ensured that ERP components of interest could be identified in the interval preceding the onset of eye movements. Thus when components of interest in the stimulus-locked ERP coincided with eye movements - operationally defined as the interval in which 95% of eye movements occurred - we additionally identified and analyzed these components in ERPs time-locked to the onset of the saccade. In these analyses, saccade-locked ERP components are measured across the 50 ms preceding saccade onset.

2.5.3 Time-frequency. We calculated pre-stimulus oscillatory power by applying Morlet wavelet transforms to individual trials. Wavelet cycles increased linearly from 1 cycle at 4 Hz to 8 cycles at 30 Hz and measures were pooled across occipital electrodes PO3/4, PO7/8, POz, O1/2, and Oz.

3. Results

3.1 Experiment 1

3.1.1 Behavior. Trials were rejected if saccades did not begin at fixation (start point >3° from fixation; 1.02% of trials), did not land at either target or distractor locations (1.99%), or if they were anticipative (<60 ms; 0.03%) or late (>2.5 standard deviations later than participant mean SRT; 2.23%). An additional 0.20% of trials were rejected due to a computer error. This led to the overall exclusion of 5.46% of trials in Experiment 1.

A paired-samples *t* test showed a greater proportion of correct saccades when the target was salient (M = 0.77 vs. 0.55), $t(19) = 5.88$, $SE = 0.04$, $p < .001$, $d = 1.63$. A two-way repeated measures analysis of variance (rANOVA) was conducted on SRTs using saliency (salient target vs. salient distractor) and saccade outcome (correct vs. incorrect) as within-participants factors. Analyses revealed a main effect of saccade outcome, $F(1, 19) = 41.34$, $MSE = 226.39$, $p < .001$, $\eta^2p = 0.69$, and

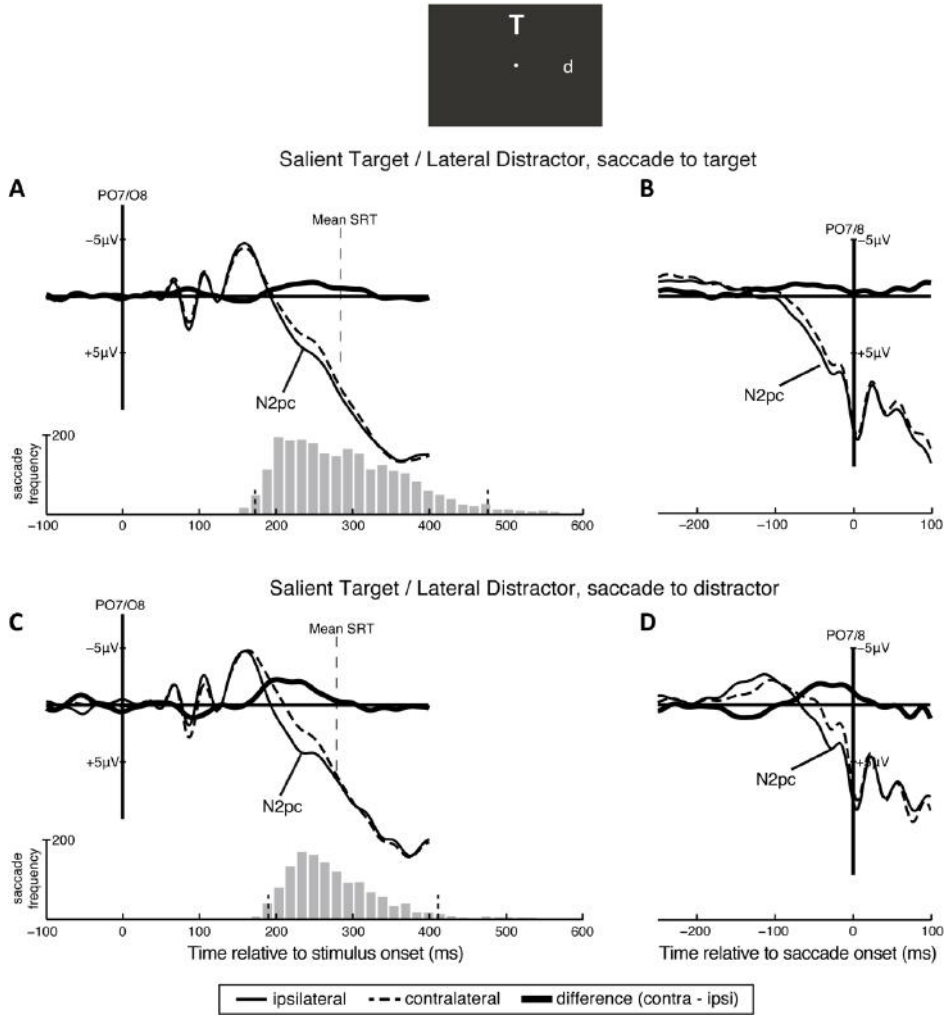

Figure 2. Stimulus-locked (A & C) and saccade-locked (B & D) lateralized event-related potentials (ERPs) for the salient target / lateral distractor display, presented in separate panels according to saccade outcome (target-directed: A & B; distractor-directed: C & D). Ipsilateral and contralateral electrode sites are plotted separately (averaged over PO7 and PO8 electrode locations). Difference waveforms were derived by subtracting relevant ipsilateral from contralateral waveforms. Negative voltages are plotted upward. Mean SRTs are indicated by the long vertical dashed line. Frequency distribution of SRTs aggregated across participants are presented below relevant ERPs. 95% of SRTs occurred within small vertical dashed lines. Paradigm schematic included as a reference, where 'T' denotes salient target and 'd' denotes the distractor.

a saliency × saccade outcome interaction, $F(1, 19) = 285.88$, $MSE = 109.68$, $p < .001$, $\eta^2p = 0.94$. Planned *t* tests showed that correct SRTs were faster when the target was salient ($M_{Salient\ Target}$ = 267 ms vs. $M_{Salient\ Distractor}$ = 318 ms; $t(19) = -8.32$, $SE = 6.13$, $p < .001$, $d = -1.01$), whereas incorrect SRTs were slower ($M_{Salient\ Target}$ = 285 ms vs. $M_{Salient\ Distractor}$ = 257 ms; $t(19) = 3.87$, $SE = 7.29$, $p < .001$, d =

0.71). Participants were thus faster and more accurate when the target was more salient than the distractor.

3.1.2 ERPs. ***3.1.2.1 Salient Target / Lateral Distractor.*** Figure 2 presents the occipital ERPs elicited by a display containing a salient target and lateral distractor as a function of saccadic behavior. In the stimulus-locked ERPs, a distractor-elicited N2pc appears both when the eyes are correctly deployed to the target (Fig. 2A) and when the eyes were erroneously deployed to the distractor (Fig. 2C). The stimulus-locked N2pc occurs in the eye-movement interval, but examination of the saccade-locked ERPs indicates that the component consistently preceded saccade onset on a trial-by-trial basis (Figs. 2B & 2D).

The deployment of selective attention, as indexed by the N2pc, thus consistently preceded the initiation of eye movements. However, the results demonstrate a clear dissociation of covert and overt selection: the lateral distractor is selected when the eyes are deployed to the location of this stimulus, but also when the eyes are deployed vertically to the target.

***N2pc*.** Statistical assessment of the stimulus-locked N2pc began with a rANOVA with factors for saccade outcome (target-directed vs. distractor-directed) and electrode laterality (ipsilateral vs. contralateral). A significant main effect of electrode laterality, $F(1, 19) = 15.83$, $MSE = 2.85$, $p < .001$, $\eta^2p = 0.45$, reflected a reliable distractor-elicited N2pc component both when the eyes were deployed to the vertical target (Fig. 2A; latency window 222–272 ms) and when they were deployed to the lateral distractor (Fig 2C; latency window 176–226 ms). The N2pc appears larger in the latter case, but this was not reliable, as reflected in a non-significant interaction ($F < 1.45$). The main effect of saccade outcome was significant, $F(1, 19) = 13.60$, $MSE = 34.96$, $p = .002$, $\eta^2p = 0.42$, reflecting slightly greater bilateral positivity when saccades were directed to the target.

As illustrated in Figures 2B and 2D, the N2pc is evident in the saccade-locked ERP as a negative difference preceding saccade onset (which occurs at graph origin). RANOVA analysis of activity in the 50 ms preceding saccadic onset revealed much the same pattern as identified in analysis of the

stimulus-locked N2pc: significant main effects for electrode laterality, $F(1, 19) = 8.96$, $MSE = 2.77$, $p = .007$, $\eta^2p = 0.32$, and saccade outcome, $F(1, 19) = 35.82$, $MSE = 8.11$, $p < .001$, $\eta^2p = 0.65$, but no evidence of an interaction, $F < 2.43$.

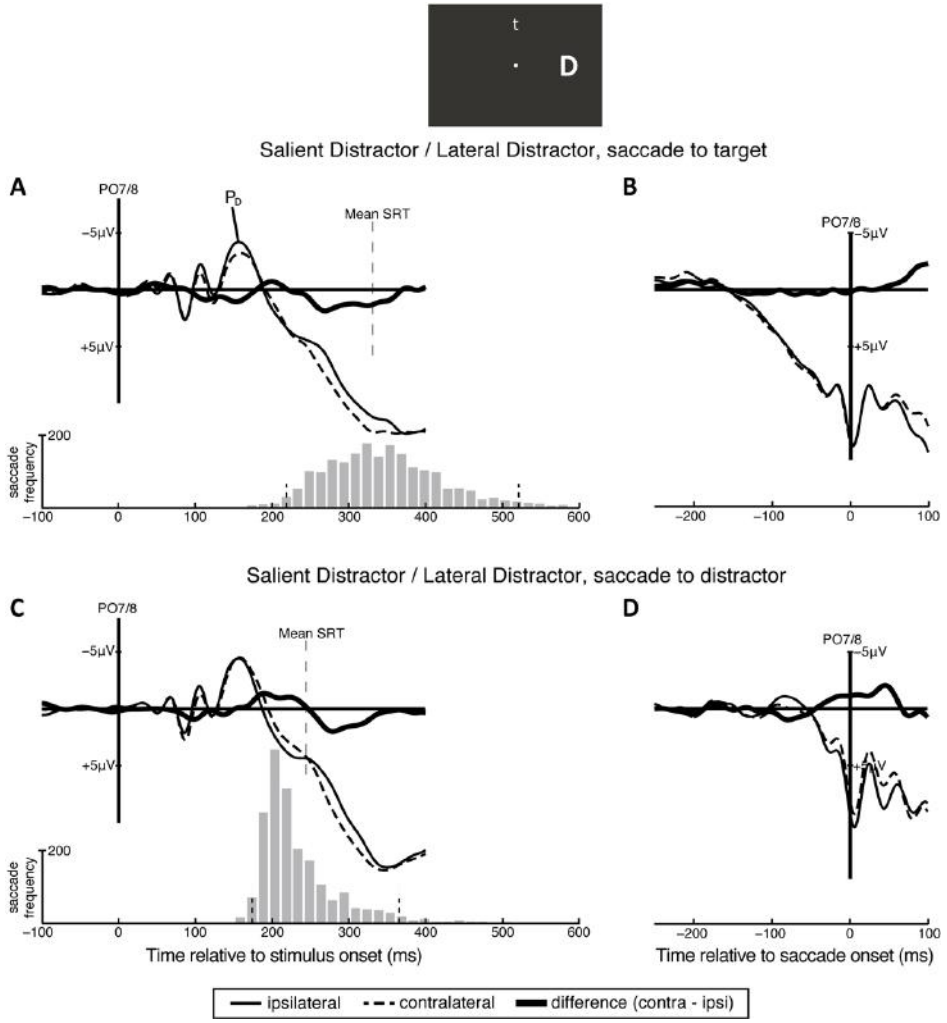

Figure 3. Stimulus-locked (A & C) and saccade-locked (B & D) ERPs for the salient distractor / lateral distractor display, presented in separate panels according to saccade outcome (target-directed: A & B; distractor-directed: C & D). Ipsilateral and contralateral electrode sites are plotted separately (averaged over PO7 and PO8). Difference waveforms were derived by subtracting relevant ipsilateral from contralateral waveforms. Negative voltages are plotted upward. Mean SRTs are indicated by the long vertical dashed line. Frequency distribution of SRTs aggregated across participants are presented below relevant ERPs. 95% of SRTs occurred within small vertical dashed lines. Paradigm schematic included as a reference, where 't' denotes the target and 'D' denotes salient distractor.

3.1.2.2 Salient Distractor / Lateral Distractor. When the salient distractor was lateral, an early distractor-elicited Pd emerged in the stimulus-locked ERP. This component importantly preceded the eye movement interval. The Pd was present only when the eyes were subsequently deployed to the target, suggesting that it plays a functional role in selective processing. Pd amplitude emerged later in the ERP, sustaining into the eye movement interval (Fig. 3A, 3C), but this late Pd was not evident in the saccade-locked ERP (Fig. 3B, 3D).

Pd. Statistical analysis of the early stimulus-locked Pd (148–158 ms) revealed main effects of saccade outcome, $F(1, 19) = 4.69$, $MSE = 2.52$, $p = .043$, $\eta^2p = 0.20$, and electrode laterality, $F(1, 19) = 8.64$, $MSE = 0.60$, $p = .008$, $\eta^2p = 0.31$, alongside an interaction between these factors, $F(1, 19) = 5.01$, $MSE = 1.11$, $p = .037$, $\eta^2p = 0.21$. The early Pd evident in Figure 3A was thus reliably larger than that elicited in the same interval in Figure 3C (see Fig. 5A for scalp topography).

Additional analyses revealed that the amplitude of the early Pd predicted the quality of target selection: as illustrated in Figure 5B, greater distractor-elicited Pd amplitude was associated with saccades that landed closer to the center of the target. $r(18) = -0.54$, $p = .013$, bootstrapped 95% CI [-.78, -.10].

Collapsing across saccade conditions in the stimulus-locked ERP, the late Pd (Figs. 3A, 3C; 244-294 ms) was reliable, as reflected in a main effect of electrode laterality, $F(1, 19) = 8.02$, $MSE = 4.57$, $p = .011$, $\eta^2p = 0.30$, but did not vary as a function of saccade accuracy (all other Fs < 0.06). Moreover, it was not evident in the saccade-locked ERP, where only a main effect of saccade outcome was significant, $F(1, 19) = 28.21$, $MSE = 24.03$, $p < .001$, $\eta^2p = 0.60$, (all other Fs < 0.96). This suggests that, unlike the early Pd, late Pd amplitude was not a determining factor in oculomotor behaviour.

N2pc. As evident in Figure 3C, a small N2pc appears to emerge when the salient distractor was lateral and the eyes were deployed to this stimulus. However, analysis of the N2pc (165–215 ms) with factors for saccade outcome and electrode laterality did not detect a significant interaction,

$F(1,19) = 2.22$, $MSE = 1.22$, $p = 0.153$, $\eta^2p = 0.10$, or a main effect of electrode laterality, $F(1,19) = 2.97$, $MSE = 2.35$, $p = 0.101$, $\eta^2p = 0.14$. The apparent N2pc in Figure 3C was thus not reliably larger than the ipsilateral vs. contralateral difference in the same time period in Figure 3A, and the N2pc did not reliably emerge when analysis was collapsed across these conditions.

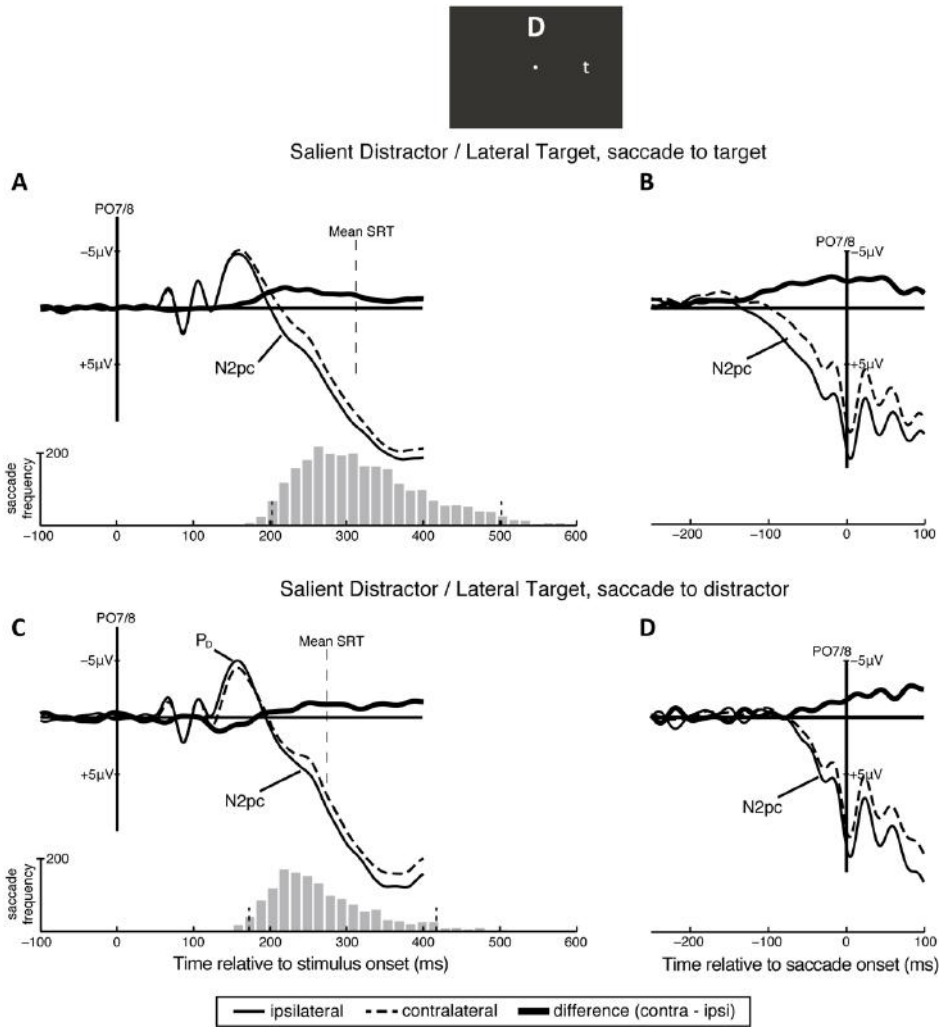

Figure 4. Stimulus-locked (A & C) and saccade-locked (B & D) ERPs for the salient distractor / lateral target display, presented in separate panels according to saccade outcome (target-directed: A & B; distractor-directed: C & D). Ipsilateral and contralateral electrode sites are plotted separately (averaged over PO7 and PO8). Difference waveforms were derived by subtracting relevant ipsilateral from contralateral waveforms. Negative voltages are plotted upward. Mean SRTs are indicated by the long vertical dashed line. Frequency distribution of SRTs aggregated across participants are presented below relevant ERPs. 95% of SRTs occurred within small vertical dashed lines. Paradigm schematic included as a reference, where 't' denotes the target and 'D' denotes salient distractor.

3.1.2.3 Salient Distractor / Lateral Target. When the less-salient target was lateral, a target-elicited N2pc was evident when the eyes were deployed to the target (Fig. 4A). When the eyes were deployed to the distractor, the same physical display elicited an early Pd followed by a small target-elicited N2pc (Fig. 4C).

Pd. Statistical analysis of the target-elicited Pd (129–139 ms latency window) revealed a main effect of electrode laterality, $F(1, 19) = 16.55$, $MSE = 0.39$, $p < .001$, $\eta^2p = 0.47$, and an electrode laterality × saccade outcome interaction, $F(1, 19) = 7.02$, $MSE = 1.11$, $p = .016$, $\eta^2p = 0.27$ (other Fs < 1). The Pd illustrated in Figure 4C was thus reliably larger than that elicited over the same interval in Figure 4A (1.20 μV vs. -0.05 μV).

N2pc. Analysis of the target-elicited N2pc (195–245 ms latency window) revealed main effects of electrode laterality and saccade outcome, Fs > 7.30, along with an interaction, $F(1, 19) = 6.88$, $MSE = 0.64$, $p = .017$, $\eta^2p = 0.27$. The increase in N2pc amplitude from Figure 4C to 4A was thus reliable (-0.66 μV vs. -1.60 μV).

The N2pc was also reliable in the saccade-locked ERP (Figs. 4B, 4C), as reflected in a main effect of electrode laterality, $F(1, 19) = 44.85$, $MSE = 1.33$, $p < .001$, $\eta^2p = 0.70$. Paralleling results from analysis of the stimulus-locked component, the saccade-locked N2pc was reliably larger when the eyes were subsequently deployed to the target (Figs. 4B vs. 4D; M = -2.41 vs -1.05), as reflected in an electrode laterality by saccade outcome interaction, $F(1, 19) = 8.70$, $MSE = 1.05$, $p = .008$, $\eta^2_p = 0.31$ (all other Fs < 2.25).

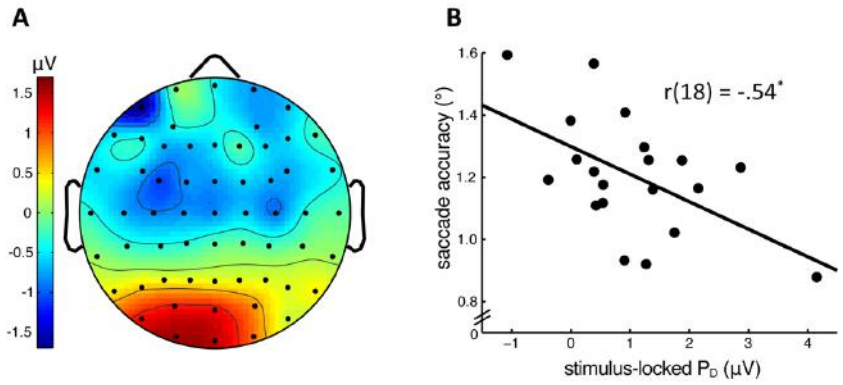

Figure 5. (A) Scalp topography for distractor positivity component (Pd), showing positivity contralateral to the lateralized salient distractor (target- minus distractor-directed saccade condition voltage; 148–158 ms). Contralateral electrode locations are mapped to the left hemisphere. (B) Correlation across participants between Pd component amplitude and accuracy of target-directed saccades (measured as degrees of visual angle from saccade endpoint to target center).

3.1.3 Time-frequency. To determine the role of pre-stimulus occipital state on oculomotor performance, we extracted EEG power spectra over the pre-stimulus interval preceding saccades to targets or salient distractors. These values were subsequently collapsed across stimulus laterality conditions before being compared at each time-frequency bin (1 Hz / ~9 ms) using paired *t* tests with false detection rate (FDR) set to .05 (Benjamini & Hochberg, 1995). Positive values in this analysis reflected bins where oscillatory power significantly increased when the eyes were deployed to the target. As illustrated in Figure 6A, target selection was associated with increased occipital power in the alpha / low-beta range (~8–18 Hz) in the 200 ms prior to stimulus onset.

Increased alpha has been linked to active suppression of visual input (Worden, Foxe, Wang, & Simpson, 2000; Kelly, Lalor, Reilly, & Foxe, 2006), suggesting that the relationship here may reflect a disruption and slowing of target and distractor processing. One possibility is that the improvement of performance associated with pre-stimulus alpha in our results is an indirect product of behavioural slowing, effectively providing more time for oculomotor control to be established (van Zoest et al. 2004). If this is the case, it should be evident in an additional relationship between oscillatory power and SRT: pre-stimulus alpha should predict slow saccadic response.

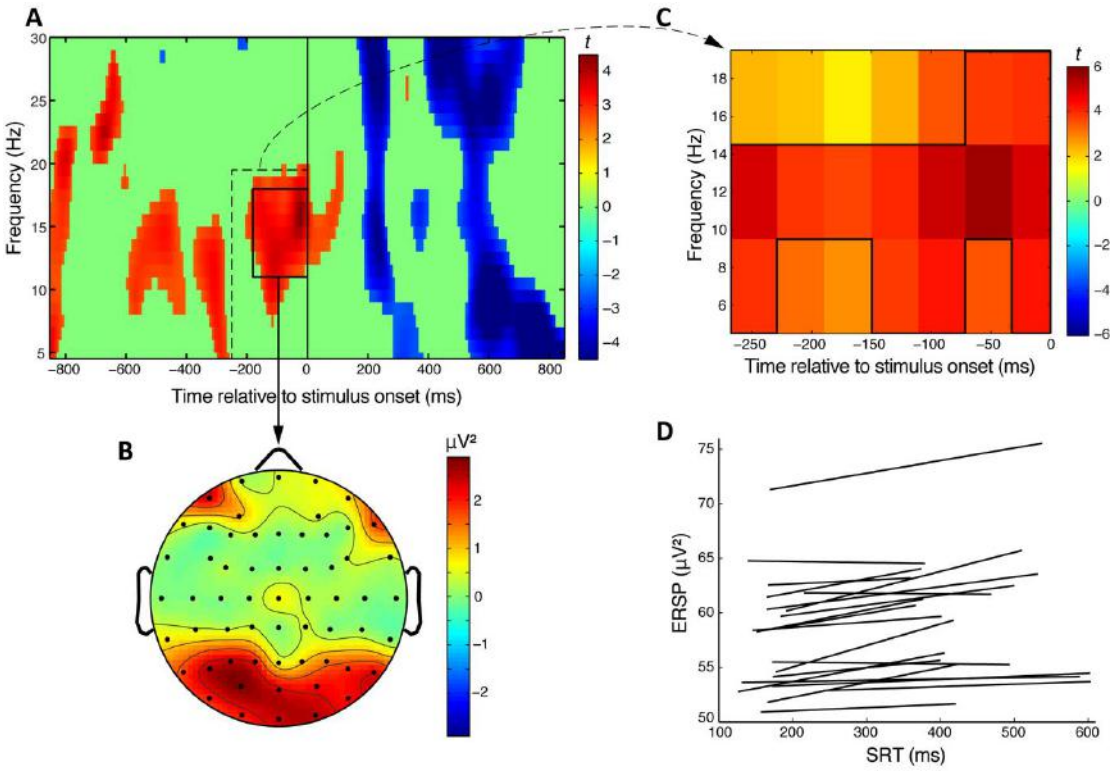

Figure 6. (A) *t* values from comparisons of oscillatory power for target- vs. distractor-directed saccades, collapsed across stimulus laterality, as a function of time and frequency (averaged across electrodes PO3/4, PO7/8, POz, O1/2, Oz). Warmer colors indicate greater power (μV^2) for saccades deployed to the less-salient target (vs. salient distractor). *t* values below FDR-corrected significance threshold have been set to green color. (B) Scalp topography for target- minus distractor-directed saccade ERSP within the final 180 ms prior to stimulus onset, in the 11–17 Hz frequency band corresponding to the solid black box highlighted in panel A. (C) One-sample *t* values on within-participants Fisher-transformed correlation coefficients for ERSPs and SRTs within the time-frequency range outlined by the dashed black box in panel A. Warmer colors indicate significant positive correlations where greater power at a given time-frequency bin predicted increased SRTs. *t* values above Bonferroni-corrected significance threshold are outlined in bold. (D) Plot of ERSP / SRT lines of least-square fit for each participant at the time-frequency bin ~70–30 ms pre-stimulus, 9.5–14.5 Hz. Line length reflects the individual participants' SRT range.

To test this hypothesis, we conducted an additional analysis in which we computed Pearson correlation coefficients between raw pre-stimulus oscillatory power and SRT for each participant across all trials. To increase our ability to detect an effect, we limited the number of analyzed bins by a.) decreasing the resolution of time-frequency bins to 5 Hz and approximately 40 ms intervals, b.) focusing on the 250 ms preceding stimulus onset, and c.) analyzing only the 5–19 Hz bandwidth

identified by the dashed line in Figure 6A. One-sample *t* tests of the Fisher-transformed correlations identified significant non-zero values across a range of alpha / low-beta frequencies, particularly within the 100 ms prior to stimulus onset (see Fig. 6C). Those that survived Bonferroni correction for multiple comparison (α = .05) are identified in Figure 6C by bold outline. These results are collapsed across target- and distractor-directed saccades; we found no reliable difference in the relationship between oscillatory power and SRT as a function of accuracy (all *t*s < 2.08, cf. corrected critical t-value threshold of 3.50 for α = .05).

Increased alpha / beta power in the interval prior to stimulus onset thus predicted slower saccadic response. Figure 6D illustrates this effect for the time-frequency bin with the strongest correlation (71–32 ms pre-stimulus, 9.5–14.5 Hz; $t(19) = 5.61$, $SE = 0.01$, $p < .001$, $d = 1.25$). Each line in this plot represents the least-square fit for the data from one participant. The generally positive slope of these lines illustrates the reliability of the positive relationship between alpha power and SRT, though the per-participant correlations between these noisy variables were individually very small ($M_R = .08$; $R^2 = 0.007$).

3.1.4 Summary

Experiment 1 supports the notion that oculomotor control relies on attentional mechanisms that act on visual representations in occipital cortex, and on distractor inhibition in particular. We find that a large N2pc to a lateralized stimulus, reflecting target selection, predicts that the eliciting object will be subsequently selected by the eyes (Figs. 2C & 4A). In contrast, early emergence of a Pd, reflecting distractor inhibition, predicts that the eyes will be deployed elsewhere (Figs. 3A & 4C). When the early Pd is elicited by a distractor, the amplitude of this component predicts the accuracy of target selection (Fig. 5B).

At the same time, results from Experiment 1 identify a dissociation between overt and covert selection. When the eyes are deployed to either a salient target or distractor on the vertical

meridian of the display, an N2pc can be observed contralateral to the lateralized stimulus (Figs. 2A & 4C). This N2pc precedes saccadic onset on a trial-by-trial basis (Figs. 2B & 4B), demonstrating that in many of these trials selective attention was deployed to the lateral stimulus in the interval immediately preceding a saccade to the salient stimulus on the vertical.

One possibility is that this reflects the concurrent attentional selection of both target and distractor in these trials. Despite many years of experimental investigation, it remains unclear if attention can be 'split' to concurrently monitor two locations in space (e.g., Müller, Malinowski, Gruber, & Hillyard, 2003; but see Jans, Peters, & De Weerd, 2010). Our data do not speak to this issue, but, critically, the core dissociation demonstrated in our results does not rely on the idea that attention is unitary. If attention is split between two objects, but the eyes are deployed to only one of these stimuli, it remains the case that the other object was covertly selected while the eyes were deployed elsewhere.

Results further demonstrate that oculomotor behavior is sensitive to the state of occipital cortex in the interval immediately preceding stimulus onset. Pre-stimulus alpha power predicted that the eyes would be deployed to the target (Fig. 6), possibly by slowing the saccadic response (Figs. 6C & 6D) and providing time for oculomotor control to be established.

As discussed above, differences of overt performance in Experiment 1 were accompanied by differences in SRT, which in some situations lead to complications of interpretation. For example, saccades that followed the distractor-elicited Pd tended to be accurate, but also slower (Figs. 3A vs. 3C). In this situation it is unclear if it is the presence of the Pd that improves accuracy, or the delay in SRT, or the combination of these factors. To allow for clearer insight into this issue, Experiment 2 was designed to limit variability in overt selection by having targets consistently appear at the same locations. Rather than focusing on saccadic accuracy, eye movement analysis in Experiment 2 examined distractor-elicited deviations in saccades to target locations.

3.2 Experiment 2

3.2.1 Behavior. Trial rejection parameters were as in Experiment 1: 1.42% of trials were rejected because saccades did not initiate at fixation; 5.37% because they did not land at either target or distractor locations; 0.12% because they were anticipative; and 2.48% because they were late. In addition, for the purposes of deviation analysis in Experiment 2, we further rejected trials where saccadic flight time was greater than 100 ms (0.14%) and where partial blinks disrupted measurement of saccade paths (0.32%). Together, these criteria led to the overall exclusion of 9.85% of trials from the 18 participants included in the primary analyses.

Previous research has found later SRTs to result in greater deviation away from distractors (e.g., McSorley, Haggard, & Walker, 2006, 2009; Mulckhuyse, Van der Stigchel, & Theeuwes, 2009; Hickey & van Zoest, 2012; for a review, see Van der Stigchel, 2010). We directly assessed the within-participants, trial-wise relationship between SRT and saccadic deviation by correlating SRT and saccadic deviation magnitude across all trials for each subject. The resulting per-participant correlations were small but reliably negative across the sample (M_R = -0.04; $t(17)$ = -2.38, SE = 0.02, p = .029, d = -0.56), indicating that long-latency saccades were consistently associated with greater deviation of saccade trajectories away from the distractor. This motivated a within-participants median split based on SRT into fast (Fig. 7) and slow (Fig. 8) saccade latency conditions.

A two-way rANOVA on accuracy revealed significant main effects of distractor salience (high vs. low) and saccade latency (fast vs. slow; Fs > 11.97), the latter showing that faster saccades were less accurate (M_{Fast} = .92 vs. M_{Slow} = .97). A significant interaction, $F(1, 17)$ = 24.97, MSE = 0.01, p < .001, η^2p = 0.59, and follow-up t tests showed an effect of distractor salience on accuracy only with fast saccades (M_{Low} = .95 vs. M_{High} = .89), $t(17)$ = 5.33, SE = 0.01, p < .001, d = 1.51; slow saccades, t < 1.74. Accuracy was, however, substantially better in Experiment 2 than was observed in Experiment 1.

An rANOVA analysis of saccadic deviations with factors for distractor salience and saccade latency revealed no significant main effects (Fs < 3.67), but, importantly, a significant salience ×

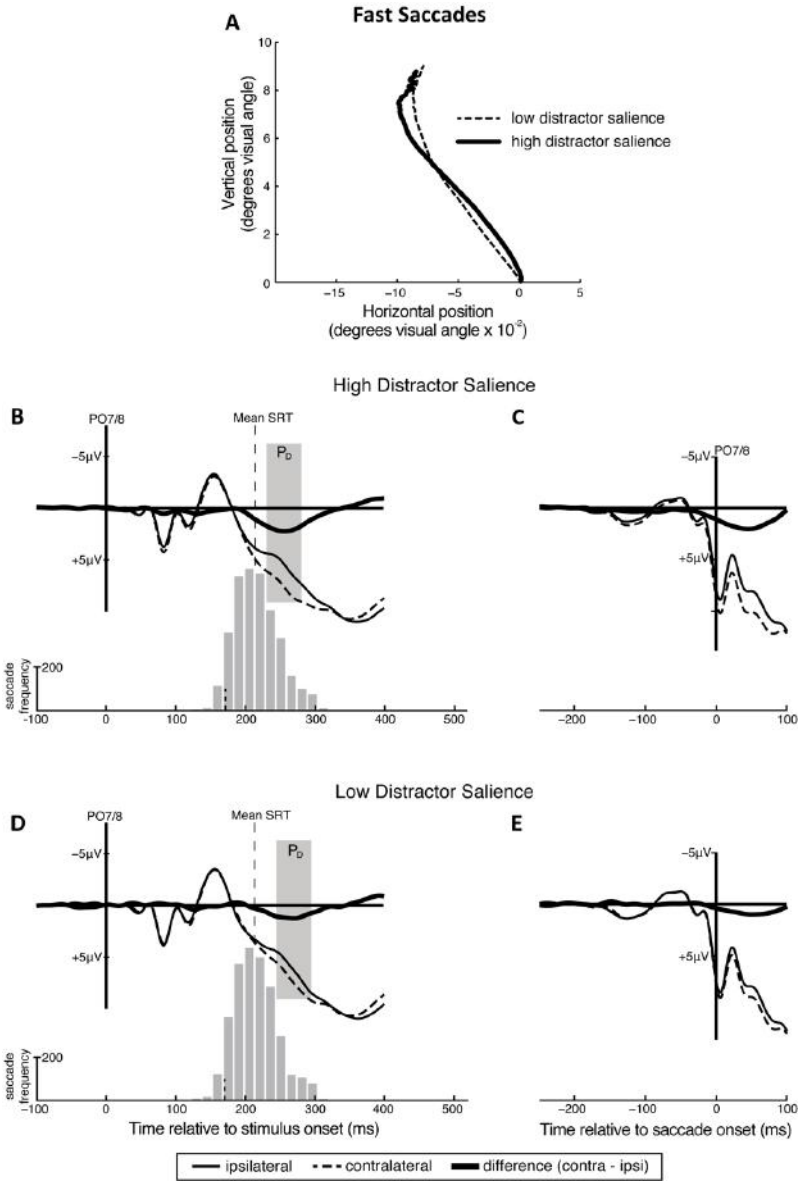

Figure 7. (A) Saccade trajectories for fast saccade condition, with horizontal scale magnified. Plotted in reference to a target in upper hemifield and distractor in upper right quadrant. Stimulus-locked (B & D) and saccade-locked (C & E) ERPs for high and low distractor salience conditions. Ipsilateral and contralateral electrode sites are plotted separately (averaged over PO7 and PO8). Difference waveforms were derived by subtracting relevant ipsilateral from contralateral waveforms. Negative voltages are plotted upward. The grey boxes indicate the peak-based latency windows used to calculate Pd amplitude. Mean SRTs are indicated by the long vertical dashed line. Frequency distribution of SRTs aggregated across participants are presented below relevant ERPs. 95% of SRTs occurred after the small vertical dashed line.

saccade latency interaction, $F(1, 17) = 4.59$, $MSE = 0.80$, $p = .047$, $\eta^2p = 0.21$. This was driven by greater distractor-elicited saccadic deviation when the distractor was of high salience, but only when saccades were slow (Fig 8; $M_{High} = -1.26°$ vs. $M_{Low} = -0.77°$), $t(17) = 3.41$, $SE = 0.15$, $p = .003$, $d = 0.57$; fast saccades: $t < 1.08$.

3.2.2 ERPs. ***3.2.2.1 Stimulus-locked ERPs*****.** Stimulus-locked ERPs from PO7/8 are presented as a function of distractor salience and saccade latency in Figures 7 and 8. Three patterns are evident. First, a distractor-elicited Pd emerges at ~200 ms in all four conditions. Second, the Pd appears larger for high- vs. low-salience distractors (Figs. 7B & 8B vs. 7D & 8D), consistent with the idea that increased salience of the distractor required stronger distractor suppression. Third, fast saccades tended to occur before the emergence of Pd (Figs. 7B & 7D), whereas the majority of slow saccades occurred once Pd was established (Figs. 8B & 8D).

Statistical analyses of the Pd began with an omnibus rANOVA with factors for distractor salience, saccade latency, and electrode laterality. A significant main effect of electrode laterality demonstrated the reliability of the Pd, $F(1, 17) = 49.18$, $MSE = 1.62$, $p < .001$, $\eta^2p = 0.74$, and an electrode laterality × salience interaction indicated that the Pd was larger when the distractors were salient ($M_{High} = 1.88$ μV vs. $M_{Low} = 1.09$ μV), $F(1, 17) = 21.02$, $MSE = 0.26$, $p < .001$, $\eta^2p = 0.55$. The electrode laterality × saccade latency interaction was not reliable ($M_{Fast} = 1.57$ μV vs. $M_{Slow} = 1.40$ μV), $F < 0.60$, suggesting that Pd amplitude did not vary as a function of saccade latency.

We approached the experiment with the expectation that distractor suppression in visual cortex – as indexed by the Pd – would show a relationship with distractor suppression in the oculomotor system – as indexed by saccadic deviation. As illustrated in Figure 9B, we observed this correlation across participants in slow trials, $r(16) = -.69$, $p = .002$, bootstrapped 95% CI [-.88, -.30], but not fast trials, $p = .371$, CI [-.59, .25].

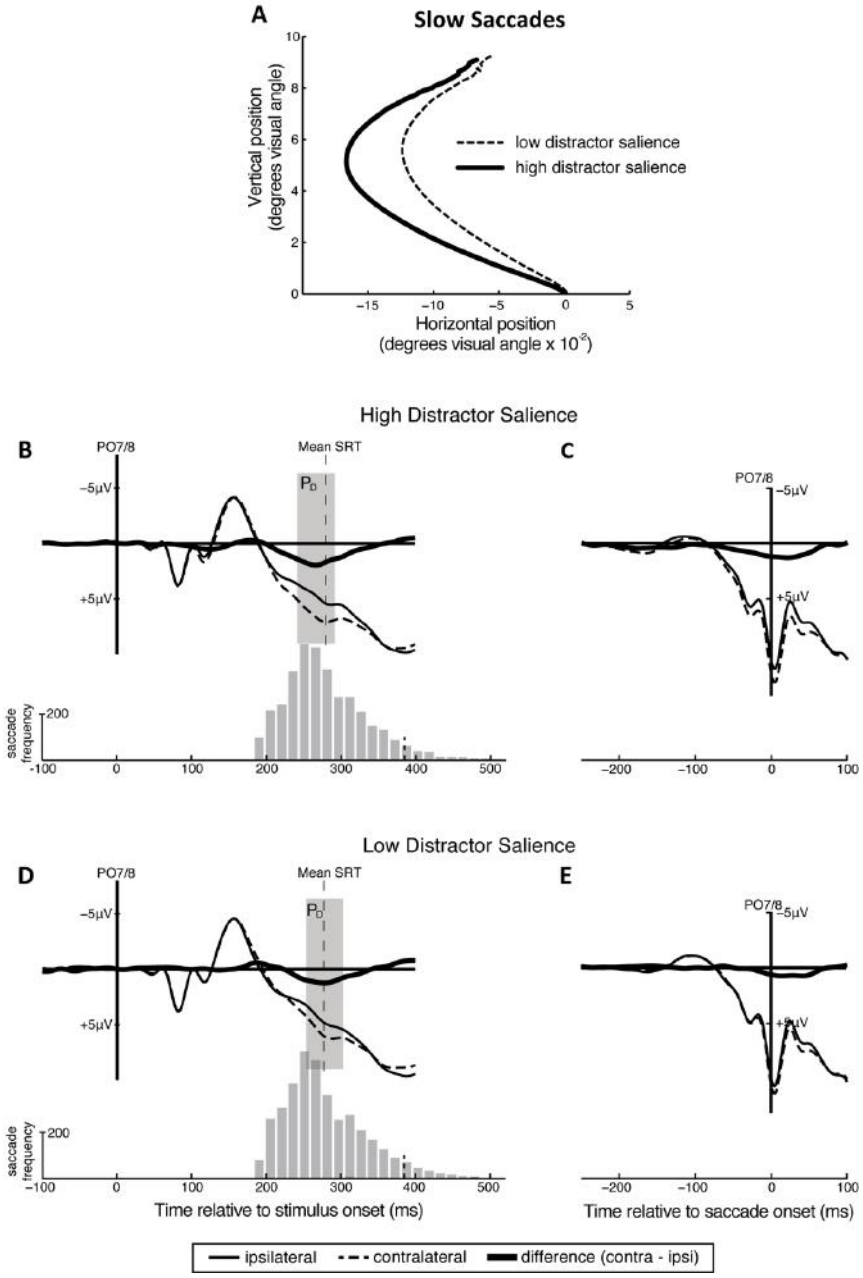

Figure 8. (A) Saccade trajectories for slow saccade condition, with horizontal scale magnified. Plotted in reference to a target in upper hemifield and distractor in upper right quadrant. Stimulus-locked (B & D) and saccade-locked (C & E) ERPs for high and low distractor salience conditions. Ipsilateral and contralateral electrode sites are plotted separately (averaged over PO7 and PO8). Difference waveforms were derived by subtracting relevant ipsilateral from contralateral waveforms. Negative voltages are plotted upward. The grey boxes indicate the peak-based latency windows used to calculate Pd amplitude. Mean SRTs are indicated by the long vertical dashed line. Frequency distribution of SRTs aggregated across participants are presented below relevant ERPs. 95% of SRTs occurred before the small vertical dashed line.

Analysis of stimulus-locked results suggests a relationship between Pd amplitude and saccadic deviation when the Pd precedes saccade onset. But the timing of saccadic response seems independent of the timing of the distractor suppression indexed in the Pd. This independence is informally illustrated in Figure 10, which presents per-trial results for two selected participants. Trials are sorted according to SRT, and the contralateral-minus-ipsilateral difference wave observed in each trial is rendered in color. Pd timing is clearly independent of variance in SRT.

3.2.2.2 Saccade-locked ERPs. The Pd elicited in the stimulus-locked ERP consistently occurred in the eye movement interval and we accordingly replicated our findings in analysis of saccade-locked ERPs. The saccade-locked Pd is evident in Figures 7C, 7E, 8C, and 8E as a positivity in the difference wave in the interval immediately before and after saccade onset.

Analysis of saccade-locked Pd began with a rANOVA paralleling that described above in analysis of stimulus-locked results. A significant main effect of electrode laterality indicated the presence of a Pd component prior to saccade onset, $F(1, 17) = 5.70$, $MSE = 1.11$, $p = .029$, $\eta^2p = 0.25$. The Pd was reliably larger when distractors were salient, as reflected in a significant electrode laterality × salience interaction ($M_{High} = 0.70$ µV vs. $M_{Low} = 0.14$ µV), $F(1, 17) = 22.50$, $MSE = 0.13$, $p < .001$, $\eta^2p = 0.57$. Additional effects of saccade latency, salience, and a salience × saccade latency interaction were detected (Fs > 7.99; all other Fs < 0.82). As in analysis of stimulus-locked Pd, we identified a reliable negative correlation between pre-saccadic Pd and saccadic deviation for slow saccades (Fig. 8C), $r(16) = -.57$, $p = .013$, bootstrapped 95% CI [-.85, -.43], but not fast saccades ($p = .222$, CI [-.73, .23]).

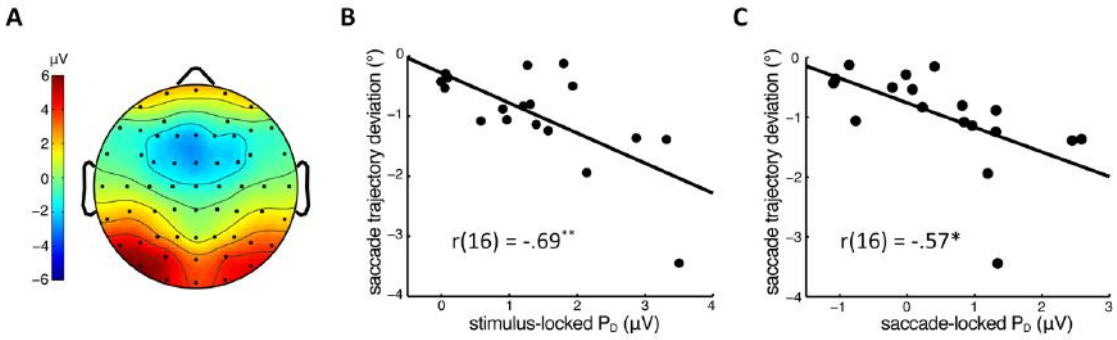

Figure 9. (A) Topographic map of raw voltage in stimulus-locked Pd interval for slow saccades, collapsed across salience conditions (244–294 ms). Contralateral electrode locations are mapped to the left hemisphere. Correlation across participants between (B) stimulus-locked or (C) saccade-locked Pd amplitude and saccadic deviation for slow saccades, collapsed across salience conditions. Negative saccadic deviation values on the y-axis indicate curvature away from the distractor.

The saccade-locked Pd onset earlier both when the distractor was of higher salience and when the saccade was relatively slow. To test these latency effects we calculated Pd onset latencies using a jackknife-based approach (Ulrich & Miller, 2001) combined with a measure of fractional area, which defines component onset as the time when a prespecified percentage of total component area has occurred (Hansen & Hillyard, 1980; Luck, 2005, 2014). Pd area was calculated as the positive area under the contralateral-minus-ipsilateral difference wave from 100 ms pre-saccade to 100 ms post-saccade. We used an onset criterion of 30% of component area (as per Kiesel, Miller, Jolicoeur, & Brisson, 2008). Analysis revealed significant main effects of salience, F_C (1, 17) = 8.75, p_C = .009, and saccade latency, F_C (1, 17) = 8.00, p_C = .012, but no interaction, F_C < 0.29. The Pd thus began earlier relative to saccade onset when the distractor was salient (M_{Low} - M_{High} = 19 ms) and when saccades were slow (M_{Fast} - M_{Slow} = 24 ms).

Taken together, results from Experiments 1 and 2 suggest that oculomotor control is determined in part by the quality of visual representation available to the saccade execution system when the saccade is programmed. Saccadic performance is accurate and target-directed when distractor suppression in visual cortex precedes saccade onset, but if the eyes are deployed before distractor suppression begins, the saccade is driven by visual salience.

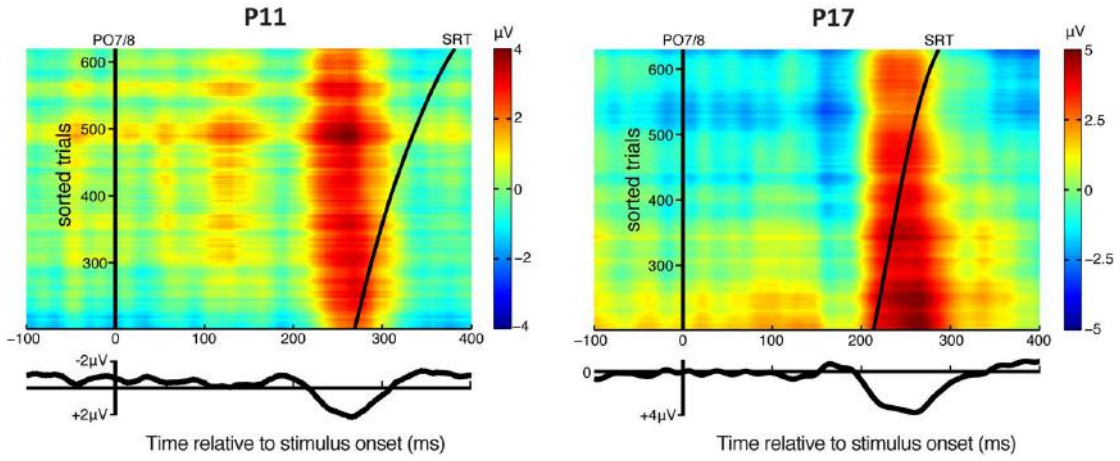

Figure 10. Single-trial stimulus-locked ERP difference waveforms (contralateral minus ipsilateral) collapsed across all conditions and sorted by SRT. A 400-point Gaussian weighted moving-average was applied across trials to smooth data. Grand average ERPs are presented in a separate panel underneath. Two exemplar participants highlight the independence of the Pd component relative to a range of SRTs tending to occur either after (left panel) or during (right panel) the Pd.

3.2.3 Time-frequency. If saccade timing is independent of the action of selective attentional mechanisms, what determines when the eyes are deployed? Results from time-frequency analysis of Experiment 1 suggest that one determining factor might be the state of the visual system in the pre-stimulus interval. To test this hypothesis in Experiment 2, we again conducted pre-stimulus time-frequency analysis of the EEG data.

We measured within-participant trial-wise relationship of raw pre-stimulus oscillatory activity to SRT, collapsed across all conditions, using the same analyses and parameters as employed in Experiment 1. One-sample Bonferroni-corrected *t* tests identified significant non-zero correlations in the low-alpha range (~5–10 Hz) approximately 150–250 ms prior to stimulus onset (Fig. 11A). Increased oscillatory activity in low alpha during this interval thus predicted slower saccadic responses. As in Experiment 1, individual participant correlation coefficients for the most significant time-frequency bin (190–151 ms pre-stimulus, 4.5–9.5 Hz) were small (M_R = .03) but had reliably positive slope ($t(17) = 4.08$, $SE = 0.01$, $p < .001$, $d = 0.96$).

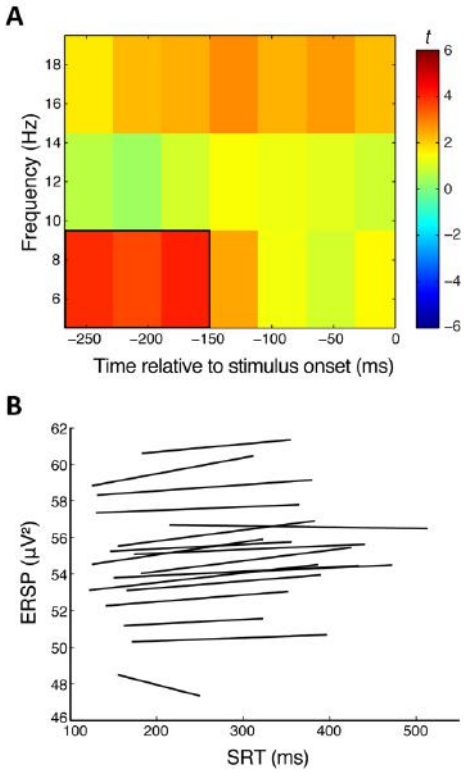

Figure 11. (A) One-sample *t* values on within-participants correlation coefficients for oscillatory power and SRTs. Warmer colors indicate that greater oscillatory power (μV^2) at a given time-frequency bin predicted increased SRTs. *t* values above Bonferroni-corrected significance threshold are outlined in bold. (B) Plot of alpha power / SRT lines of least-square fit for each participant at the time-frequency bin ~190–150 ms pre-stimulus, 4.5–9.5 Hz. Line length reflects the individual participants' SRT range.

In Experiment 1, this relationship between pre-stimulus oscillatory power and saccadic accuracy emerged across a broader frequency spectrum and across a greater number of latency bins, consistent with another recent report (Bompas, Sumner, Muthumumaraswamy, Singh, & Gilchrist, 2015). One possibility is that the subtle featural discrimination required in Experiment 1 rendered saccadic performance more sensitive to the pre-saccadic state of the visual system, causing this effect to emerge across a broader frequency band.

3.2.4 Summary

Experiment 2 extends Experiment 1 in several important ways. First, it underscores the close relationship between attentional inhibition in visual cortex and inhibition in oculomotor behavior. Saccadic trajectory deviation away from a distractor increases both as a function of the salience of the distractor and as the saccadic response occurs later in time (Figs. 7A & 8A). In trials with slow saccades, the eye movement tends to follow the onset of the distractor-elicited Pd (Figs. 8B–E) and we find a robust correlation between saccadic deviation amplitude and Pd amplitude (Fig. 8B & 8C).

However, results from Experiment 2 also extend Experiment 1 by providing additional demonstration of the independence of attentional selection and saccadic latency. Though latency of the Pd in no way predicts the latency of the saccadic response, when the saccade is initiated following the onset of this component, the path of the eye movement will deviate away from the distractor.

4. General Discussion

Our experimental results broadly support two assertions. First, we find that saccadic behavior is strongly linked to the operation of attentional mechanisms in visual cortex. In Experiment 1, accurate saccades to targets were preceded by attentional selection of the target, as reflected in large-amplitude target-elicited N2pc (Fig. 4A), but also by attentional suppression of the distractor, as evident in distractor-elicited early Pd (Fig. 3A). Similarly, in Experiment 2 the strength of distractor suppression, again indexed by Pd, predicted the degree to which the eyes would deviate away from the distractor on their way to the target (Figs. 8B & 8D).

At the same time, covert and overt selection are clearly dissociated. In Experiment 1, we observe that lateralized target stimuli are attentionally selected – generating a reliable N2pc – even when saccades land at the location of the distractor (Fig. 4C). Importantly, the target-elicited N2pc only slightly precedes mean SRT, indicating that attentional selection of the target occurs at much

the same time as saccades are deployed to the distractor. A second dissociation is evident in the relative independence of saccade latency and timing of covert attentional mechanisms reflected in the ERPs. This is clear in both experiments, but particularly in Experiment 2, where the distractor suppression indexed by Pd occurs at a consistent latency regardless of variation in SRT (Fig. 10).

The conflict between these observations is only superficial. It can be reconciled if we accept three principles regarding the nature of eye movements and their relationship to spatial attention: first, that the temporal programming and spatial programming of saccades are relatively independent processes; second, that the deployment of covert selective mechanisms only weakly impacts saccade timing; and, third, that motor sequencing of the saccade takes time, such that the direction and accuracy of the saccade reflects the state of the oculomotor system some tens of milliseconds prior to SRT. All of these principles are in line with findings in the literature. There is strong evidence of the independence of spatial and temporal sequencing in eye movement preparation (see Findlay & Walker, 1999, for a review), and this characteristic of the oculomotor system is reflected in influential models (e.g., Abrams & Jonides, 1988; Findlay & Walker, 1999). Similarly, spatial cues do not appear to have any substantive impact on saccade latency: sometimes they provide a small benefit (Megaw & Armstrong, 1973), other times they have no effect (Walker, Kentridge, & Findlay, 1995), and occasionally they create a cost (Sheliga, Riggio, & Rizzolatti, 1995; Sheliga, Craighero, Riggio, & Rizzolatti, 1997). Finally, saccade-related spike activity in the superficial layers of monkey SC precedes onset of the actual eye movement by at least 20 ms, with the intervening time presumably spent in brainstem programming (e.g., Boehnke & Munoz, 2008).

The first two of these principles – that the timing and direction of saccades are independent with attention impacting only the latter – together provide an account for the dissociation of saccade latency and N2pc / Pd latency, suggesting that eye movements will reflect attentional mechanisms only when saccades are executed after these mechanisms have had the opportunity to act. Thus in Experiment 2, fast target-directed eye movements that precede the distractor-elicited

Pd show no deviation. However, when the saccade is slower and the Pd appears prior to motor execution, the saccade will curve away from the distractor with a strength predicted by Pd amplitude.

The third principle – that there is a small delay between the cognitive call for a saccade and its actual execution – accounts for the dissociation of saccade direction and attentional focus observed in Experiment 1. In those results, we find that a target-elicited N2pc roughly co-occurs with distractor-directed saccades. However, this target-elicited N2pc is preceded by an early target-elicited Pd, reflecting rapid suppression of the eliciting stimulus. It appears that the pre-motor representation of the saccadic response is programmed during this interval of target-suppression. The actual execution of the eye movement occurs some tens of milliseconds later, at which time the initial suppression has been corrected and attention has been deployed to the target.

The three principles together define an account of the relationship between covert attention and overt saccadic control that we call *temporal dependency*. At the core of this account is the simple idea that saccadic performance can reflect the influence of attentional mechanisms only when there is time enough prior to saccade onset for these mechanisms to operate (cf. van Zoest et al., 2010). With this insight, we believe that temporal dependency carves a middle ground through existing discussion of the relationship between attention and oculomotor control. This discussion has been characterized by strong, dichotomous views: the *premotor theory of attention* on one side, proposing that oculomotor and attentional control are essentially the same thing (Rizzolatti, Riggio, Dascola & Umilta, 1987; Rizzolatti, Riggio, & Sheliga, 1994), and numerous reports of the dissociation of attention and eye movements on the other (e.g., Klein, 1980; Kingstone & Klein, 1993; Klein & Taylor, 1994; Stelmach, Campsall, & Herdman, 1997; Thompson, Bichot, & Schall, 1997; Fischer, 1999; Corbetta & Shulman, 2002; Wu & Remington, 2003; see Wright & Ward, 2008, for a review). In line with the premotor theory, our results demonstrate a strong dependency of oculomotor behavior on the deployment of attention, but we add to this the idea that covert selection can

impact overt performance only when saccade timing allows for it. Our results demonstrate two dissociations of attention and saccadic control that are caused by the misalignment of attentional and saccadic timing; similar timing effects may underlie other demonstrations of independent oculomotor and attentional systems in the literature.

The attentional inhibition indexed in our results could be mechanistically related to oculomotor inhibition in at least two ways. Eye movement programming may depend directly on the quality of the object representation in visual cortex. In this case, a change to the visual representation through attentional inhibition could directly cause variance in the quality of the saccadic response. This is a simple but plausible account: visual input plays a role in the definition of oculomotor salience maps in LIP, FEF, and SC (e.g., Fecteau & Munoz, 2006). It is also lent support by results in the current study showing that greater pre-stimulus occipital alpha power predicted slower saccadic responses: the pre-stimulus state of visual cortex clearly impacts eye movement behaviour, suggesting that the post-stimulus state of visual cortex is also likely to influence the eyes.

The alternative is that the observed covariance in attentional and oculomotor inhibition reflects mutual dependence on shared control structures or intermediary mechanisms. Such a point of intersection could be relatively high-level, for example at DLPFC or FEF. However, our results also demonstrate a tight coupling of attentional and oculomotor inhibition, with Pd amplitude in Experiment 2 predicting up to 48% of variance in saccadic trajectory deviations across participants (Fig. 9B,C). This degree of correspondence suggests a closer convergence within the visual system, possibly at the level of shared salience maps in posterior parietal areas such as LIP or via a subcortical connection involving the pulvinar nucleus of the thalamus (LaBerge, 1997; Saalmann, Pinsk, Wang, Li, & Kastner, 2012).

If covert attentional mechanisms drive the quality but not the timing of saccades, what creates the variance in SRT that we observe? The pre-stimulus state of the visual system plays some role here. Consistent with another recent report (Bompas et al., 2015), we find in both experiments that

pre-stimulus oscillatory power over visual cortex in the alpha-to-beta range predicts slow SRTs (see Figs. 6A & 11A). In Experiment 1, where saccadic errors are common, increased pre-stimulus alpha also predicts an improvement in saccadic accuracy. At first glance this may seem counter-intuitive: pre-stimulus alpha has generally been associated with task disengagement and thus poorer performance (e.g., Pfurtscheller, 2001; Mazaheri, DiQuattro, Bengson, & Geng, 2011; but see Klimesch, Sauseng, & Hanslmayr, 2007; Bonnefond & Jensen, 2012). Again, the timing of the saccadic response appears critically important: by slowing visual processing, pre-stimulus alpha appears to create the opportunity for attentional mechanisms to strategically resolve visual input and in this way contribute to oculomotor control.

Our discussion has so far focused on implications of the results to our understanding of attention and eye movements, but the data also add to our knowledge of the Pd component. First, we confirm existing reports of a very early Pd (Sawaki & Luck, 2010). Importantly, this early Pd only appears in the current results when the eliciting stimulus is not selected by the eyes (Figs. 3A & 4C) and it predicts the accuracy of target selection (Fig. 5B). These findings both argue in favor of a distractor suppression interpretation and distinguish the component from other early positivity components in the literature that have been linked to visual salience (e.g., the Ppc; Leblanc, Prime, & Jolicœur, 2008; Corriveau et al., 2012; Fortier-Gauthier, Moffat, Dell'Acqua, McDonald, & Jolicœur, 2012). Second, the pattern of Pd results observed here lends support to a developing theory regarding the functional role of the component. Sawaki and Luck (2010, 2011) have suggested that salient stimuli may be automatically detected by the visual system, producing an obligatory 'attend-to-me' signal (see also, Gaspelin, Leonard, & Luck, 2015). This signal can draw attention, as indexed by the N2pc, when the eliciting stimulus matches target templates or when attentional control is not well established. When attentional control is instantiated, this signal can be suppressed, as indexed by the Pd, to avert attentional capture by the salient distractor, thereby preventing it from interfering with goal-driven behavior. A similar sequence occurs when attentional selection of a

target must be terminated (Sawaki et al., 2012). In the current results, it appears that saccades initiated in the short interval after initial salience is signaled - but before the Pd and distractor suppression - can be driven by raw salience toward the irrelevant distractor (cf. van Zoest et al., 2004).

To conclude, we used concurrent recording of eye movements and electrical brain activity to investigate the role of attentional mechanisms, and distractor suppression in particular, in the control of oculomotor behavior. Our results strongly support the notion that attentional mechanisms play a role in determining saccadic behavior. However, critically, saccade timing is not contingent on the deployment of attention, and this creates a temporal dependency in the relationship: attention can impact oculomotor behavior only when attentional mechanisms can act before the eyes are deployed.

5. Acknowledgments

This project was supported by the Autonomous Province of Trento, Italy (call 'Grandi Progetti 2012,' project 'Characterizing and improving brain mechanisms of attention – ATTEND'). The authors declare no competing financial interests.

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