Research Report

Isolating event-related potential components associated with voluntary control of visuo-spatial attention

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ABSTRACT

Attention-directing cues presented at fixation evoke several lateralized event-related potential (ERP) components prior to the onset of visual targets. These components have been associated with the control of visuo-spatial attention, but the neuro-cognitive operations and neural generators of the components are still largely unknown. Here, we isolated cue-elicited ERP activity in different ways to home in on different neuro-cognitive operations and to gain a better understanding about the possible neuroanatomical sources of the cue-elicited ERP activities. To isolate lateralized cue-ERP activity, we compared shift-left and shift-right cue ERPs to shift-up cue ERPs. To measure all of the ERP activity related to attentional control, including spatially nonspecific activity that is removed in the process of isolating lateralized cue-ERP components, we compared shift-cue ERPs to neutral-cue (i.e., no-shift) ERPs. Isolated lateralized-ERP activity was seen in the contralateral–occipital lobe in the early phase of the cue-target interval and in the ipsilateral–occipital lobe in the late phase. The later, ipsilateral activity indicates that the late directing attention positivity (LDAP) reflected processing of the to-be-ignored location. The neutral-cue isolation revealed a shift-related positivity over posterior scalp regions and a shift-related negativity over more anterior scalp regions. The spatio-temporal sequence of shift-related activity observed on the scalp, together with estimates of distributed source activity underlying the shift-related ERP components, indicated that frontal and parietal regions of cortex participated in the control of attention and led to pre-target biasing in visual cortical areas.

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1. Introduction

Voluntarily directing attention to a particular location of the visual field enhances the perception of objects that appear at that location relative to objects that appear at unattended locations (e.g., Carrasco et al., 2004). This perceptual change results in faster and more accurate detection and identification of attended targets than unattended targets (Luck et al., 1996; Prinzmetal et al., 2005). Attention-induced changes in perception and performance are accompanied by changes in the brain’s electrical responses to visual targets. Typically, stimuli that appear at attended locations elicit larger amplitude event-related potential (ERP) components that arise from extrastriate visual cortex (e.g., P1, posterior N1) than do stimuli that appear elsewhere in the visual field (for review, see Hillyard et al., 1998; Mangun, 1995). Such effects occur when attention is selectively maintained at a particular location for several trials (e.g., Eason, 1981, Mangun and Hillyard, 1987) and when attention is shifted on a trial-by-trial basis in response to symbolic cues that predict the location of an
impending target (e.g., Luck et al., 1994; Mangun and Hillyard, 1991).

Several fundamental cognitive operations are hypothesized to take place when observers shift attention covertly in response to a symbolic visual cue (Posner, 1980; Woldorff et al., 2004). The ERP method is well suited to investigate these operations because the scalp-recorded electrical fields provide precise information about the timing of neural activity as it unfolds across the cortex. Although the spatial resolution of the ERP method is lower than that of hemodynamic-based neuroimaging, its high temporal precision enables easier separation of activity related to the control and deployment of attention and the subsequent attentional modulation of sensory cortical areas in anticipation of the target stimulus.

Several investigators have examined the ERPs elicited by centrally presented cues that trigger shifts of attention to locations in the left and right visual hemifields (e.g., Harter et al., 1989; Hopf and Mangun, 2000; Mangun, 1994; Nobre et al., 2000). To identify the neural processes associated with shifting attention in space, researchers initially focused on lateralized-ERP components elicited by the centrally presented cues. Such lateralized components are likely associated with the cognitive operations that take place between the presentation of the cue and subsequent target. Some symbolic cues that have been used traditionally to investigate the behavioural consequences of attention (e.g., physically asymmetrical arrows) may inadvertently lead to lateralized sensory activity due to the contralateral nature of the geniculo-striate visual pathways. For this reason, ERP researchers have adopted the use of laterally symmetric cues, such as overlapping pointers (e.g., Nobre et al., 2000), bilateral pointers (e.g., Van Velzen and Eimer, 2003), and individual letters (Grent-'t-Jong and Woldorff, 2007). Low-level sensory responses elicited by these symmetric cues are balanced more evenly across the left and right cortical hemispheres, thereby giving researchers the opportunity to associate lateralized activity to cognitive operations involved in deploying attention to the left or right side of the visual field.

Lateralized-ERP components in the cue-target interval are typically identified by comparing waveforms recorded contralateral and ipsilateral to the cued location. By convention, contralateral-ipsilateral ERP differences are described as increased voltages in the waveforms recorded contralateral to the to-be-attended location, although it is possible that they reflect modulations of the waveforms recorded ipsilateral to the cued location (i.e., contralateral to the uncued location on the opposite side of fixation; Nobre et al., 2000; Praamstra et al., 2005). Lateralized cue-elicited components reported to date include a contralateral negativity over the posterior scalp beginning 200–300 ms after cue onset (early-directing attention negativity, EDAN; Harter et al., 1989), a contralateral negativity over the anterior scalp 300–500 ms after cue onset (anterior-directing attention negativity, ADAN; Eimer et al., 2002), and late contralateral positivities (late directing attention positivity, LDAP; Harter et al., 1989) and negativities (bias-related negativity, BRN; Grent-'t-Jong and Woldorff, 2007) over the posterior scalp toward the end of the cue-target interval.

The lateralized-ERP components elicited by visual attention-directing cues – EDAN, ADAN, and LDAP/BRN – have been associated with successive control operations underlying voluntary deployment of attention in visual space. However, the specific control operation tied to each lateralized component, as well as the neural generators of each component, are still largely unknown. Originally, the EDAN was considered to reflect early parietal activity related to the deployment of attention to the cued location, but subsequent work indicated that the EDAN may be an N2pc (known to be generated primarily in occipito-temporal cortex; Hopf et al., 2000) elicited when participants attend to a lateralized portion of the cue itself (such as an arrowhead; van Velzen and Eimer, 2003). The ADAN has been considered to reflect attentional-control activity in the frontal cortex based on its anterior topography and presence in some nonvisual cuing tasks (e.g., Eimer et al., 2002), but recent work has indicated that the ADAN does not reflect critical attentional-control operations (Green et al., 2005, 2008; Green and McDonald, 2006; but see also Seiss et al., 2007) and arises from multiple cortical regions (Green et al., 2008). The LDAP has been considered to reflect anticipatory biasing of occipito-temporal regions involved in processing of the target (Green et al., 2005; Harter et al., 1989; Hopf and Mangun, 2000), marking of the to-be-attended location (Hopf and Mangun, 2000), an attentional trace of the expected visual target (Hopf and Mangun, 2000), and parietal activity related to the deployment and maintenance of attention at the cued location (Eimer et al., 2002).

Some of the difficulty in identifying specific attentional-control operations by examination of cue-elicited ERPs is likely due to the conventional approach used to identify lateralized-ERP activity. This approach, which involves comparison of ERP waveforms recorded contralateral and ipsilateral to the cued location (or alternatively, a comparison of ERPs elicited by leftward-directing and rightward-directing cues), has two limitations. First, this approach is insensitive to spatially nonspecific activity. If an attentional-control region were involved in the control of covert shifts of attention to both left and right visual fields, activity in that region would go undetected by the lateralized-ERP approach. Because much of the attentional-control activity in the fronto-parietal network may be spatially nonspecific (Praamstra et al., 2005; Woldorff et al., 2004), there is a need to complement the lateralized-ERP approach with a different approach that enables measurement of spatially nonspecific ERP activity. Researchers have started to examine spatially nonspecific attentional-control activity by comparing ERPs elicited by leftward and rightward cues to ERPs elicited by spatially noninformative (i.e., neutral) cues (Praamstra et al., 2005; Slagter et al., 2005; Talsma et al., 2007; Talsma et al., 2005) or interpret cues that signify no target will appear (Grent-'t-Jong and Woldorff, 2007). These studies indicate that there may be substantial bilateral activity in frontal and parietal cortices during the cue-target interval.

Second, the conventional approach does not enable researchers to determine whether the lateralized-ERP components reflect changes in the electrical fields at electrodes located contralateral to the cued location, ipsilateral to the cued location, or both. This limitation is made clear by conventional methods for mapping the topography of the lateralized-ERP components. One such method is to plot the amplitude of the left-cue minus right-cue difference
waveforms across the scalp (e.g., Hopf and Mangun, 2000; Nobre et al., 2000; Eimer et al., 2002); a second method is to plot the contralateral-ipsilateral difference on just one side of the scalp (Green et al., 2005; Praamstra et al., 2005); a third method is to invert the amplitude of the contralateral-ipsilateral difference and plot it on one side of the scalp along side the half-head map of the noninverted contralateral-ipsilateral differences (antisymmetric mapping, Praamstra et al., 1996; see also Green et al., 2008). Neither the half-scalp method nor the antisymmetric mapping method allow for the determination of whether changes in voltage are arising from ipsilateral scalp sites, contralateral scalp sites, or some combination of the two. The two full-scalp methods also make it difficult to estimate the locations of underlying neural sources, because the opposite-polarity foci might be attributed incorrectly to opposite ends of a single dipolar source located between the foci. Moreover, the subtraction technique used to produce the antisymmetric maps can introduce spurious sources if the activities are not actually symmetrical (Oostenveld et al., 2003).

The goal of the present study was to provide a more detailed picture of attentional-control activity elicited by symbolic visual cues. In addition to measuring the lateralized-ERP components using conventional methods, we set out to isolate attentional-control activity in two ways. First, we compared ERPs elicited by leftward-directing and rightward-directing cues to ERPs elicited by upward-directing cues to isolate the lateralized cue-ERP activity. This isolation method was premised on the assumption that deployments of attention to lateralized and nonlateralized locations activate the same fronto-parietal network of attentional control and lead to pre-target biasing of activity in the visual areas, but that deployments of attention to lateralized locations would lead to more lateralized activations. Based on the nominal view of the LDAP, we predicted that the isolated LDAP would show up as a positive voltage focused contralateral to the to-be-attended location.

Second, we compared ERPs elicited by leftward-directing and rightward-directing cues to ERPs elicited by a spatially noninformative cue to examine both spatially specific and spatially nonspecific activities related to attentional control and preparation. Based on prior ERP studies that employed spatially noninformative cues (Praamstra et al., 2005; Slagter et al., 2005; Talsma et al., 2005, 2007; Grent-‘t-Gong and Woldorff, 2007), we expected to find broadly distributed shift-related activities on the scalp, which would be suggestive of a distributed attentional-control system. We investigated the potential neural sources of the shift-related activities, as well as the isolated lateralized-ERP components, using a distributed source modeling technique called standardized low resolution brain electromagnetic tomography (sLORETA). We predicted to find shift-related activities in frontal and parietal regions that have been implicated in attentional control (by fMRI, EEG, and ERP) as well as in extrastriate visual areas, where anticipatory biasing of activity has been shown to occur (fMRI: Corbetta and Shulman, 2002; EEG/ERP: Green and McDonald, 2008; Grent-‘t-Gong and Woldorff, 2007). Although a number of fMRI and ERP studies have suggested that top-down attentional control is initiated in frontal cortex (e.g., Corbetta and Shulman, 2002; Grent-‘t-Gong and Woldorff, 2007), based on the results of a recent EEG study (Green and McDonald, 2008) we predicted that the shift-related activities would be seen in parietal cortex prior to frontal cortex.

We recorded ERPs from seventeen participants during a visual discrimination task, in which a cue presented at fixation indicated the likely location of the task-relevant visual target (Fig. 1a). Each trial began with a cue that either predicted the location of an impending target (predictive-cue trials; 80%) or did not predict the target’s location (neutral-cue trials; 20%). To ensure laterally balanced physical stimulation, we used a symmetric cue that consisted of three colored boxes positioned immediately to the left and right, as well as above, fixation. The positions of the colored cue boxes were consistent with three potential target locations in the upper visual field. The position of one colored cue box was informative of the impending target’s location (counter-balanced across participants). This colored box was present on predictive-cue trials and absent on nonpredictive-cue trials (Fig. 1b). The target appeared at the cued location on 80% of the predictive-cue trials (valid trials) and at an uncued location on
20% of the predictive-cue trials (invalid trials). Participants indicated the orientation of a masked target grating by means of a two-alternative-forced-choice response (horizontal or vertical).

2. Results

2.1. Behavioral performance

On average, 8.9% of the trials were discarded due to eye-movement and EEG artifacts. An additional 2.1% of the trials were discarded because responses were too fast (i.e., anticipatory; RT<100 ms), too slow (RT>2500 ms), or fell too far from the mean (3 SDs). Response accuracy and median RT were calculated from the remaining trials for each observer in each Validity×Location condition.

As illustrated in Fig. 2, target-discrimination accuracy was affected by Cue Type, $F(2,38)=21.9$, $P<0.00001$, with highest accuracy on valid-cue trials (mean=77.2%; SEM=1.6%), intermediate accuracy on neutral-cue trials (mean=74.3%; SEM=1.6%), and lowest accuracy on invalid-cue trials (mean=70.5%; SEM=1.4%). The effect of Cue Type did not interact with Target Location, $F(4,76)<1$. Planned t-tests revealed that the accuracy on valid-cue trials was higher than the accuracy on neutral-cue trials ($t(19)=2.74$, $P=0.013$) and invalid-cue trials ($t(19)=6.61$, $P<0.00001$) and that the accuracy on neutral-cue trials was higher than the accuracy on invalid-cue trials ($t(19)=3.68$, $P=0.002$). All of these pairwise differences were significant after Bonferroni correction for multiple comparisons. Accuracy was also affected by Target Location, $F(2,38)=5.31$, $P=0.013$, with highest accuracy for right targets (77.1%; SEM=2.1%), intermediate accuracy for central targets (74.3%; SEM=1.9%), and lowest accuracy for left targets (70.6%; SEM=1.5%). Pairwise differences in accuracy for identifying left, right, and central targets were not tested because we had no a priori hypotheses about the effect of Target Location.

RT was also affected by Cue Type, $F(2,38)=16.9$, $P=0.0001$. RT was shortest for valid-cue trials (mean=701 ms; SEM=25 ms), intermediate for neutral-cue trials (mean=752 ms; SEM=26 ms), and longest for invalid-cue trials (mean=782 ms; SEM=31 ms) (Fig. 2). The effect of Cue Type did not interact with Target Location, $F(4,76)<1$. Planned t-tests revealed that the RT on valid-cue trials was shorter than the RT on neutral-cue trials ($t(19)=-3.62$, $P=0.00004$) and invalid-cue trials ($t(19)=-4.79$, $P=0.0001$). Both of these differences were significant after Bonferroni correction for multiple comparisons. RTs on neutral-cue and invalid-cue trials were nonsignificant ($t(19)=1.93$, $P=0.068$). The RT was also affected by Target Location, $F(2,38)=6.22$, $P=0.005$, with longer RT for left targets (770 ms; SEM=27 ms) than for central (731 ms; SEM=29 ms) and right targets (733 ms; SEM=28 ms). Pairwise differences in RTs for left, right, and central targets were not.

![Fig. 2](image-url) - Effects of spatial cueing on behavioral performance. The asterisk (*) denotes statistical significance after applying the Bonferroni correction for multiple comparisons; ns denotes a nonsignificant difference after Bonferroni correction.

![Fig. 3](image-url) - Grand-average ERP waveforms elicited by symbolic cues. Cue onset occurred at time=0 ms; Target onset occurred at time=900 ms.
tested because we had no a priori hypotheses about the effect of Target Location.

2.2. ERPs to attention-directing cues

Fig. 3 displays the ERP waveforms elicited by each of the four different types of cues at representative electrode sites across the scalp. All of the cues elicited similar sequences of positive and negative ERP peaks in the initial 200 ms time window. The major deflections in this interval included a negative peak at 110 ms that was maximal at parietal-occipital electrodes and a negative peak (N1) at 180 ms that was maximal at lateral-occipital electrodes. Little or no P1 (90–120 ms) was observed at posterior electrodes, most likely because of spatio-temporal overlap with the first negative peak (possibly a C1 delayed by focal presentation of the cue) and a slow negative potential that began prior to cue onset. No attempt was made to remove the anticipatory negative potential because it did not vary as a function of cue type. After the initial 200 ms following cue onset, the cue-elicited ERP waveforms consisted of a positive peak at 250 ms, which was maximal at fronto-central electrode sites, and a slow negative shift over the posterior scalp, which remained until the onset of the target. The timing and scalp topography of the positive peak resembled those of the P3a component, which is most commonly seen in response to infrequent nontarget deviants in three-stimulus oddball tasks (Comerchero and Polich, 1999; Soltani and Knight, 2000).

2.2.1. Conventional lateralized-ERP activity

As can be seen in Fig. 3, there were subtle differences between the ERPs elicited by the three types of shift cues and larger differences between these shift-cue ERPs and the neutral-cue ERPs. To examine these differences more closely, we first measured the lateralized cue-ERP components elicited by shift-left and shift-right cues using a conventional method (Green et al., 2008). Fig. 4a shows the ERPs recorded contralateral and ipsilateral to the to-be-attended location, collapsed over shift-left and shift-right cueing conditions. Over the lateral-occipital scalp (e.g., PO7/8), the contralateral waveforms were more negative than the ipsilateral waveforms in the 150–350 ms post-cue interval. This voltage difference reversed later in the cue-target interval (500–700 ms), and by the end of the cue-target interval the differences between contralateral and ipsilateral waveforms disappeared. Over the lateral frontal scalp (e.g., F5/6), the contralateral waveforms were more negative than the ipsilateral waveforms beginning 350 ms after cue onset until the end of the cue-target interval. Statistical analyses of mean voltages at frontal and occipital sites confirmed the following lateralized cue-ERP effects: (1) a contralateral negativity over the occipital scalp in the 200–300 ms interval, \( t(19)=5.11, P=0.00006 \); (2) a contralateral negativity over the frontal scalp in the 300–500 ms interval, \( t(19)=2.01, P=0.05 \); (3) a contralateral positivity over the occipital scalp in the 500–700 ms interval, \( t(19)=-2.26, P=0.03 \). The topographical distributions of these lateralized cue-ERP differences are displayed in Fig. 4b. The frontal contralateral negativity was marginally significant in the 500–700 ms and 700–900 ms intervals \( P=0.06 \) and \( P=0.07 \), respectively, whereas the late contralateral positivity over the occipital scalp was clearly absent in the 700–900 ms interval, \( t(19)=.59, P=0.57 \).

2.2.2. Lateralized activity isolated using shift-up cue

Following our conventional analysis of lateralized cue ERP activities, we compared the ERPs elicited by shift-left cues and shift-right cues to the ERPs elicited by the shift-up cue to provide a more accurate picture of the lateralized-ERP activities over contralateral and ipsilateral scalp regions. Differences in ERP voltages elicited by shift-left cues, shift-right cues, and shift-up cues became apparent over the lateral–occipital scalp by 100–200 ms (see Fig. 3). To examine the spatio-temporal characteristics of these differences more closely, we subtracted

Fig. 4 - Grand-averaged ERP waveforms elicited by shift-left cues and shift-right cues, collapsed to show the conventional lateralized cue-ERP components. (a) Cue ERPs recorded contralateral and ipsilateral to the cued locations at anterior sites (F5/6) and posterior sites (PO7/8). Shaded areas denote time intervals of the EDAN, ADAN, and LDAP components. Time = 0 ms denotes cue onset. (b) Topographical voltage maps of the contralateral-ipsilateral difference waveforms during time intervals of the EDAN (200–300 ms), ADAN (300–500 ms), and LDAP (500–700 ms).
the ERPs elicited by shift-up cues from the ERPs elicited by the shift-left and shift-right cues. The \( L^{-U} \) and \( R^{-U} \) differences were then combined after remapping electrodes to preserve information about lateralization (see Section 4.6.2). Fig. 5a shows the combined \( L^{-U}/R^{-U} \) difference waves, with electrodes contralateral to the to-be-attended lateral location on the right side of the scalp. Distinct negative peaks occurred over the lateral-occipital scalp in two temporally overlapping phases. In the first phase, which peaked 200–300 ms after cue onset, a negative peak was seen predominantly over occipital scalp sites contralateral to the laterally cued location. In the second phase, which peaked 550–600 ms after cue onset, a negative peak was seen predominantly over occipital scalp sites ipsilateral to the laterally cued location. Statistical tests revealed that the early negative difference was significant at contralateral–occipital sites in the 100–400 ms interval whereas the later negative difference was significant at ipsilateral–occipital sites in the 300–700 ms interval (Fig 5a). In addition to these occipital negative peaks, an early (100–150 ms) negative peak was significant at most electrodes. There also appeared to be a small positive peak at anterior sites (450–500 ms), primarily over the ipsilateral scalp, but this positive voltage difference was nonsignificant in each of our statistical tests.

To investigate the scalp distributions of the isolated lateralized cue-ERP activities more thoroughly, we created topographical maps of the \( L^{-U}/R^{-U} \) comparison

### Table 1 – Locations of significant distributed source activations in \( L^{-U}/R^{-U} \) comparison

<table>
<thead>
<tr>
<th>Interval (ms)</th>
<th>BA</th>
<th>MNI coordinates (mm)</th>
<th>Region</th>
<th>Lateralization</th>
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<tr>
<td></td>
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<td>250–300</td>
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</table>

Abbreviations: SFG, superior frontal gyrus; LingG, lingual gyrus; MFG, middle frontal gyrus; MOG, middle occipital gyrus.
ms time intervals. Fig. 5b shows maps of voltages and corresponding scalp current densities (SCDs) in two time intervals. The first time interval (250–300 ms) corresponded to the early phase of L–U/R–U negativity; the second time interval (550–600 ms) corresponded to the late phase of L–U/R–U negativity. As can be seen in the figure, the early negative voltage was tightly focused over the contralateral–occipital scalp (plotted on the right side of the map). In contrast, the late negative voltage was focused primarily over the ipsilateral–occipital scalp. The contralateral and ipsilateral–occipital negativities overlapped in time; thus, some negative voltage remained over the contralateral scalp in the late time interval.

We plotted SCD maps to examine further the possible number and locations of cortical generators of the lateralized negative voltages. Unlike voltages, the SCDs are unaffected by the choice of the reference electrode. The resulting SCD maps show estimations of the radial sources and sinks of electrical currents on the scalp (Perrin et al., 1989). The SCD map corresponding to the early negative voltage showed a focus of activation over the contralateral–occipital scalp, whereas the SCD map corresponding to the late negative voltage showed a strong activation over the ipsilateral–occipital scalp and a weaker activation over the contralateral–occipital scalp.

To investigate the neural sources of the isolated lateralized-ERP activity in the cue-target interval, distributed source activity was estimated using the sLORETA algorithm (Pascual-Marqui, 2002). Fig. 5c shows statistically significant source activations in the time intervals of the peak occipital negative voltages (250–300 ms and 550–600 ms). In the early time interval, distributed source activity was seen along the medial surface of the occipital lobe contralateral to the to-be-attended lateral location. This activity was centered on the lingual gyrus.

Fig. 6 – Attentional-control cue-ERP activity isolated using the neutral cue. (a) Left-neutral/right-neutral difference waveforms (L–N/R–N) recorded at contralateral and ipsilateral electrodes (on right and left of head, respectively). The column on the right shows the results of statistical t-tests of mean amplitudes of the difference waveforms in 50-ms intervals. Gray boxes denote statistical significance ($P < 0.05$). (b) Topographical maps of mean voltages in the time intervals of the peak difference-waveform activities, along maps of corresponding scalp current densities (SCDs). (c) Statistically significant sLORETA source estimations of attentional-control activity.
voltage peak was also observed over the contralateral more posterior focus at the ipsilateral parietal sites. A negative over the scalp, with one focus at midline frontal sites and a shift-related positive peak was distributed broadly in this time interval. A shift-related negativity appeared over the frontal, fronto-central scalp in the 450–500 ms interval, intensified and shifted to the contralateral hemisphere in the 650–700 ms interval, and then weakened in the 750–800 ms interval. The SCD maps showed foci of activation primarily over lateral-occipital areas in each time interval.

Fig. 6c shows statistically significant distributed source activities in the four time intervals used to show topographical maps of the L–N/R–N difference waves. Table 2 lists the coordinates for the centroids of significant source activations. In the 250–300 ms interval, significant activity was seen primarily in ventral occipito-temporal regions in both hemispheres (contralateral: middle temporal gyrus; ipsilateral: cuneus). In the 450–500 ms interval, significant activity was seen in the middle temporal gyrus (contralateral) as well as in the inferior parietal lobe (contralateral), middle frontal gyrus (contralateral), superior frontal gyrus (ipsilateral), middle frontal gyrus (contralateral), anterior cingulate cortex, and middle occipital gyrus (bilateral). In the 650–700 ms interval, significant activity was seen in the superior frontal gyrus (ipsilateral), middle frontal gyrus (contralateral), anterior cingulate cortex, and middle occipital gyrus (bilateral). Finally, in the 750–800 ms interval, significant activity was seen in the middle frontal gyrus (contralateral), anterior cingulate cortex, and middle occipital gyrus (bilateral).

Table 2 – Locations of significant distributed source activations in L–N/R–N comparison

<table>
<thead>
<tr>
<th>Interval (ms)</th>
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<th>Lateralization</th>
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<td>ACC</td>
<td>Midline</td>
</tr>
</tbody>
</table>

Abbreviations: MFG, middle frontal gyrus; MedFG, medial frontal gyrus; SFG, superior frontal gyrus; ACC, anterior cingulate cortex; MTG, middle temporal gyrus; IPL, inferior parietal lobe; MOG, middle occipital gyrus.

(3.1). Additional distributed source activity was seen on the lateral cortical surface in the superior frontal gyrus. In the later time interval, distributed source activity was seen in the occipital lobe ipsilateral to the to-be-attended lateral location within the lingual gyrus and middle occipital gyrus. Additional distributed source activity was seen ipsilaterally in the precuneus and middle frontal gyrus.

2.2.3. Attentional-control activity isolated using neutral cue
In the third step of our ERP analysis, we compared the ERPs elicited by shift-left cues and shift-right cues to the ERPs elicited by the neutral cue. Differences in ERP voltages elicited by the shift cues and the neutral cues were apparent throughout most of the cue-target interval (see Fig. 3). To examine the spatio-temporal characteristics of these differences more closely, we subtracted ERPs elicited by the neutral cue from the ERPs elicited by the shift-left and shift-right cues. The L–N and R–N differences were then combined after remapping electrodes to preserve information about lateralization (see Section 4.6.2). Fig. 6a shows the combined L–N/ R–N difference waves, with electrodes contralateral to the to-be-attended location on the right side of the scalp. Statistical analysis of the difference waves revealed the following effects: (1) a positive peak at frontal, fronto-central, central, and parietal electrodes in the 200–300 ms interval, (2) a positive peak at occipital electrodes in the 250–550 ms interval, (3) a negative peak at frontal, fronto-central, and central electrodes in the 500–800 ms interval.

To investigate the scalp distributions of the attentional-control activity more thoroughly, we created topographical maps of the L–N/R–N difference waves in 50-ms time intervals. Fig. 6b shows maps of voltages and corresponding SCDs in four time intervals. During the 250–300 ms time interval, a shift-related positive peak was distributed broadly over the scalp, with one focus at midline frontal sites and a more posterior focus at the ipsilateral parietal sites. A negative voltage peak was also observed over the contralateral-occipital scalp in this time interval. During the 450–500 ms interval, a shift-related positive peak was focused over the contralateral-occipital scalp and extended to the ipsilateral-occipital scalp. A shift-related negativity appeared over the fronto-central scalp in the 450–500 ms interval, intensified and shifted to the contralateral hemisphere in the 650–700 ms interval, and then weakened in the 750–800 ms interval. The SCD maps showed foci of activation primarily over lateral-occipital areas in each time interval.

3. Discussion

3.1. Lateralized-ERP activity in cue-target interval
There has been considerable debate about the specific types of cognitive operations associated with the lateralized cue-ERP components. Initial studies associated the EDAN with control operations involved in shifting attention to the cued location, but a recent study showed that the EDAN likely reflects...
attentional selection of lateralized features of the cue stimulus itself (Van Velzen and Eimer, 2003). Specifically, van Velzen and Eimer showed that when the cue stimulus is reversed so that a feature on one side of fixation is used to direct attention to a location on the opposite side of fixation, the EDAN reverses polarity whereas the subsequent ADAN and LDAP components are unaffected. Based on these findings, van Velzen and Eimer concluded that the EDAN is an increased negativity contralateral to the informative side of the cue stimulus (i.e., an N2pc to part of the cue). The scalp topography of the isolated EDAN observed in the present study, which showed a clear negative focus over the contralateral-occipital scalp, is consistent with this conclusion. Our study was not designed to test the N2pc account of the EDAN, but future studies could do so by determining whether the isolated EDAN flips polarity when the relevant part of the cue (e.g., a red box) is used to direct attention to a potential target location on the opposite side of fixation.

The N2pc account of the EDAN has a potentially important implication for theories of attentional control. Namely, if the EDAN is not generated by processes involved in the deployment of attention to the cued location, then one of the other lateralized cue ERPs might reflect the initiation of attentional control. Researchers have hypothesized that the ADAN reflects the initiation of attentional control in frontal cortex because it occurs before the LDAP and is maximal over the anterior scalp (Eimer et al., 2002). Dipole source modeling has provided support for the presumed anatomical locus of the ADAN generator in premotor regions of the frontal lobe (Mathews et al., 2006; Fraamstra et al., 2005; van der Lubbe et al., 2006). However, the specific neuro-cognitive operation indexed by the ADAN has remained unclear. The conclusion that the ADAN reflects initiation of attentional control has been called into question by the results of several auditory and audio-visual spatial cueing studies, in which symbolic auditory spatial cues failed to elicit the ADAN despite the presence of theLDAP and cue effects on target processing (Green and McDonald, 2006; Green et al., 2008; Green et al., 2005; Störmer et al., in press; but see also Seiss et al., 2007).

In the present study, a small ADAN was found by conventional means (Fig. 4), but no isolated ADAN was found when we compared shift-left and shift-right cue ERPs to shift-up cue ERPs (Fig. 5). It is unlikely that low signal-to-noise led to the absence of the isolated ADAN, because an isolated LDAP was found even though the conventional LDAP was as small as the conventional ADAN. Together with the results from auditory cueing studies, the absence of the isolated ADAN suggests that this lateralized component is not an electrophysiological marker of the initiation of top-down attentional control. However, it is possible that some unknown aspect of our experimental procedure led to the absence of an isolated ADAN.

Both the LDAP and the isolated LDAP peaked at 500–650 ms in the present study. Neither of these “late” lateralized-ERP components was sustained until the appearance of the target stimulus. These results are in accord with previous findings (e.g., Hopf and Mangun, 2000; van Velzen et al., 2002). The early offset of the LDAP indicates that this component probably does not reflect anticipatory target preparation, although the duration of preparation might be associated with the time at which some critical threshold of activity is reached rather than the time at which the target is presented (Hopf and Mangun, 2000). Researchers have surmised that the LDAP might reflect the coding of the to-be-attended location (Hopf and Mangun, 2000), the control of the deployment of attention (Eimer et al. 2002; van Velzen et al., 2002), or the establishment of a representation of the expected target (i.e., an attentional trace; Hopf and Mangun, 2000). The present findings are inconsistent with the hypothesis that the LDAP reflects attentional-control activity in the parietal lobe (Eimer et al., 2002). Specifically, we showed that the isolated LDAP is maximal over the lateral-occipital scalp, and our distributed source analysis indicated that the isolated LDAP is generated in occipital cortex, not parietal cortex.

The present study revealed novel results about the polarity and lateralization of the LDAP. Specifically, the isolated LDAP appeared as a negative voltage over the ipsilateral-occipital scalp rather than as a positive voltage over the contralateral-occipital scalp. Consistent with the pattern of ERP activity observed on the scalp, the distributed source analysis indicated that the isolated LDAP was generated in regions of the occipital lobe that were ipsilateral to the cued locations. One possible explanation for these unexpected findings is that the procedure used to isolate the lateralized components led to a mirror imaging and polarity inversion of the isolated ERP components. For example, if a shift-up cue elicited a +2 μV positive deflection on both sides of the scalp while a shift-right cue elicited a +2 μV positive deflection on the left side of the scalp and a 0 μV positive deflection on the right side of the scalp, our isolation subtraction (right-up) would yield a difference of −2 μV over the left side of the scalp. In other words the positive voltage over the right hemisphere would have been transformed into a negative voltage over the left hemisphere. However, this explanation would also have to account for the fact that the isolated EDAN was expressed as a contralateral negativity and not as an unexpected ipsilateral positivity.

A second explanation for the unexpected pattern of results is that the LDAP may reflect processing of a to-be-ignored location rather than the to-be-attended location. This explanation is in line with conclusions stemming from recent studies of cue-related changes in alpha-band EEG oscillations (Worden et al., 2000; Kelly et al., 2006; Rihs et al., 2007). These studies showed that event-related increases in alpha synchronization are found over occipital scalp regions ipsilateral to the to-be-attended location when there is a potential target location or concurrent distractor on the opposite side of fixation. In other words, the increased alpha occurred over the occipital scalp regions contralateral to the to-be-ignored locations. These alpha-band increases have been interpreted in terms of active suppression of the unattended objects or locations. The similarity between the lateralization of the isolated LDAP and the lateralization of the alpha-band increases suggests that the isolated LDAP could also reflect suppression of the to-be-ignored location. However, the isolated LDAP appears to differ from the increases in alpha-band synchrony in at least one important way: the former peaks at 500–650 ms and disappears before target onset, whereas the latter appears to develop gradually and remain until target onset. This may indicate that multiple attentional-control operations involve suppression of distractor information.
3.2. Attentional-control activity isolated using neutral cue

The pattern of shift-neutral difference wave activity observed in the present study bears similarity to patterns reported in previous studies that used neutral cues to isolate attentional-control activities. Several studies have reported shift-related positivities and negativities in the first 350 ms of the cue-target interval (Slagter et al., 2005; Talsma et al., 2005, 2007; see also Störmér et al., in press). Early shift-related positivities and negativities over the posterior scalp have been interpreted mainly in terms of attentional processing of the cue itself (Slagter et al., 2005; Talsma et al., 2007). In contrast, early effects over the anterior scalp have been taken to reflect rapid activation of fronto-parietal control systems, which may happen when the cue-target SOA is short and the cue stimulus is easy to interpret (Talsma et al., 2007). The specific neurocognitive operations that give rise to these early effects likely depend on methodological factors, such as the interpretability of the cue stimulus and the duration of the cue-target interval.

In the present study, which used a relatively long cue-target SOA and a somewhat complex cue, the earliest effects were seen primarily over the posterior scalp between 250 and 300 ms. It is unlikely that this early effect reflected a purely sensory response to the shift cues because the shift cues and neutral cues were nearly physically identical. However, the shift cue contained a color that was known in advance to be predictive of target location, whereas the neutral cue did not contain the relevant color. It is possible that this difference enabled an attentional boost to sensory signals arising from shift cues relative to the sensory signals arising from the neutral cue. This interpretation is in line with several recent findings. First, peripheral visual cues elicit larger occipital N1 components when they contain a feature that matches an observer’s attentional set than when they lack the task-relevant feature (Arnott et al., 2001). Second, a recent study of cue-related changes in theta-band EEG activity showed that early shift-related activation of occipital cortex occurs when centrally presented colour boxes are used to cue the target location but not when centrally presented letters are used to cue-target location (Green and McDonald, 2008). In other words, the early shift-related differences in occipital cortex went away when shift cues and neutral cues did not differ on the basis of a salient feature. Third, auditory shift cues that are easily discernable from auditory neutral cues appear to boost neural activity in auditory cortex as early as 200 ms (Störmér et al., in press).

The spatio-temporal sequence of the remaining shift-related activity points to the involvement of a distributed attentional-control network that biases activity in visual cortical areas prior to target onset. A shift-related positivity was observed over the posterior contralateral scalp between 300 and 500 ms, and a shift-related negativity was observed over frontal, central, and parietal scalp regions beginning at 450 ms and lasting until the end of the cue-target interval. No shift-related positivity or negativity was observed over the occipital scalp toward the end of the cue-target interval. To determine whether this was at least partially due to the use of mastoids as the common reference, we re-computed the L–N/R–N difference waves using an average reference. This confirmed that the difference wave voltages recorded at lateral–occipital sites were similar to the voltages recorded at the mastoids. The SCD maps, which provide reference-free estimates of radial current flow, showed clear foci of activity over the occipital scalp toward the end of the cue-target interval.

To gain a better understanding of the neural origins of the shift-related activities in the cue-target interval, we estimated the distributed sources of the shift-neutral difference wave for each participant and then used nonparametric tests to find regions of statistically reliable source activity across participants. The resulting distributed source estimates are affected by several factors, such as the assumptions that are incorporated into the inverse solution algorithm. However, such distributed source analysis techniques have several advantages over dipole source modeling, including the ability to estimate source activity without specifying the number of sources in advance (for more discussion, see Michel et al., 2004).

Several recent studies have modeled the neural sources of the conventional lateralized ERPs (Praamstra et al., 2005; Mathews et al., 2006; Grent’-t-Gong and Woldorff, 2007; van der Lubbe et al., 2006), but only two prior studies have modeled the neural sources of shift-neutral ERP differences (Grent’-t-Jong and Woldorff, 2007; Slagter et al., 2005). One of these studies constrained the locations of dipoles based on fMRI data to focus on the timing of activity in the presumed fronto-parietal network (Grent’-t-Jong and Woldorff, 2007). The other study allowed the locations of the dipoles to vary (Slagter et al., 2005). The results of the present study help to clarify some of the tentative conclusions from these past studies. In particular, in the Slagter et al. (2005) study, a single pair of best-fitting dipoles located in the occipital lobes accounted for the shift-related ERP activities observed at ~550 ms post-cue. Rather than interpreting this solution solely in terms of pre-target biasing in visual cortical areas, Slagter et al. (2005) speculated that additional sources in parietal cortex, frontal cortex, or both, contributed to the shift-neutral ERP differences. In the present study, significant source activity was observed in distinct regions of frontal, parietal, and occipito-temporal cortices, beginning 450 ms after cue onset. These findings are in line with the tentative conclusions of Slagter et al. (2005) and with the pattern of results that has emerged from event-related fMRI studies (e.g., Corbetta et al., 2000; Hopfinger et al., 2000; Woldorff et al., 2004).

In the present study, analyses of distributed source activity showed shift-related activities in the inferior parietal lobe and superior frontal gyrus 450–500 ms after the cue onset. These results suggest that parietal and frontal cortices become involved in attentional control at approximately the same time in spatial cueing tasks. A similar co-activation of parietal and frontal regions was observed during shifts of auditory attention (Störmér et al., in press). However, in that study frontal activity was short-lived, and was followed by activity in right parietal lobe and subsequent preparatory activity in temporal lobe. In the present study, activity in the frontal cortex continued through later time intervals (650–800 ms), in tandem with the late activities observed in occipital cortex. These differences could reflect different attentional orienting mechanisms for the auditory and visual modalities, such as activation of the frontal eye fields to a greater extent in the visual modality. However, the cues
in the auditory study were also not predictive of the upcoming target location, which could also influence the structures that are activated and the sequence in which they operate.

The pattern of distributed source activity observed here differed from the pattern that was observed when we used beamformer spatial filters to study cue-elicited changes in theta-band EEG across the human cortex (Green and McDonald, 2008). Theta-band attentional-control activity was observed first in parietal cortex, then in frontal cortex, then again in parietal cortex, and finally in occipital cortex. Based on those results, we argued that attentional control is initiated by the parietal lobe, not the frontal lobe, when observers shift their attention voluntarily in response to centrally presented symbolic cues. In the present study, sLORETA analysis did not aid in determining whether activity in parietal or frontal cortices initiated attentional control. In general, not much activity was observed in the parietal cortex, at least compared to the study of cue-elicited theta-band EEG activity.

The differences in source estimation are likely due to two factors. First, cue-elicited changes in ERPs and theta-band EEG oscillations contain different information. The ERP difference waves examined here contained information about a wide range of frequencies (0.1–25 Hz) but contained no information about induced changes in electrical brain activity that are canceled out in the course of ERP averaging (because induced responses are not phase-locked). The theta-band EEG activity that was examined in our previous study contained information about evoked (phase-locked) and induced (not phase-locked) changes in electrical brain activity but only within a limited range of frequencies. To gain a broader understanding of attentional control, it is important to look at evoked activity (ERPs) as well as induced changes in various frequency bands. Second, different source localization method have different advantages and disadvantages. The method used here, sLORETA, has relatively low spatial resolution but localizes activity without error under ideal conditions (Pascual-Marqui, 2002). Beamformers may be able to estimate activity with higher spatial resolution, but unfortunately the BESA beamformer cannot be applied to evoked activity at this time (BESA ver. 5.1).

4. Experimental procedures

All experimental procedures were approved by the Simon Fraser University research ethics board.

4.1. Participants

Twenty neurologically typical university students participated in the experiment after providing informed written consent. Each volunteer participated in one of two variants of the experiment. Eleven people participated in Experiment 1a, and nine different people participated in Experiment 1b. All participants (16 females; mean age 22.2 years) were right-handed and had normal or corrected-to-normal vision. A different analysis of the data from Experiment 1a was previously reported in Green and McDonald (2008).

4.2. Apparatus

The experiment was conducted in a sound attenuated and electrically shielded chamber that contained a 19-in CRT monitor. Participants sat in an adjustable chair and viewed the monitor from a distance of 65 cm. A Windows-XP-based PC running Presentation (Neurobehavioral Systems Inc., Albany, CA, USA) controlled stimulus presentation and registered the participants’ responses that were made on a gamepad device (Logitech). A second Windows-XP-based PC running custom software controlled EEG acquisition. The acquisition PC housed a 64-channel A-to-D board (PCI 6071e, National Instruments, Austin, TX, USA) that was connected to an EEG amplifier system with high input impedance (SA Instrumentation, San Diego, CA, USA).

4.3. Stimuli

Visual stimuli were presented on a black monitor with a background luminance of 0.02 cd/m². Three unfilled, gray squares (2.5°×2.5°, RGB=201, 201, 201) were presented throughout the experiment to highlight potential target locations. These target landmarks were positioned 8° (centre-to-centre) from a small gray fixation box, which was visible continuously at the center of the monitor. Two target landmarks were positioned to the left and right of the fixation box, 1.5° above the horizontal meridian, and one target landmark was positioned directly above the fixation box (Fig. 1). Three smaller boxes that were used to cue the locations of target stimuli surrounded the fixation box (each box 25°×25°; all within a 1° radius of fixation). Two of these cue boxes were positioned to the left and right of the fixation box, and one cue box was positioned directly above the fixation box. All cue boxes were grey until the beginning of each trial, at which point each cue box assumed a different color. This color change constituted the cue stimulus. Colors of the cue boxes were selected from red (RGB=255, 0, 0), green (RGB=0, 225, 0), blue (RGB=0, 204, 255), and violet (RGB=204, 102, 204). The color change lasted for 300 ms (Experiment 1a) or until the target was presented (Experiment 1b). We increased the duration of the cue in Experiment 1b to ensure that the offset of the cue at 300-ms in Experiment 1a was not affecting the ERP effects observed during the cue-target interval. Target stimuli consisted of five horizontally or vertically aligned bars presented within one of the three target landmarks for 50 ms. The luminance of the target was varied across trials to maintain accuracy at ∼75% (initial RGB=100, 100, 100). The mask was a checkerboard pattern that remained visible until a response was made.

4.4. Procedure

Participants were instructed to maintain fixation on the fixation box throughout each block of trials. In Experiment 1a, an inter-trial interval (ITI) of 500 ms occurred between the previous response and the presentation of the attention-directing cue. In Experiment 1b, we introduced a random ITI of 500–900 ms in an attempt to eliminate slow anticipatory potentials that may have been caused by the constant interval employed in Experiment 1a. Following the ITI, a
multi-colored cue stimulus was presented at fixation. One of the four possible cue colors was predictive of the target location (counterbalanced between participants). The cue stimulus contained the predictive color along with two nonpredictive colors on 80% of all trials (shift-cue trials). On the remaining 20% of all trials, the cue stimulus contained three nonpredictive colors (neutral-cue trials). When present, the predictive-cue color indicated the correct location of the impending target with 80% accuracy. Trials on which the predictive color appeared left of fixation (shift-left cue), right of fixation (shift-right cue), or above fixation (shift-up cue) were equiprobable and pseudo-randomly intermixed. After a 900-ms cue-target SOA, a target was presented at one of the three possible target locations. A checkerboard mask then appeared at the same target location and remained onscreen until participants made a manual response. The task was to discriminate the orientation of the target and respond as accurately as possible before the next trial by pressing a corresponding response button (stimulus-response mappings counterbalanced between participants). To motivate participants to attend to the cued location whenever possible the task was made difficult by adapting the luminance of the target bars to keep target-discrimination accuracy across all trials at 75%. Participants were told that the target would appear at the cued location on most trials and that the luminance of the target would be changed across trials to make the task moderately difficult. Each participant was instructed to direct attention to the cued target location whenever the cue contained the predictive color (i.e., attend left when predictive color presented to the left of fixation box) and to keep attention directed at the fixation box until the target appeared whenever the cue did not contain the predictive color (i.e., on neutral-cue trials). Participants were discouraged from making eye movements during the experiment and were informed that eye position was being monitored (by horizontal electro-oculogram; see below).

Each participant performed in a single one-hour session. The session was comprised of 30 blocks of trials separated by short rest periods. Trial types were presented pseudo-randomly within each block. In total, there were 288 left-cue trials, 288 right-cue trials, 288 up-cue trials, and 216 neutral-cue trials.

4.5. Electrophysiological recording

EEGs were recorded using 62 tin electrodes mounted on an elastic cap and one additional electrode fixed directly to the left mastoid. All but five of these electrodes were positioned at standard 10-10 locations (FP1, FPz, FP2, AF3, AF4, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FC5, FC3, FC1, FCz, FC2, FC4, FC6, T7, T5, C3, C1, Cz, C2, C4, C6, T8, CP5, CP3, CP1, CPz, CP2, CP4, CP6, P9, P7, P5, P3, P1, Pz, P2, P4, P6, P8, P10, PO7, PO3, POz, PO4, PO8, O1, Oz, O2, Iz, and M1; American Electroencephalographic Society, 1994). The remaining five electrodes were positioned at nonstandard locations inferior to the standard row of occipital electrodes to provide better spatial sampling of the visual ERPs maximal over the occipital scalp. All EEG electrodes were referenced to an electrode fixed to the right mastoid (M2) and were re-referenced off-line to the algebraic average of the two mastoids. The horizontal electro-oculogram (HEOG) was recorded bipolarly using two electrodes positioned lateral to the external canthi. All electrode impedances were kept below 10 kΩ. EEGs and HEOG were amplified (gain 20,000) in a bandpass of 0.1–100 Hz (−12 dB/ Octave) and digitized at 500 Hz.

Epochs of EEG that were time-locked to the cues were extracted and averaged separately for different conditions. A semi-automated artifact rejection procedure (Green et al., 2008) was performed to identify and remove trials on which the EEG epochs were contaminated by horizontal eye movements, blinks, and amplifier blocking. Artifact-free data were then used to create the averaged ERP waveforms. The averaged ERPs were digitally low-pass filtered (≥3 dB point at 25 Hz) to remove high-frequency noise (e.g., muscle artifact).

4.6. Data analysis

4.6.1. Behavioral performance

Spatial cuing effects on behavioral performance were assessed by conducting separate ANOVAs on target-discrimination accuracies and RTs, with factors for target location (left, centre, right) and cue type (valid, invalid, neutral). Paired-samples t-tests were then performed to examine the costs and benefits of spatial cueing separately. Costs were assessed by comparing performance on invalid-cue trials and neutral-cue trials, and benefits were assessed by comparing performance on valid-cue trials and neutral-cue trials. These planned pairwise comparisons were two-tailed and Bonferroni adjusted to maintain familywise error rates at .05.

4.6.2. Cue-elicited ERPs

The first step of the cue-ERP analysis focused on the well-known EDAN, ADAN, and LDAP components. ERPs elicited by shift-left and shift-right cues were collapsed to reveal waveform-contralateral and ipsilateral to the cued location. Then, for each participant, we measured the mean amplitudes of the contralateral and ipsilateral waveforms at lateral frontal (F5/F6) and occipital (PO7/PO8) scalp sites in four time intervals: 200–300 ms, 300–500 ms, 500–700 ms, and 700–900 ms. The mean amplitudes of the contralateral and ipsilateral waveforms were analyzed separately for each combination of scalp location and time interval using paired-samples t-tests.

The second step of the cue-ERP analysis focused on lateralized cue-ERP activities that were isolated with respect to the shift-up cue. Shift-up cue ERPs were subtracted from corresponding shift-left and shift-right cue ERPs to yield left-minus-up (L–U) and right-minus-up (R–U) difference waves. The R–U difference waves were then re-mapped by swapping waveforms measured at homologous sites over the left and right scalp hemispheres (e.g., F1 swapped with F2; difference waves recorded at midline sites were unchanged). This enabled us to combine the L–U and R–U difference waves while maintaining information about lateralized-ERP activity. Specifically, difference waves over the left scalp were recorded ipsilateral to the cued location, whereas difference waves over the right scalp were recorded contralateral to the cued location. Mean amplitudes of the combined L–U/R–U difference waves were then measured in 18 consecutive 50-ms time windows at six pairs of
lateralized electrodes spanning from the anterior scalp to the posterior scalp (see Fig. 5a). For each electrode and time interval, separate t-tests were performed to determine if the amplitude of the L−U/R−U difference wave was significantly different than 0 μV.

In the third step of the cue-ERP analysis, we isolated shift-left and shift-right activity using the neutral cue. Neutral-cue ERPs were subtracted from corresponding shift-left and shift-right cue ERPs to yield left-minus-neutral (L−N) and right-minus-neutral (R−N) difference waves. The R−N difference waves were re-mapped by swapping waveforms measured at homologous sites over the left and right scalp hemispheres, and then the L−N and re-mapped R−N difference waves were combined to yield difference waves recorded ipsilateral and contralateral to the cued location. Mean amplitudes of the combined L−N/R−N difference waves were then measured in 18 consecutive 50-ms time windows at the same six pairs of lateralized electrodes used to examine the isolated lateralized difference waves. For each electrode and time interval, separate t-tests were performed to determine if the amplitude of the L−N/R−N difference wave was significantly different than 0 μV.

In the fourth and final step of the cue-ERP analysis, we subtracted the neutral-cue ERPs from the shift-up ERPs and measured mean amplitudes of the resulting up-neutral (U−N) difference waves in 18 consecutive 50-ms time windows at the same six pairs of lateralized electrodes used to examine the L−U/R−U and L−N/R−N difference waves. For each electrode and time interval, separate t-tests were performed to determine if the amplitude of the U−N difference wave was significantly different than 0 μV.  

4.6.3. Topographical mapping and source estimation

We used a variant of the antisymmetric mapping method (Green et al., 2008; see also Praamstra et al., 1996) to characterize the scalp topographies of the conventional lateralized-ERP components. Grand-averaged contralateral-ipsilateral voltage differences measured at homologous left and right electrode sites (e.g., F5/6) were projected to one side of the scalp and copied to the other side of the scalp with their polarities inverted. Values at midline electrodes were set to 0 μV. Isopotential contour maps of the antisymmetric data were plotted for three time intervals corresponding to the EDAN (200–300 ms), ADAN (300–500 ms), and LDAP (500–700 ms). Next, we created isopotential contour maps of the L−U/R−U difference waves, L−N/R−N difference waves, and C-N difference waves in successive 50-ms time intervals. In all cases, voltages were interpolated using spherical splines (Perrin et al., 1989). Topographical maps of associated SCDs were also created.

We estimated the cortical generators of the isolated cue-ERP activities using the sLORETA distributed linear imaging method (Pascual-Marqui, 2002). The sLORETA algorithm estimates the activities of current dipoles distributed evenly throughout a volumetric head model based on the Montreal Neurologic Institute (MNI) average template brain. The method is similar to the minimum-norm technique (Hämäläinen and Ilmoniemi, 1993), except that sLORETA outputs standardized estimates of the minimum-norm current densities (see Dale et al., 2000, for an alternative method of standardization). The current-density standardization yields information about the statistical reliability of the estimated signal at each point, thereby making the output more analogous to statistical parametric mapping of fMRI. We output sLORETA images on an individual-participant basis for each successive 50-ms time interval using the L−U/R−U, L−N/R−N, and U−N difference waves. We then performed nonparametric statistical tests (as implemented in the sLORETA software) to determine statistical reliability of current-density estimates across participants. Significant activity (P<0.05) was then displayed on a standardized surface-rendered brain.

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Appendix A. Supplementary data


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