

COGNITIVE NEUROSCIENCE

Prepare for conflict: EEG correlates of the anticipation of target competition during overt and covert shifts of visual attention

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Abstract

When preparing to make a saccadic eye movement in a cued direction, perception of stimuli at the target location is enhanced, just as it is when attention is covertly deployed there. Accordingly, the timing and anatomical sources of preparatory brain activity accompanying shifts of covert attention and saccade preparation tend to exhibit a large degree of overlap. However, there is evidence that preparatory processes are modulated by the foreknowledge of visual distractor competition during covert attention, and it is unknown whether eye movement preparation undergoes equivalent modulation. Here we examine preparatory processes in the electroencephalogram of human participants during four blocked versions of a spatial cueing task, requiring either covert detection or saccade execution, and either containing a distractor or not. As in previous work, a typical pattern of spatially selective occipital, parietal and frontal activity was seen in all task versions. However, whereas distractor presence called on an enhancement of spatially selective visual cortical modulation during covert attention, it instead called on increased activity over frontomedial oculomotor areas in the case of overt saccade preparation. We conclude that, although advance orienting signals may be similar in character during overt and covert conditions, the pattern by which these signals are modulated to ameliorate the behavioral costs of distractor competition is highly distinct, pointing to a degree of separability between the overt and covert systems.

Introduction

Selection of elements of our visual environment for prioritized processing can be achieved overtly, with eye movements, and covertly, i.e. without eye movements. The intuitive notion that these operations must be closely linked has been borne out in experiments using multiple behavioral and neurophysiological techniques. Behavioral studies have shown that covert attention to a location facilitates saccades to that location, that perceptual identification is improved at saccade goals, and that attempts to uncouple the locus of attention from a saccade goal necessarily involve a sacrifice in either saccadic or perceptual performance (Kowler *et al.*, 1995; Deubel & Schneider, 1996). Non-human primate neurophysiological studies have shown that parts of the cortical network supporting visuomotor behavior are mutually involved in covert and overt orienting. For instance, the cortical area most directly implicated in generating eye movement commands, the frontal eye field (FEF; Robinson & Fuchs, 1969), has

been shown to actively participate in covert target selection in the absence of eye movements (Thompson *et al.*, 2005; Thompson & Bichot, 2005) and, when electrically stimulated, to excite area V4 neurons involved in visual discrimination (Moore & Armstrong, 2003). Meanwhile, the lateral intraparietal area, which is thought to guide attention through its encoding of behaviorally relevant locations (Gottlieb *et al.*, 1998; Bisley & Goldberg, 2003), is known to be involved in the generation of saccades (see Andersen & Buneo, 2002). Similar functional overlap has been seen in the superior colliculus (SC; Kustov & Robinson, 1996; McPeck & Keller, 2002). Human neuroimaging studies have accordingly demonstrated a large amount of overlap in the anatomical structures activated during covert and overt orienting (Corbetta *et al.*, 1998; Nobre *et al.*, 2000a).

While the presence of a link between covert and overt orienting mechanisms is clear, the precise nature of the link is still under debate. Some investigators have put forward the notion that the link is not only embodied in shared anatomical regions, but also in shared mechanisms (e.g. Kustov & Robinson, 1996). On the extreme end of this thinking, the pre-motor theory of attention proposed by Rizzolatti *et al.* (1987, 1994) questions whether there is any need for a separate construct of covert spatial attention at all. In this view, attention shifts

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are a byproduct of oculomotor planning; that is, the behavioral facilitation classically attributed to covert attention arises from cases where a specific motor program is activated but not executed. Inconsistent with this, however, are recent behavioral studies showing that attention can be allocated to specific locations remote from the upcoming saccade goal during pauses in a sequence (Gersch *et al.*, 2008, 2009). Moreover, recent lesion studies showed that attentional enhancement contralateral to a damaged parietal lobe can be impaired in the absence of any impairment in saccade execution (Khan *et al.*, 2009), and even in a case where parietal damage did impair contralateral saccade execution, pre-saccadic facilitation remained intact while covert discrimination was severely impaired (Blangero *et al.*, 2009).

Recently, the event-related potential (ERP) technique has been employed to demonstrate links between overt and covert control mechanisms (Van der Lubbe *et al.*, 2006; Van der Stigchel *et al.*, 2006; Eimer *et al.*, 2007). ERPs provide a high-resolution measure of the temporal dynamics of cortical activity observable across the scalp and are thus informative with regard to discrete processes that unfold over time following sensory or cognitive events. These studies employed variants of a classical spatial cueing paradigm (e.g. Posner, 1980), where a directional cue (e.g. an arrow) informs an observer of the likely or relevant location of an upcoming imperative target, allowing examination of preparatory processes occurring in the intervening cue-to-target period. In the standard case where covert discrimination is required upon target presentation, a sequence of spatially selective lateralized processes are routinely observed, identified as divergences in the cue-locked ERP over lateral scalp sites for cues pointing to the contralateral vs. ipsilateral hemifield (Harter *et al.*, 1989; Nobre *et al.*, 2000b; Talsma *et al.*, 2005). Under alternative conditions where subjects were required to make an immediate saccade to spatially pre-cued targets, the pattern of lateralized activity was highly similar to the covert case (Van der Lubbe *et al.*, 2006; Van der Stigchel *et al.*, 2006; Eimer *et al.*, 2007). This overlap in preparatory activity was taken as evidence for the pre-motor theory (see Eimer *et al.*, 2007).

There is evidence that the expression of preparatory set is dependent on task demands. For example, cue-related ERP components have been shown to modulate depending on the non-spatial stimulus properties to be discriminated (Dale *et al.*, 2008) and task difficulty (Hopf & Mangun, 2000). A major factor known to affect attention allocation in space is the presence of distractors. In fact, prominent theories have defined attention explicitly with reference to the biased competition between targets and distractors (Desimone & Duncan, 1995; Kastner *et al.*, 1998; Reynolds *et al.*, 1999). It has been shown that the degree of biasing against distractor interference can be regulated through top-down mechanisms based on prior knowledge of distractor probability (Awh *et al.*, 2003), target location probability (Geng & Behrmann, 2006) and distractor presence (Ruff & Driver, 2006). In the latter study, the behavioral cost of a distractor was reduced with foreknowledge of its appearance opposite the cued location, and this was accompanied by anticipatory modulation of blood oxygenation level-dependent (BOLD) activity in occipital areas processing the expected distractor location, along with anticipatory activation of distinct parietal and frontal structures. A recent ERP study also showed modulation of cue-evoked frontal activity with the knowledge that distractors will appear adjacent to the target (Seiss *et al.*, 2009).

The presence of visual distractors can also inhibit or delay saccadic eye movements. While presentation of two visual stimuli close together in visual space tends to produce saccades directed to a position in between the two (Ottens *et al.*, 1984; Edelman & Keller, 1998; Chou *et al.*, 1999), presentation of two stimuli far apart tends to

produce saccades directed at one or the other target, but with increased reaction time (Levy-Schoen & Blanc-Garin, 1974; Chou *et al.*, 1999; Edelman *et al.*, 2007). Even when a target or its expected location has been selected, saccades can be inhibited or delayed by the presence of a visual distractor (Walker *et al.*, 1995, 1997; Reingold & Stampe, 2002; Edelman & Xu, 2009).

Considering the overlap in anticipatory processing during overt and covert attention, and the parallels in the behavioral cost of distractors, the question arises whether the anticipatory processes undergo equivalent regulation to meet the demands of distractor competition. If covert attention deployment and saccade preparation were truly one and the same thing, one would expect that they be regulated in the same way with prior knowledge of distractor presence. Whereas neurophysiological and imaging studies of the expression and resolution of stimulus competition for covert attentional selection have tended to focus on extrastriate cortex (e.g. Desimone, 1998; Reynolds *et al.*, 1999; Fink *et al.*, 2000; Geng *et al.*, 2006), studies of saccadic competition have focused on downstream oculomotor structures such as the SC and cortical eye fields (e.g. Schall *et al.*, 1995; Munoz & Istvan, 1998; McPeck & Keller, 2002; Dorris *et al.*, 2007). This highlights the possibility that competition-related regulation of anticipatory signals during overt and covert attention may be quite distinct. We test this here by examining anticipatory electrophysiological processes during overt and covert selection of pre-cued target locations, with foreknowledge of the presence or absence of distractors. We predicted that anticipatory orienting signals during overt selection would be regulated more strongly in frontal areas known to encode preparatory set for saccades (e.g. pre-frontal cortex, FEF and supplementary eye fields; e.g. Schall, 1991a, b; Schlag-Rey *et al.*, 1997; Everling & Munoz, 2000; Nagel *et al.*, 2008), whereas in the case of covert detection, the biasing of upstream visual occipital and parietal regions, known to be relied upon for task performance (e.g. Sylvester *et al.*, 2007; Kelly *et al.*, 2009), would be more strongly regulated.

To investigate the above predictions, we chose five key dependent measures on which to assess the effects of distractor presence in overt and covert scenarios. We measured the preparatory activity of frontomedial pre-motor areas in a slow negative potential at midline fronto-central electrodes, widely associated with stimulus expectancy (the 'contingent negative variation' or CNV; Walter *et al.*, 1964) and/or pre-saccadic preparation (the 'pre-saccadic negativity' or PSN; Kurtzberg & Vaughan, 1982; Evdokimidis *et al.*, 1992; Everling *et al.*, 1997). We probed anticipatory activity in lower-tier visual areas by measuring a broadband ERP component known as the LDAP (late-directing attention positivity), defined by relatively positive amplitude contralateral to the direction of a central spatial cue (Harter *et al.*, 1989; Hopf & Mangun, 2000), as well as lateralization of alpha-band (8–14 Hz) amplitude to the visual hemisphere ipsilateral to cue direction (Worden *et al.*, 2000). Both the LDAP and alpha lateralization have been associated with the anticipatory modulation of excitability in early visual areas responsible for processing an upcoming target (Worden *et al.*, 2000; Kelly *et al.*, 2005, 2006, 2009; Talsma *et al.*, 2005; Simpson *et al.*, 2006; Thut *et al.*, 2006; Gomez-Ramirez *et al.*, 2009). In addition, we tested for effects on two other spatially selective (i.e. defined by an interaction between hemisphere and attention direction) ERP processes typically observed at lateral parietal (200–300 ms post-cue) and frontal (300–500 ms) sites, respectively labeled the EDAN (early-directing attention negativity) and ADAN (anterior-directing attention negativity). While the EDAN has been attributed to the initiation of an attention shift (Harter *et al.*, 1989; Yamaguchi *et al.*, 1994) or cue interpretation (van Velzen & Eimer, 2003), the ADAN has been linked with frontal attentional control processes (Nobre *et al.*, 2000b; Talsma *et al.*, 2005; but see

Green *et al.*, 2008). Thus, this set of five dependent measures allowed us to cover possible effects of distractor presence on visual biasing activity, frontomedial pre-motor activity, and parietal and frontal lateralized, spatially selective activity during covert and overt orienting.

Materials and methods

Participants

Sixteen (five female) neurologically normal, paid volunteers, aged between 19 and 40 years participated in the study. All subjects provided written informed consent, and the Institutional Review Board of The City College of New York approved the experimental procedures. All subjects provided written informed consent and the institutional Review Board of The City College of New York approved the experimental procedures, which were in accordance with the Declaration of Helsinki. All subjects reported normal or corrected-to-normal vision.

Stimuli and task

The experiment comprised four spatial cueing tasks crossing the factors of task type (COVERT or SACCADE) and whether a distractor was presented simultaneously with the target stimulus in the opposite hemifield (SINGLE or DISTRACTOR). Eight separate trial blocks of each task were run within each session, with blocks interleaved such that each consecutive set of four blocks contained one of each task, in counterbalanced order. Subjects were seated 150 cm away from a 19-in CRT monitor with a resolution of 1024×768 and 60 Hz refresh rate. The subject's head was stabilized using a chin rest. All stimuli were presented on a mid-gray background. The trial structure was the same across all task versions (Fig. 1): a trial began with a small white fixation point (diameter 0.1°) appearing at the center of the screen. After 700 ms, a small arrow cue was presented (size 0.4° , duration 100 ms), pointing with equal probability to the left or right, indicating with 100% validity the hemifield in which the upcoming target will appear. The target was presented 817–1033 ms after cue onset within

the cued hemifield at one of three equiprobable, unmarked positions defined by polar angles of 45° , 0° and -45° relative to the horizontal meridian, and an equal eccentricity of 6.25° . The target consisted of a Gabor pattern of spatial frequency 6 cycles/degree, with a diameter of 1° at half-contrast, which could be oriented at 45° or 135° with equal probability so that subjects had no prior knowledge of orientation. The following trial began 917–1033 ms after target onset.

In the COVERT task type subjects were instructed to maintain fixation on the central point at all times and covertly deploy attention to the cued hemifield in anticipation of the target. A response was required on detection of a ring of reduced luminance in the Gabor pattern with a diameter of 0.8° and thickness 0.11° , which randomly occurred on 25% of trials. This covert detection task is known to invoke strong attentional deployments, as evidenced by modulation of ERPs to the standard Gabor stimuli at the onset of visual cortical activity and beyond (see Kelly *et al.*, 2008). To discourage the execution of saccades, targets appeared only for 100 ms, and the fixation point was extinguished 500 ms after target onset. In the SINGLE condition, targets appeared alone in the cued hemifield. In the DISTRACTOR condition, a second distractor Gabor pattern appeared on every trial at the mirror-symmetric location in the opposite hemifield, which could also contain a darkened ring with 25% probability. Subjects were instructed to respond only when the ring appeared superimposed on the target, not when it was superimposed on the distractor.

In the SACCADE task type subjects maintained fixation during the cue–target interval but prepared to make a saccade to the target in the cued hemifield, to be executed immediately on its appearance. Targets in this case were of longer duration (500 ms) to allow time to fixate the pattern before returning gaze to the center on its offset. As in the COVERT task, the fixation point was extinguished 500 ms after target onset, in this case coincident with target offset. Gabor patterns did not contain rings on any trial and no button press responses were required. As in the COVERT task, targets appeared alone in the cued hemifield in the SINGLE condition, whereas a symmetrically located distractor Gabor pattern appeared on every trial in the DISTRACTOR condition.

A total of 72 trials were presented per block with cue direction and target position randomly ordered but equally represented in each. Subjects completed a total of 32 blocks (eight of each task), with breaks of varying duration in between.

Data acquisition

Continuous electroencephalographic (EEG) data, digitized at 512 Hz, were acquired from 164 scalp electrodes, two horizontal electrooculographic (EOG) electrodes placed at the outer canthi of the eyes and two on the nose (nasion and supranasion). Off-line, the data were low-pass filtered up to 45 Hz (4th order Butterworth) and re-referenced to the nasion. Noisy channels were identified automatically by comparing the standard deviation of amplitude over ~ 40 -s data segments at each channel to that of the six closest surrounding channels. If the standard deviation of a channel was more than twice that of at least three of the six neighboring channels, the channel was interpolated using a linear combination of the six neighboring signals, weighted by the inverse-squared distance.

Eye tracking

Eye position was continuously recorded during all tasks. An ISCAN eye tracker sampling eye position at a rate of 120 Hz was used for six subjects, and an EYELINK 1000 (SR-Research) sampling at 500 Hz

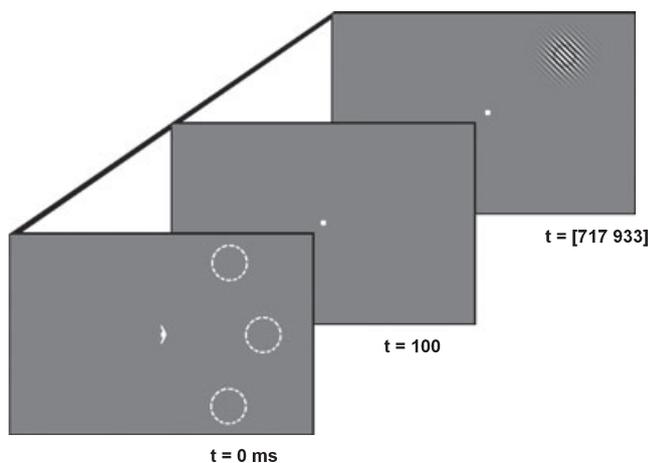


FIG. 1. Stimuli and task. An arrow cue was presented in advance of an imperative target appearing at one of three locations (dashed rings shown only for illustration) in the cue hemifield. In four separate blocked task types, subjects prepared to either covertly detect a 'go' target (COVERT condition; shown in the illustrated case) or to make a visually triggered saccade to the target (SACCADE condition), and had foreknowledge of whether a distractor would appear directly opposite on every trial (SINGLE vs. DISTRACTOR).

was used for the remaining 10. Calibration using a nine-point array of dots was carried out at the beginning of the recording session and repeated before resuming after any breaks throughout the session. Eye position data were analysed off-line to obtain measures of saccadic reaction time (SRT). To ensure unbiased estimates of SRT across eye tracker systems, we incorporated the simultaneously recorded EOG data in our measurement of saccade onset. We first detected timepoints at which eye movement velocity exceeded $75^\circ/\text{s}$ based on the eye tracker data. If any such points were detected prior to target onset, the trial was rejected. Otherwise, we proceeded to refine our measure of onset using the differential EOG (left channel minus right) data. Specifically, for each data point in the EOG trace, a straight line was fit to the 30-ms window ending at that point and for the 30-ms window starting at that point, respectively. We then calculated the slope of the lines in the forward and trailing windows, and took the difference between them at each timepoint. In the resulting waveform, we found the local maximum or minimum (depending on saccade direction) that lay closest to the movement detected in the eye tracker data, and marked this as the saccade onset. This corresponds to detection according to an acceleration criterion, and is appropriate in this case where EEG activity immediately following the detected onset timepoint is dramatically affected by the eye movement itself. It also provides the most accurate timing with respect to the target trigger in the EEG and enabled the derivation of saccade-locked ERPs.

For all analyses of both SACCAD and COVERT blocks, trials were rejected if eye gaze deviated by more than 0.5° at any point during the cue–target interval. In addition, SACCAD trials were rejected if a saccade was not made within the 500 ms duration of the target, while COVERT trials were rejected if a saccade was made in the same time-frame. Four subjects for whom eye movements were detected during the cue–target interval on more than 25% of trials were excluded from all further analyses.

Data analysis

Cue-locked ERPs were derived for leftward cues ('cue-L') vs. rightward cues ('cue-R'), separately for each of the four task conditions. EEG data were epoched from -200 ms before to 1000 ms after cue onset, and baseline-corrected with respect to the interval -100 – 0 ms, with an artifact rejection threshold of $\pm 80 \mu\text{V}$ applied. In the SACCAD task, only trials with saccades made in the correct direction and with a latency longer than 80 ms were accepted. In both tasks, only trials with cue–target stimulus onset asynchronies longer than 875 ms were accepted, so that late component time-intervals could extend to 900 ms after cue onset.

We tested for effects of the main task manipulations (task type and distractor presence) on five well-known ERP/EEG processes evoked by a central arrow cue: the EDAN, ADAN, LDAP, alpha lateralization and a fronto-central late negativity. The latter resembles both the classic CNV (Walter *et al.*, 1964) and the PSN (Kurtzberg & Vaughan, 1982) defined in saccade-locked ERP studies, but is here labeled 'Nfc' in the interest of neutrality. Each of these five processes was reduced to a single measure for each of the four blocked task conditions (SACCAD/COVERT \times SINGLE/DISTRACTOR) for each subject. For the spatially selective ERP components, amplitude was integrated across appropriate time-intervals (chosen by inspection of collapsed waveforms in Fig. 2A, and for consistency with previous studies) and across clusters of four–five electrodes at symmetrical, lateral scalp sites (EDAN: 240 – 320 ms, PO7/8; ADAN: 360 – 440 ms, F3/4; and LDAP: 500 – 900 ms, PO7/8). These three processes are defined by an interaction of hemisphere and cue direction on amplitude at these

symmetric sites. Therefore, each was reduced to a single double-subtraction metric by subtracting amplitude for rightward cues from leftward cues over both hemispheres, then subtracting the right hemisphere direction effect from the left (see, e.g. Harter *et al.*, 1989; Jongen *et al.*, 2006 for a similar approach). This is equivalent to summing opposite differences across hemispheres according to the formula (LHcueL–LHcueR) + (RHcueR–RHcueL). Thus, contralateral negativities (EDAN and ADAN) take on negative values, whereas the LDAP should appear positive. Average alpha amplitude waveforms were derived by filtering each epoch with a passband of 8 – 14 Hz, rectifying (so that negative values are made positive), averaging across trials, then smoothed by averaging data points within a sliding 100 -ms window. The alpha effect was captured in a double-subtraction metric in the same way as for the three ERP components, using the same time-interval and electrode clusters as for the LDAP. Because the alpha biasing effect is defined by a relative decrease for attention directed to the contralateral hemifield, this metric should take on negative values. Finally, the Nfc was measured as the difference in amplitude at midline fronto-central sites in the interval 800 – 900 ms relative to that in the interval 500 – 600 ms. In this case leftward and rightward cue conditions were averaged.

Results

Behavior

Reaction times (RT) were recorded as the saccade onset latency relative to target onset in the SACCAD task, and as the button press latency on 'go' targets in the COVERT task. We carried out a $2 \times 2 \times 3$ ANOVA with factors of cued Hemifield [left, right visual field (LVF, RVF)], Distractor Presence (SINGLE, DISTRACTOR) and target Position (upper, middle, lower) on RT for each task type. Mean RT for all four blocked task conditions are listed in Table 1. Of primary interest was an overall slowing in reaction time of 9 ms with the presentation of a distractor for both the COVERT and SACCAD tasks.

SACCAD task

There was a significant main effect of Distractor Presence on saccadic RT ($F_{1,11} = 50.06$, $P < 0.001$). There was also a main effect of Position ($F_{2,22} = 26.64$, $P < 0.001$), with pair-wise comparisons showing faster saccadic RTs to the middle position compared with the lower position and faster again to the upper position compared with the middle (both $P < 0.005$), replicating previously reported patterns (Heywood & Churher, 1980). This Position effect interacted with Distractor Presence ($F_{2,22} = 4.23$, $P < 0.05$), which was driven by a smaller (but nevertheless significant, $P < 0.05$) SINGLE-DISTRACTOR difference at lower positions compared with both the upper and middle positions (both $P < 0.05$). Subjects incorrectly made saccades into the hemifield opposite the cue on only $0.43 \pm 0.37\%$ of DISTRACTOR trials, demonstrating that they followed the cue as instructed.

COVERT task

There was an interaction between Distractor Presence and Hemifield ($F_{1,11} = 5.55$, $P < 0.05$). In follow-up comparisons the RT slowing in the DISTRACTOR conditions relative to the SINGLE conditions reached significance for the LVF (14 ms; $P < 0.05$) but not for the RVF (4 ms; $P > 0.1$; overall main effect n.s., $P = 0.13$). There was also a main effect of Position on RT ($F_{1,11} = 5.92$, $P < 0.01$), driven by faster RT for stimuli in the middle position compared with both upper and lower stimuli (both $P < 0.05$). Subjects detected targets

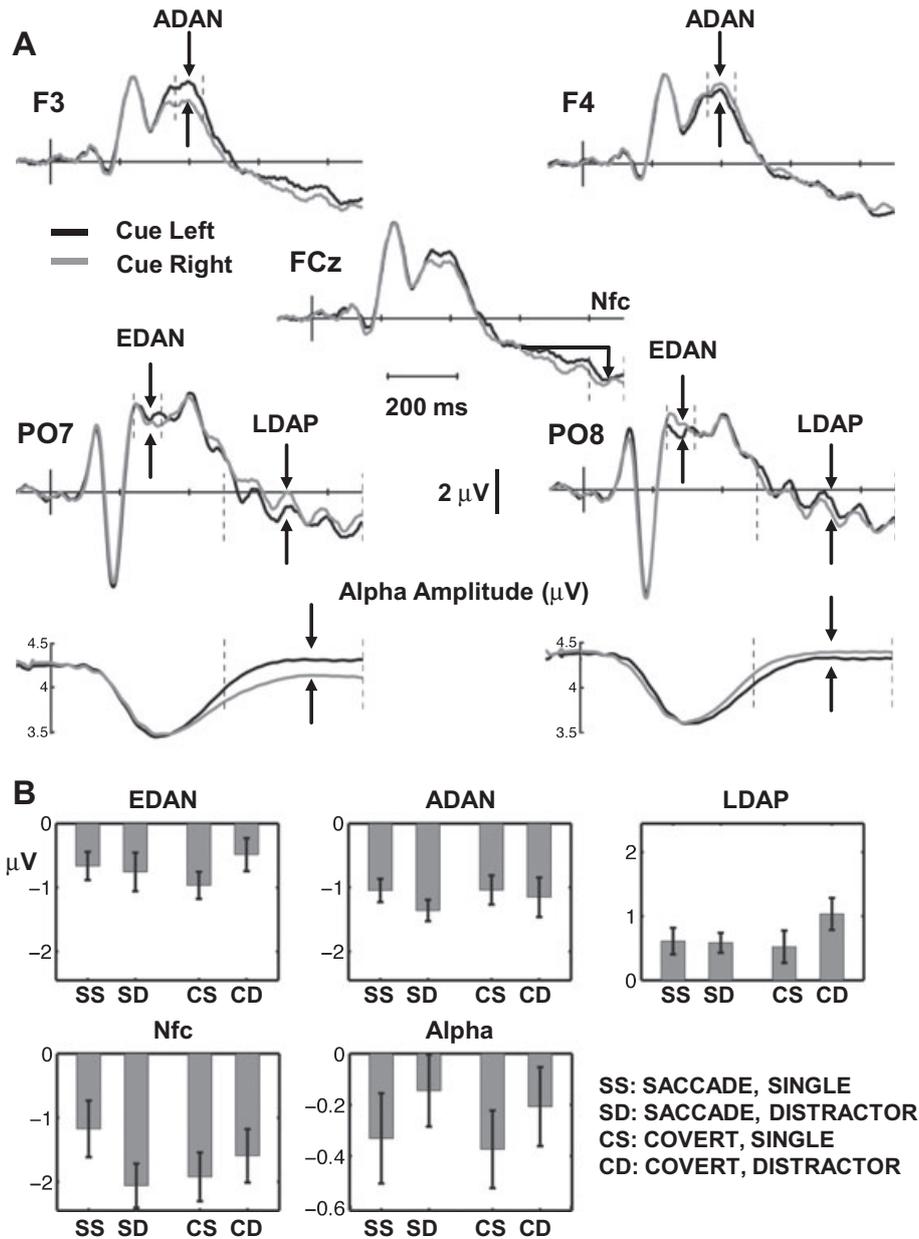


FIG. 2. (A) Collapsed cue-evoked ERP waveforms (i.e. averaged across the four task conditions) at lateral frontal, midline fronto-central and lateral ventral parieto-occipital sites, and alpha amplitude timecourses at the same ventral parieto-occipital sites, illustrating the derivation of the five dependent measures: the EDAN (early-directing attention negativity), ADAN (anterior-directing attention negativity), LDAP (late-directing attention positivity), alpha lateralization and a fronto-central late negativity (Nfc). Dashed vertical lines demarcate the time-intervals used for measurement of each process. (B) Metrics capturing each of the five processes, averaged for each task condition. All were significantly different than zero (corresponding to absence of the process) for each of the four task conditions ($P < 0.05$), and a significant interaction between task type (COVERT/SACCADE) and distractor presence (SINGLE/DISTRACTOR) is evident for the EDAN, LDAP, Nfc and alpha lateralization.

with a mean ($\pm\text{SD}$) hit rate of $89 \pm 11\%$, which was not found to depend on any task conditions ($P > 0.1$). False alarms were made on $2.6 \pm 2.8\%$ of DISTRACTOR trials with a target appearing on the uncued distractor side, demonstrating that subjects followed the cue as instructed.

Electrophysiology

Figure 2A demonstrates the derivation of the five dependent measures, which were all significantly different than zero for each of the four task conditions ($P < 0.05$). Collapsed cue-evoked ERP waveforms

(i.e. averaged across the four task conditions), derived over left and right frontal sites (the sites of the ADAN), midline fronto-central (the slow negative 'Nfc'), and ventral parieto-occipital (EDAN/LDAP) sites are shown for illustration, along with alpha amplitude timecourses (all waveforms broken out by task condition are shown in Supporting information, Fig. S1, while the waveforms from which the five dependent measures were derived appear in supporting Fig. S2). The metrics capturing the five cue-evoked processes for each task condition are plotted in Fig. 2B. Task type and distractor presence had differential effects on several of the cue-locked processes: the EDAN, LDAP, alpha lateralization and the Nfc.

TABLE 1. RTs for saccade onset in the SACCAD task and for button press on 'go' targets in the COVERT task

Position of target stimulus	SACCAD task RT (ms)		COVERT task RT (ms)	
	SINGLE	DISTRACTOR	SINGLE	DISTRACTOR
LVF				
Upper	164 ± 17	178 ± 15	452 ± 57	479 ± 73
Middle	173 ± 21	188 ± 22	445 ± 60	448 ± 44
Lower	188 ± 24	195 ± 23	462 ± 60	473 ± 60
RVF				
Upper	158 ± 17	165 ± 16	471 ± 69	472 ± 70
Middle	168 ± 24	179 ± 20	446 ± 61	447 ± 60
Lower	185 ± 23	190 ± 20	460 ± 53	470 ± 58
Overall means	173	182	456	465

Data are presented as means ± SD. RT, reaction time; LVF, left visual field; RVF, right visual field.

A 2 × 2 ANOVA with factors of Task Type (SACCAD vs. COVERT) and Distractor Presence (SINGLE vs. DISTRACTOR) was carried out for each process. Significant interactions between Task Type and Distractor Presence were found for the EDAN ($F_{1,11} = 6.58$, $P < 0.05$), the LDAP ($F_{1,11} = 9.85$, $P < 0.01$) and the Nfc ($F_{1,11} = 6.86$, $P < 0.05$). Both the EDAN and LDAP were modulated by distractor presence in the COVERT tasks, but not in the SACCAD tasks – the EDAN was marginally greater for the SINGLE condition ($P = 0.056$), whereas the LDAP was stronger for the DISTRACTOR condition ($P < 0.05$). In contrast, the non-lateralized Nfc was enhanced in the DISTRACTOR condition relative to the SINGLE condition in the SACCAD task but was not significantly modulated in the COVERT task ($P > 0.1$). To verify that the interaction for the LDAP is not merely a temporal extension of that found for the EDAN, which was in the same direction (see Fig. 2B), we tested the intervening interval 320–500 ms, and found no interaction (both $P > 0.1$).

An unexpected effect was revealed for alpha lateralization – the relative decrease of alpha contralateral to cue direction was greater when a distractor was not present than when present (main effect of Distractor Presence: $F_{1,11} = 9.94$, $P < 0.01$), and this did not depend on task type. Plotting alpha amplitude measures broken out by all factors (Hemifield, Hemisphere, Distractor Presence, Task Type) shows that hemispheric differences may lie at the root of this effect (Fig. 3). To further examine this, we conducted a separate 2 × 2 ANOVA for each hemisphere assessing the factors of cued Hemifield and Distractor Presence with the COVERT/SACCAD factor collapsed. Over the left hemisphere, alpha power was marginally lower for right (contralateral) cues than left cues ($F_{1,11} = 3.85$, $P = 0.075$), which did not depend on Distractor Presence. For the right hemisphere, there was an interaction ($F_{1,11} = 9.19$, $P < 0.02$); follow-up comparisons revealed that alpha power was lower prior to contralateral (LVF) targets than ipsilateral (RVF) targets for the SINGLE condition ($P < 0.02$), but not for the DISTRACTOR condition ($P > 0.1$). Figure 3 illustrates this virtual disappearance of the cue-differential over the right hemisphere during the DISTRACTOR blocks.

To further examine the modulations by distractor presence of late non-spatially selective processes like the Nfc, we mapped the scalp distribution (default spline interpolation function of BESA analysis package, <http://www.besa.de>) of the DISTRACTOR-SINGLE difference in the late pre-target interval (800–900 ms) for the SACCAD and COVERT tasks, with cue direction collapsed (Fig. 4). The

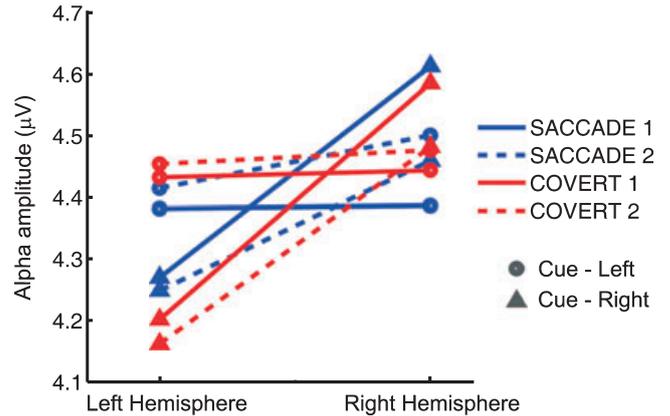


FIG. 3. Measures of alpha amplitude in the late pre-target time-interval, broken out by all factors to highlight hemispheric differences in the modulation of the alpha cueing differential due to distractor presence. In the DISTRACTOR conditions (dashed lines, '2'), the alpha differential (left vs. right cues) is absent over the right hemisphere.

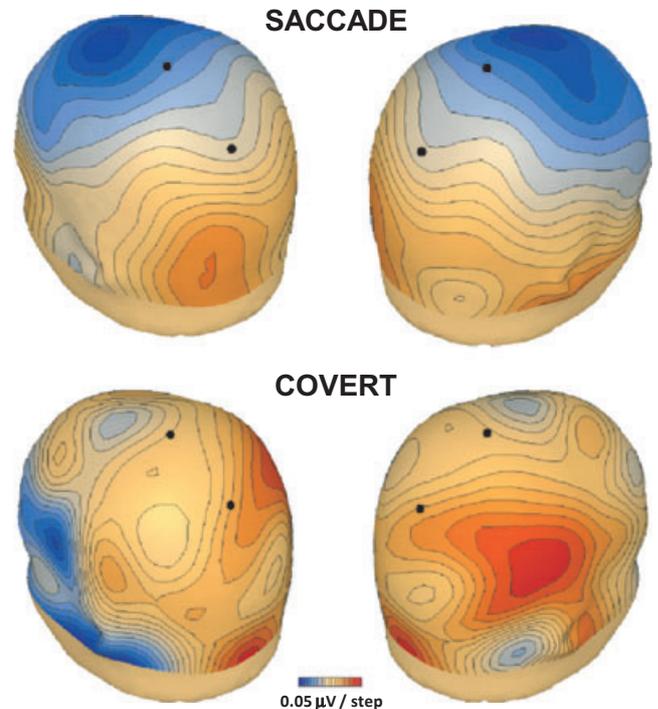


FIG. 4. Scalp topographical maps of the difference due to distractor presence (DISTRACTOR – SINGLE) for each task type in the late pre-target interval, averaged across cue direction. In the SACCAD task, the distractor presence-related difference is dominated by an upregulation of the midline fronto-central negativity (Nfc), as quantified in Fig. 2B. In the COVERT task, a distinct pattern is seen, where a relatively positive posterior right-lateralized focus appears concurrently with a left-lateralized, relatively negative frontal focus. For reference, black dots mark the locations of standard electrode placements Cz and Pz.

enhancement of the Nfc in the presence of distractors in the SACCAD task can be seen to be focused over midline fronto-central scalp. Interestingly, the same collapsed difference topography for the COVERT task (note the LDAP would be cancelled out and so is not visible here) reveals two dominant foci – one positive focus over right parietal scalp and one negative focus over left frontal scalp.

Saccade-locked ERPs

The Nfc component bears a resemblance to the PSN, a similarly slow and fronto-centrally distributed saccade-locked ERP component previously ascribed to preparatory activity in frontal pre-motor areas (Kurtzberg & Vaughan, 1982; Everling *et al.*, 1997). It was thus of interest to examine pre-saccadic activity in the saccade-locked ERP in our data. The PSN typically begins 0.5–1 s prior to saccade onset over midline sites, and does not differ for leftward vs. rightward cues. Because the pre-saccadic epoch is contaminated by visually evoked activity, we utilized the COVERT data to subtract out the target-evoked ERP in the SACCADE trials. This was achieved using the following steps: data were first epoched from –600 ms before to 500 ms after target onset for both the SACCADE and COVERT blocks. Average target-locked ERPs were constructed for the COVERT blocks separately for the SINGLE and DISTRACTOR conditions, and for each cue direction and target position. For each single trial in the SACCADE blocks, the average COVERT target ERP of the matching conditions was subtracted from the stimulus-locked SACCADE epoch. The saccade-locked single-trial waveform was subsequently extracted from this trace using an epoch of –600–150 ms relative to saccade onset. These waveforms were baseline corrected relative to the interval –600 to –500 ms, and averaged for each cue direction and target position. Figure 5A shows the saccade-locked ERP for the SINGLE and DISTRACTOR conditions, averaged across cue directions and target positions. A broad negativity resembling the PSN component can be seen for the DISTRACTOR

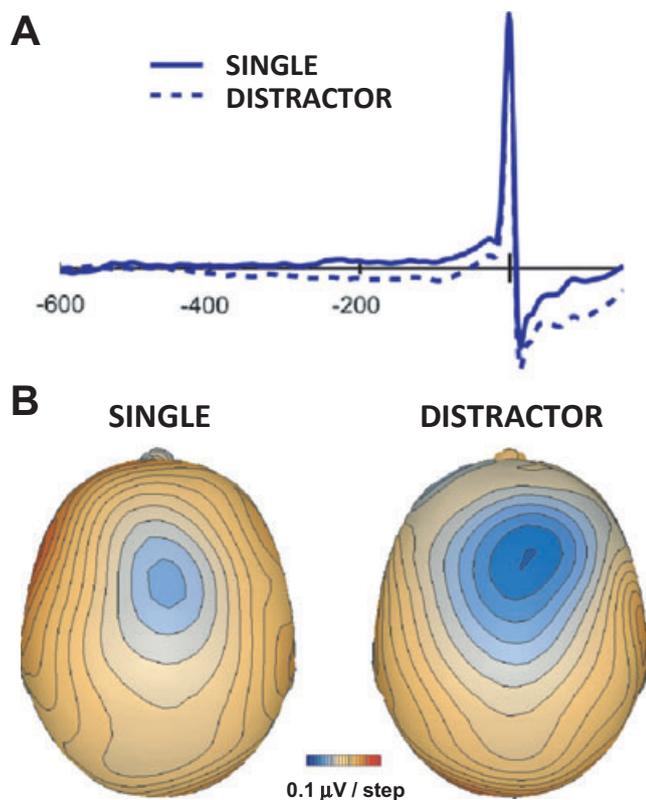


FIG. 5. (A) Saccade-locked ERP averaged over five electrodes centered on standard electrode site FCz. (B) Scalp topographies of the PSN (–200 to –100 ms relative to saccade onset) for SINGLE and DISTRACTOR conditions. Note that scalp topographies are ‘reference free’, thus a local minimum over fronto-central cortex in the SINGLE condition is represented in blue shading, even though the nasion-reference waveforms appear slightly positive.

condition, enhanced relative to that for the SINGLE condition. PSN amplitude, measured in the interval –200 to –100 ms, was submitted to a $2 \times 2 \times 3$ ANOVA with factors of Cue, Target Position and SINGLE/DISTRACTOR. There was a main effect of SINGLE/DISTRACTOR ($F_{1,11} = 5.22$, $P < 0.05$), with no other effects reaching significance. Figure 5B shows the scalp topographies of the PSN for both conditions.

Discussion

The close links between saccadic eye movements and shifts of covert attention have long been a subject of interest, and have been demonstrated by human psychophysics (Kowler *et al.*, 1995; Deubel & Schneider, 1996; Gersch *et al.*, 2004), non-human primate neurophysiological recordings (Kustov & Robinson, 1996; Andersen & Buneo, 2002; Goldberg *et al.*, 2006), and human neuroimaging (Corbetta *et al.*, 1998; Nobre *et al.*, 2000a) and electrophysiology (Van der Lubbe *et al.*, 2006; Van der Stigchel *et al.*, 2006; Eimer *et al.*, 2007). Visual distractors are known to impair effective target selection in both covert (Theeuwes, 1994) and overt (Theeuwes *et al.*, 1998) situations. In this study we set out to contrast the anticipatory neural processes invoked to resolve target competition in the covert and saccadic orienting systems. We compared ERPs and alpha-band (8–14 Hz) activity during the cue–target interval of four different versions of a spatial cueing task, involving either covert attentional shifts or preparation for target-triggered saccades, either in the presence or absence of an oppositely located, concurrent distractor. We found differences in the pattern of modulation of anticipatory processes invoked to handle target competition in the covert and overt tasks, evident in both lateralized and non-lateralized activity. We found that whereas biasing in lateralized low-level visual areas was more strongly affected by distractor presence during covert attentional deployments, late pre-target activity over more anterior midline areas was more strongly affected during saccade preparation.

Lateralized spatially selective activity

A late posterior contralateral positivity (‘LDAP’) was evident in all versions of our spatial cueing task, but whereas it increased in strength with distractor presence in the covert task, it remained the same in the saccade task. Given its timing and focus over ventral visual areas, the LDAP has been thought to reflect the influence of the peripheral allocation of attention on extrastriate visual areas (Hopf & Mangun, 2000; Talsma *et al.*, 2005; Simpson *et al.*, 2006). Recently it was shown that the LDAP significantly predicts reaction time on subsequent target discrimination (Kelly *et al.*, 2009). In one other study where the upcoming locations of both a saccade target and distractor were cued in advance (Van der Stigchel *et al.*, 2006), an LDAP was not observed; rather, a contralateral negativity broadly distributed over frontal and posterior scalp was measured in the late pre-target interval. This discrepancy with respect to our results may be due to critical differences in the task used in that study – lateral target locations were only in the lower visual field, and in these trials the distractor always appeared not in the opposite location but in a position directly below center on the vertical meridian. A target-alone condition was not run in that study, so it is not possible to assess the effect of distractor presence. Aside from target-distractor proximity, another interesting possibility is that an LDAP was not observed because no further target processing was required beyond the target’s onset at a pre-determined location. In our covert task a Go-NoGo decision was required based on the detection of a lower-luminance

ring inside the Gabor patch. In our saccade task, though no discrimination was required, the precise location of the target within the cued hemifield was uncertain, and thus had to be identified prior to movement. Thus, the LDAP may reflect anticipatory visual biasing specific to the expectation of stimulus attributes to be discriminated. Consistent with this, an LDAP was not observed in a condition where anticipatory target-directed saccades were allowed to occur before the target actually appeared (Evdokimidis *et al.*, 1992). In that situation a saccade was prepared without the expectation of a target at a peripheral retinal location – the target was rather expected on the fovea after the anticipatory saccade was executed.

In addition to the modulation of the LDAP in the covert task, we found that the earlier posterior EDAN was relatively enhanced with the knowledge that distractors would not appear. This is interesting because it has been posited that the EDAN reflects the selection of lateralized physical attributes (typically an arrowhead) of the cue to decode its spatial instruction rather than a genuine attention-directing process (see van Velzen & Eimer, 2003). The cues were physically the same in all conditions in the present study, yet the EDAN modulated specifically in the covert task with knowledge of distractor presence. This may indicate that the EDAN plays a more active role in the directing of attention, though why it is relatively stronger without distractors is currently unclear and may merit further investigation.

Non-lateralized anticipatory activity

We observed a slow negative potential over midline fronto-central cortex prior to target appearance in all task conditions, but whereas it was enhanced with knowledge of distractor presence in the saccadic task, it did not modulate in the covert task. This component, which we have labeled the Nfc, belongs to a general class of negative-going slow potentials that have long been observed in task contexts where a behavioral contingency is formed between successive but temporally discontinuous events (Walter *et al.*, 1964; Fuster, 1984; Brunia, 1999). Referred to as the CNV when measured with respect to a leading cue, this component has been said to reflect a prospective code or preparatory 'set' in pre-frontal areas that facilitates perception of and reaction to expected events (e.g. Fuster, 1984). Recent simultaneous EEG–functional magnetic resonance imaging (fMRI) data showed that CNV amplitude correlates with BOLD activation in the supplementary motor cortex, as well as in the anterior cingulate cortex and the thalamus (Nagai *et al.*, 2004). A similar slow negativity has been observed in ERPs time-locked to the onset of saccadic eye movements, most often labeled PSN (Kurtzberg & Vaughan, 1982; Evdokimidis *et al.*, 1992; Richards, 2003). The PSN is larger in naive subjects, an effect attributed to increased volitional effort (Evdokimidis *et al.*, 1992), and is larger prior to anti-saccades than pro-saccades (Everling *et al.*, 1997; Klein *et al.*, 2000). The latter findings parallel those of non-human primate studies showing that preparatory set activity preceding anti-saccades is reduced in FEF (Everling & Munoz, 2000) and increased in supplementary eye fields (SEFs) (Schlag-Rey *et al.*, 1997), relative to pro-saccades. Taken together with the abovementioned fMRI correlates of the CNV, these findings suggest that modulations in fronto-central surface-negative activity may reflect adjustment of preparatory set in frontal areas involved in higher level motor planning to facilitate correct behavior in situations containing response conflict. The distractor-related Nfc/PSN enhancement in our saccade task, evident both when we aligned ERPs to the onset of the cue (Nfc) and when we aligned them to saccade onset (PSN), may reflect such an adjustment. That is, medial areas such as the SEF, which likely contribute to the PSN (Everling *et al.*, 1997),

may play a larger role in saccade programming when there is response conflict, whether this conflict arises from the selection of a cued target over a simultaneous distractor (our DISTRACTOR condition), or from the requirement to direct saccades away from a suddenly appearing stimulus (the anti-saccade task). Whatever the precise mechanism underlying modulations of fronto-central activity for target competition, the most interesting aspect of the current results was that these modulations were not observed in the covert case, indicating that target competition is resolved by distinct preparatory mechanisms in the overt and covert orienting systems.

A recent non-human primate ERP study replicated the finding of increased PSN for anti-saccades relative to pro-saccades and further showed that the pre-saccadic positivity (PSP), shortly following the PSN just before (~150 ms) saccade onset, is reduced or absent prior to anti-saccades (Sander *et al.*, 2010). The same finding in humans was originally thought to reflect the suppression of the automatic pro-saccade (Evdokimidis *et al.*, 1996), but it was pointed out in the more recent non-human primate study that the PSP may be generated in the FEF and may be reduced before anti-saccades due to overlap from the PSN generated in the neighboring SEF (Sander *et al.*, 2010). In the current study a PSP was apparent (Fig. 5A), but we did not observe any modulations of this component with distractor presence, despite seeing a modulation for the preceding PSN/Nfc. The requirement to suppress a pre-potent pro-saccade response may be equally low in our task conditions because the hemifield of the target/distractor is pre-designated.

When plotting the scalp distribution of the distractor-related modulations with cue direction collapsed, which enables clear visualization of the Nfc enhancement, we observed an interesting topography in the covert case. Though no appreciable fronto-central focus could be seen, confirming the lack of modulation of the frontal oculomotor planning areas seen in the saccade task, clear foci could be seen over the right temporo-parietal and left frontal cortex (Fig. 4). This is consistent with the BOLD activations that were modulated by distractor presence in the recent fMRI study of Ruff & Driver (2006). Those foci were located specifically in the right angular gyrus, and the left anterior and dorsomedial superior pre-frontal gyrus. Though such directionally unspecific lateralized processes were not the intended focus of the present study, the parallel we observed here with those fMRI activations is interesting to note, and may warrant following up.

Modulation of alpha-band biasing with distractor presence

We found that the expectation of a distractor also influenced the levels of EEG power in the alpha-band (8–14 Hz) range, although this influence did not differ between overt and covert task types. There is considerable evidence that alpha power is relatively increased over the posterior cortex ipsilateral to the hemifield to be attended (Worden *et al.*, 2000; Kelly *et al.*, 2005, 2006, 2009; Thut *et al.*, 2006; Gomez-Ramirez *et al.*, 2009). This effect is thought to index a suppression of sensory processing of distractor locations (Foxe *et al.*, 1998; Kelly *et al.*, 2006). In light of this, one would expect that the alpha biasing effect be enhanced in a situation where a distractor is known to appear contralateral to the target, because more active inhibitory processes would be necessary to prevent the visual response elicited by the distractor from attracting attention or engaging movement planning processes. However, we found that alpha biasing was 'weaker' when a distractor was expected. This might suggest that alpha power reflects stimulus expectancy rather than attention *per se*; that is, the expectation of a stimulus in a particular hemifield, regardless of whether it is to be attended or suppressed, may be the principal factor

driving alpha amplitude. However, our results specifically show that this reduction in the cueing differential is entirely restricted to the right hemisphere. Alternative explanations should thus be considered.

Several key attentional functions that would be implicated in our tasks appear to be right-lateralized in the brain. For example, right inferior parietal regions have been implicated in non-spatial functions of sustaining attention, detecting salient events in a sequence and controlling attention over time (Husain & Nachev, 2007); lesions of the right posterior parietal cortex specifically affect action planning under response conflict (Coulthard *et al.*, 2008); a hypothesized ventral network (including the temporoparietal junction and ventral frontal cortex) serving a 'circuit breaker' function in detecting salient events with bottom-up relevance has been described as strongly right-lateralized (Corbetta & Shulman, 2002); finally, Ruff & Driver (2006) found right-lateralized angular gyrus activation associated with top-down mechanisms invoked to reduce the cost of an expected distractor. Alpha is known to be generated not only in early visual areas but also in higher regions – for example, O'Connell *et al.* (2009) found a focal increase in alpha over the right inferior parietal cortex leading up to a lapse in sustained attention, reflecting the drifting offline of a parietal control process involved in a temporal expectancy task. Assuming that right-lateralized attentional processes such as those mentioned above are equally invoked for rightward and leftward cues in our task and are also strong generators of alpha, it is very conceivable that changes in lower-level visual alpha would be masked. This would occur because oscillatory amplitude does not sum linearly between adjacent generators as broadband amplitude does, on account of phase variations – amplitude modulations of one alpha generator are visible less and less on the scalp as the power of another more dominant alpha generator increases. Thus, the finding of a reduced alpha cueing differential over the right posterior cortex here should be interpreted with caution, especially considering the higher overall levels of alpha over that hemisphere (see Figs 2 and 3).

Anticipatory spatial processes when the specification of the saccade or attentional goal is not precise

The present data have corollary implications for the question of how spatially circumscribed an attentional deployment target needs to be in order to provide attentional benefits. Does attentional deployment entail the specification of a precise covert target locus or saccadic endpoint, as is eventually required for saccade execution? Generally, saccadic motor preparation is conceived as a vector-specific process, in which a movement with a specific saccade endpoint is programmed by a population of cells in the FEFs or brainstem (though see Edelman & Keller, 1998). In contrast, reports that multiple non-contiguous loci can be simultaneously attended (Müller *et al.*, 2003; McMains & Somers, 2004; Lalor *et al.*, 2007) indicate that visual attention can be deployed in more complex configurations. In previous covert and overt spatial cueing studies, imperative stimulus locations have been fixed so that a cue points to a single circumscribed position in space, enabling the preparation of a well-defined saccadic vector. This then leads to the question of whether these preparatory processes would be exhibited in a situation where information regarding target location is partial but incomplete. In the present study, a single horizontal hemifield was cued, and stimuli could appear at one of three locations in the hemifield spanning 120° in polar direction. In both the covert and saccade tasks, responses were found that were similar to those found when a single discrete location has been cued. This suggests that lateralized preparatory processes can be established for both overt and covert orienting without requiring the specification of a single position.

A consideration of the pre-motor theory

The question of whether areas in posterior parietal and frontal cortex represent motor commands or peripheral attention deployments has long generated considerable controversy. One difficulty in resolving this question is the close connection between these two processes. On one hand, suddenly appearing visual targets both attract attention and elicit reflexive saccades. On the other hand, it is thought that spatial selection processes preceding saccades require the peripheral deployment of visual attention. On the basis of these strong links between saccadic and covert attentional shifts and their shared anatomical substrates, it has been postulated that covert spatial attention is a behavioral phenomenon that emerges from planned but unexecuted saccades (Rizzolatti *et al.*, 1994) – the pre-motor theory of attention. Our results suggest that while there are broad similarities in the lateralized brain processes subserving saccadic and covert orienting, some orienting signals display important dissociations under certain task conditions – specifically, spatially selective visual cortical modulation is upregulated to deal with competition among covert targets, whereas frontomedial preparatory activity instead receives a boost in advance of competing saccade targets. This finding may detract from the most absolute pre-motor view of wholly identical systems for covert and overt orienting.

Supporting Information

Additional supporting information may be found in the online version of this article:

Fig. S1. Cue-evoked ERP waveforms for each of the four task conditions at lateral frontal, midline fronto-central and lateral ventral parieto-occipital sites, and alpha amplitude timecourses at the same ventral parieto-occipital sites, as in Fig. 2A.

Fig. S2. Waveforms for each of the four task conditions (SACCADE/COVERT, SINGLE/DISTRACTOR) from which the five dependent measures were derived.

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Abbreviations

ADAN, anterior-directing attention negativity; BOLD, blood oxygen level-dependent; CNV, contingent negative variation; EDAN, early-directing attention negativity; EEG, electroencephalogram; EOG, electrooculogram; ERP, event-related potential; FEF, frontal eye field; fMRI, functional magnetic resonance imaging; LDAP, late-directing attention positivity; LVF, left visual field; PSN, pre-saccadic negativity; PSP, pre-saccadic positivity; RT, reaction time; RVF, right visual field; SC, superior colliculus; SEF, supplementary eye field; SRI, saccadic reaction time.

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