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Research Report

The orienting of visuospatial attention: An event-related brain potential study

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Abstract

This study investigated the electrophysiological correlates of shifting, maintaining, and relaxing the focus of attention, using a symbolic cuing task. Cues and imperative stimuli were presented in rapid succession, and the ADJAR procedure was used to remove the contribution of event-related potential (ERP) activity associated with the imperative stimulus from the cue-related ERP waveforms. Initial analyses, comparing left and right attention-directing cues, replicated previous findings of early directing attention negativity (EDAN) and anterior directing attention negativity (ADAN) effects. To isolate ERP activity that is common to leftward and rightward attention shifts, the combined ERP activity elicited by attention-directing cues was compared to the ERP activity elicited by non-informative cues. This analysis revealed a strong and broadly distributed early positivity followed by a sustained central negativity, possibly reflecting the controlled orienting and subsequent maintenance of attentional focus. Finally, imperative stimuli preceded by non-informative cues were characterized by an enhanced posterior P2 effect, with a scalp distribution indicative of generators in visual areas. This result suggests a relatively late (re)activation in visual areas associated with the processing of stimuli that had not been cued in advance.

Theme: Neural basis of cognition
Topic: Cognition

Keywords: Attention; Cuing; ERP; ADJAR; Spatial

1. Introduction

To focus on task-relevant information and ignore what is irrelevant, the human mind is equipped with a mechanism that is known as selective attention. Current neurophysiological models of attention [12,25,26] make a distinction between control and expression mechanisms. Attentional control mechanisms can selectively influence sensory processing and are presumably located in anterior and posterior association areas, more specifically the dorsolateral prefrontal cortex and superior parietal cortex [3,13], as well as the anterior cingulate areas [33,39], which act in concert with subcortical structures [1,2,24,25]. Expression mechanisms, on the other hand, have been associated with sensory brain areas, such as the extrastriate visual areas [32,44], and produce attentional modulation of sensory processing. Single cell recordings in animals [29,35], electrophysiological scalp recordings in humans [18], as well as human neuroimaging studies [19] have provided evidence for the hypothesis that the activation level in perceptual areas can be modulated by attentional control systems.

A common behavioral paradigm for studying shifts of visuospatial attention is the spatial cuing paradigm: on each

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trial, subjects are required to respond to an imperative stimulus. Each imperative stimulus is preceded by a cue indicating at which location the imperative stimulus is most likely to appear, and subjects are instructed to make use of this information by switching their attention to the location indicated by the cue [37,38,40]. Although spatial cuing paradigms have been used most widely in the behavioral literature, an increasing number of event-related potential (ERP) studies have used the paradigm to isolate the electrophysiological correlates of attention shifts from those associated with the imperative stimulus and subsequent response [10,15,31,36]. ERPs following symbolic cues directing attention to left and right lateral locations typically consist of an early posterior negativity, extending from about 200 to 400 ms after cue onset, over the hemisphere contralateral to the direction indicated by the cue. Harter and Anllo-Vento [14] labeled this negativity the "early directing attention negativity" (EDAN). The EDAN has been proposed to reflect the appreciation of the meaning of the symbolic cue and the resulting redirecting of attention, originating from parietal areas [14,18, but see 48]. Yamaguchi, Tsuchiya, and Kobayashi [54,55] have described a component similar to the EDAN that they labeled "attention-related negativity". This component was present, not only over posterior scalp sites, but also over anterior scalp sites at later time intervals (between 300 and 500 ms following the cue). Other studies [9,36], however, identified this as a separate component and labeled this component the "anterior directing attention negativity" (ADAN). The ADAN has been proposed to reflect the activation of frontal structures involved in controlling visuospatial attention. Finally, some studies have shown that the EDAN and ADAN are followed in time by a "late directing attention positivity" (LDAP; [9,14,30]), which is a broad positivity over the hemisphere contralateral to the direction indicated by the cue, superimposed upon a negative slow wave. It has been suggested that the LDAP reflects a biasing of activity in visual sensory areas, driven by a supra-modal attention-directing process [9,14].

The studies described above have shown that ERPs to cues can be helpful in teasing apart the processes involved in shifting visual attention to locations in space. However, most of these ERP studies differed in one or more aspects from behavioral spatial cuing studies. First, behavioral studies typically compare the costs and benefits of shifting attention by comparing performance associated with validly and invalidly cued imperative stimuli with performance in a baseline condition, in which the cue does not indicate the location of the imperative stimulus. In contrast, most ERP studies have investigated the electrophysiological correlates of shifting attention by comparing the ERP waveforms associated with left and right attention-directing cues. Although this comparison reveals the effects of directing attention to a specific direction, a limitation of this approach is that attention is always directed somewhere, making it impossible to fully isolate the ERP correlates of shifting attention as such. Thus, the time course and scalp distribution of such manifestations of visuospatial attention shifts have remained largely unexplored. Second, to avoid overlap of the waveforms elicited by cues and imperative stimuli, most ERP studies have used relatively long cue–stimulus intervals, typically on the order of about 600–1200 ms (e.g., [30]) or even longer [53]. The main problem with this approach is that long cue–stimulus intervals allow subjects to delay the shift of attention to the imperative stimulus, giving the experimenter less control over the timing of attentional orienting. Using shorter intervals presumably prevents subjects from adopting this "waiting strategy" and therefore heightens the time-locking of the attention-directing process to the onset of the cue.

The present ERP study sought to isolate brain activity associated with attention-directing processes while addressing the above two issues. This was done by including non-informative cues in the task design and by using short and variable time intervals between cues and imperative stimuli. On 80% of the trials, an attention-directing symbolic cue was presented that pointed to a predefined location in the left or right hemi-field. After a variable time interval between 200 and 800 ms, the imperative stimulus was presented at either the location indicated by the cue (*valid cue*; 60% of all trials) or the opposite location (*invalid cue*; 20% of all trials). On the remaining 20% of the trials, the imperative stimulus was preceded by a *non-informative* cue, which did not direct attention to either of these two locations. To deal with the problem of overlapping waveforms, we used the ADJAR correction technique to remove the overlapping ERP components elicited by imperative stimuli from the cue-related ERP waveforms [51]. ADJAR is a post-experimental correction technique to estimate and remove from the ERP waveform the overlap that results from adjacent trials in fast-rate sequences. ADJAR estimates this overlap by convolving the full averaged ERP waveforms (i.e., including the overlap) with the event distributions of the preceding and succeeding events. These overlap estimates are then subtracted from the distorted waveform. Because the procedure starts with averages that are distorted by overlap, the program iteratively uses the corrected ERP waveforms to make better overlap estimates until the solutions from multiple iterations converge.

The analysis of the cue-related ERPs consisted of three stages: first, we compared the ERPs elicited by left and right attention-directing cues in an attempt to replicate previously reported early ERP effects associated with shifting attention in specific directions. Second, we examined the effects of shifting attention per se by collapsing ERPs elicited by attention-directing cues and comparing these to ERPs elicited by the non-informative cues. To our knowledge, only a limited number of previous ERP studies have investigated the differences between attention-directing and non-informative cues [14,28,30,53]. In the third stage of the analyses, we examined attention-directing ERP effects separately for short (200–400 ms), intermediate (400–600 ms), and long (600–

800 ms) intervals between cues and stimuli. This allowed us to study putative late attention-directing effects for long intervals separately. The inclusion of shorter intervals, for which these later processes might have terminated upon presentation of the imperative stimulus, might have resulted in a substantial weakening of these late effects. Note that the longest cue–stimulus intervals used in the present study correspond with the shortest cue–stimulus intervals used in previous studies (e.g., [30]). In addition, this approach also allowed us to address the question whether or not the focusing of attention would relax after the termination of the imperative stimulus. Because the focusing of attention is presumably an effortful process, it might be expected that the brain relaxes this focus immediately after the imperative stimulus is processed. If this were the case, we would predict that late slow-wave ERP activity associated with attention-directing processes would terminate and return to baseline levels earlier in time for short cue–stimulus intervals than for long cue–stimulus intervals. Finally, to confirm the effectiveness of our attentional manipulation, we contrasted the ERPs elicited by imperative stimuli preceded by valid, non-informative, and invalid cues.

2. Methods

2.1. Participants

Fourteen volunteers (age 18–35, mean 24, 7 males) participated in the present study. All participants had normal or corrected-to-normal vision. None of them reported a history of mental or sustained physical illness. All participants gave informed consent and received credits as part of an introductory psychology course requirement.

2.2. Stimulus presentation and design

Fig. 1 illustrates the basic layout of the present design. Each trial started with a centrally presented symbolic cue, which was presented for 150 ms, and then replaced by a fixation cross. In 60% of the trials, the cue correctly indicated the location of the forthcoming imperative stimulus (valid cue). In 20% of the trials, the opposite location was cued (invalid cue), and in the remaining 20% of the trials, a non-informative cue was presented. Hence, of the attention-directing cues, 75% pointed to the correct location, and participants were made aware of this fact. The attention-directing cues were left- and right-pointing arrows, subtending a horizontal angle of about 3.5°. The non-informative cue was a horizontally oriented bar with a similar size and shape to the arrows but lacking the arrow head.

The imperative stimulus followed the cue after a random interval of 200–800 ms and could be a target (i.e., requiring a response; 25%) or non-target (75%). The identities of the target and non-targets (the letters E and F, subtending an angle of about 3.5°) were balanced across participants. Participants were instructed to respond to each target letter by making a speeded response with their left or right index finger. The use of the left and the right hand was balanced across participants. The imperative stimulus was presented for 100 ms at an angle of about 7.5° to the left or right side of the fixation cross. To increase the demands placed on the attentional system, the stimuli appeared randomly in either an intact or in a degraded version. Degraded stimuli were included to motivate participants to focus their attention as strongly as possible. In the intact version, the letters were presented in a clear print, whereas in the degraded form, black and white pixels were randomly interchanged, making the appearance noisy. Each experimental block was composed of 24 different trial types, based on the factorial combination of cue type (valid, invalid, or neutral), stimulus location (left or right), stimulus quality (intact or degraded), and stimulus type (target or non-target). A total of 2800 trials were presented throughout the experiment. Each trial was randomly assigned to 1 of 20 task blocks, each containing 140 trials.

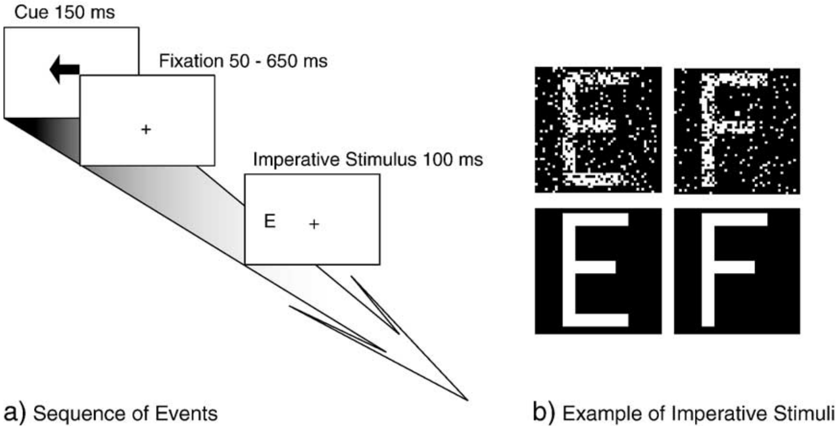

Fig. 1. Outline of the paradigm. (a) Schematic representation of the sequence of stimuli presented on each trial. (b) Examples of the intact and degraded imperative stimuli.

2.3. Procedure

For each participant, a new randomized stimulus order was generated. Participants were told to keep their eyes focused on the central fixation cross and to avoid blinking as much as possible. They were further instructed to move their attention to the location indicated by attention-directing cues, and they were informed that this was the most likely location of the subsequent imperative stimulus. Participants were also instructed to maintain their attention at fixation following the presentation of a non-informative cue. Finally, they were required to respond to each target stimulus, irrespective of whether the cue was valid or invalid.

After attachment of the electrodes, participants completed a block of practice trials to make sure they understood the instruction and to familiarize them with the stimuli and procedure. After completion of the practice block, the experimental phase started. Participants were allowed to take breaks between task blocks.

2.4. Instrumentation and recording

Stimuli were presented on a 21-in. computer monitor, located at a distance of 60 cm from the participant. Stimulus presentation was controlled by a personal computer, which ran an in-house developed MS-DOS-based application to ensure exact timing. Electroencephalographic (EEG) signals were recorded from 30 electrodes mounted in an electrocap: FPz, AFz, Fz, Cz, Pz, Oz, FP1, FP2, F7, F3, F4, F8, FC5, FC6, T7, C3, C4, T8, CP5, CP1, CP2, CP6, P7, P3, P4, P8, PO3, PO4, O1, and O2. These electrodes were referenced against the right ear lobe. Horizontal and vertical eye movements were measured using bipolar recordings from electrodes placed on the outer canthi of the two eyes and from electrodes placed approximately 1 cm above and below the participant's right eye. Electrode impedance was kept below 5 kΩ. All signals were amplified by a Nihon-Kohden Neurotop system, low-pass filtered at 35 Hz, digitized with a sample frequency of 250 Hz, and digitally stored for off-line analysis.

2.5. Data analysis

2.5.1. Behavioral data

Average correct response times, hit rates, and false alarms (i.e., responses to non-targets) were calculated for each participant, separately for each condition and separately for the short (200–400 ms), intermediate (400–600 ms), and long (600–800 ms) cue–stimulus intervals. These measures were submitted to repeated-measurement analyses of variance (ANOVAs) with within-subject factors Cue–stimulus Interval (short, intermediate, or long), Cue Type (valid, invalid, or non-informative), Stimulus Location (left or right from fixation), and Stimulus Quality (intact or degraded). Greenhouse–Geisser correction was applied to all tests involving the factors Cue Type and Cue–stimulus Interval.

2.5.2. ERP analyses

During off-line analysis, cue-locked and stimulus-locked epochs of 2048 ms, including a pre-stimulus baseline of 1024 ms, were selected for averaging. Trials that contained amplifier saturations, spike artifacts (50 μV/4 ms), or slow drifts (20 μV/s) were excluded from the analysis. In addition, ocular artifacts were corrected using a frequency-domain multiple regression method [45]. Cue-locked and stimulus-locked ERPs were then computed, separately for each condition of interest. All ERPs included both target and non-target trials. This was justified for the stimulus-locked ERPs because we were primarily interested in early attention effects over visual areas (i.e., N1/P1), which usually do not differ between target and non-target stimuli [7,16,27].

Overlap correction was performed using the ADJAR level-2 method [51]. Cue-locked ERPs were used to estimate and remove the overlap of cue-related ERP activity with the stimulus-related ERPs and vice versa. In each case, the cue ERPs and stimulus ERPs were based on the same trials. ADJAR is an iterative process that converges to better and better overlap estimates with increasing numbers of iterations. It was found that the overlap estimates converged and did not change appreciably after eight iterations (that is, changes between successive iterations were smaller than the noise levels of the single-subject data). For this reason, all ADJAR analyses were conducted using eight iterations.

Most ERP effects were statistically tested by computing mean amplitudes in consecutive time windows of 20 ms and submitting these to repeated-measurement ANOVAs. The amplitudes of the stimulus-elicited P1, N1, and P2 were defined as the peak amplitude in a specific time window (P1: 120–200 ms; N1: 180–240 ms; P2: 240–260 ms).

3. Results

3.1. Behavioral results

3.1.1. Response times

Fig. 2 shows average response times as a function of cue–stimulus interval and stimulus quality and separately for intact and degraded imperative stimuli. Response times were slower to degraded target letters than to intact target letters, which was expressed in a main effect of Stimulus Quality ($F(1,13) = 35.4$, $P < 0.0001$). The attention-directing effectiveness of the cue was expressed in a significant main effect of Cue Type ($F(2,26) = 13.1$, $P < 0.001$), indicating that responses to validly cued target letters were significantly faster than responses following non-informative or invalid cues. Although Fig. 2 suggests that the cuing effect was relatively small for short cue–stimulus intervals and

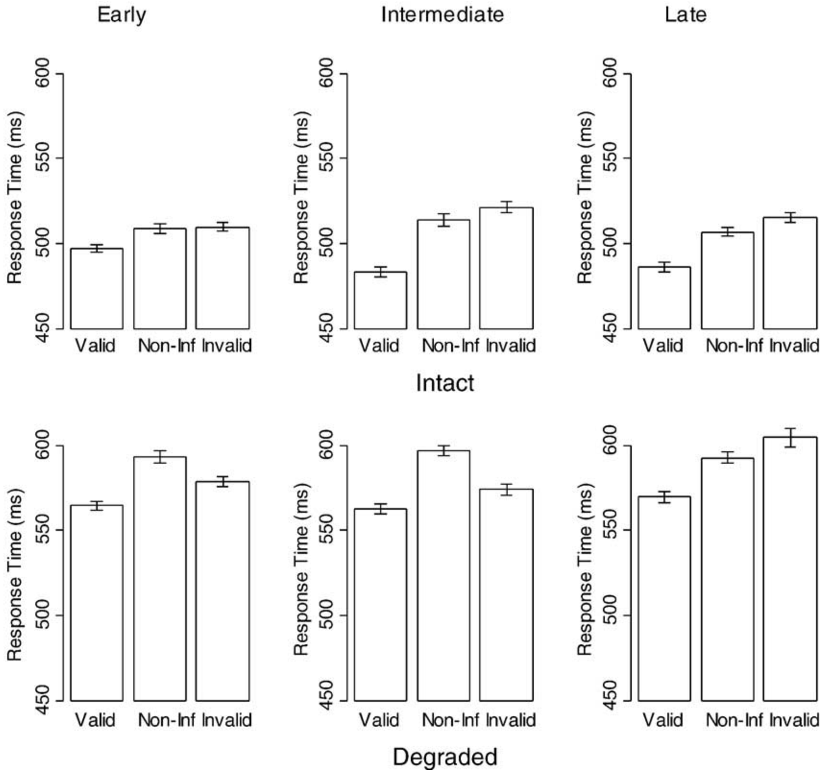

Fig. 2. Average response times as a function of cue type (valid, non-informative, invalid), stimulus quality (intact or degraded), and cue–imperative stimulus interval (short: 200–400 ms; intermediate: 400–600 ms; or long: 600–800 ms).

gradually developed as the cue–stimulus interval increased, the interaction between Cue Type and Cue–stimulus Interval failed to reach significance ($F(4,52) = 1.9$, $P > 0.1$). Similarly, although Fig. 2 suggested that the effects of attentional cuing developed differently for intact than for degraded stimuli, the three-way interaction between Cue Type, Cue–stimulus Interval, and Target Type did not reach significance ($F(4,52) = 1.1$, $P = 0.33$).

3.1.2. Accuracy measures

Hit rate percentages were significantly lower for degraded targets than for intact targets (80.0% vs. 99.2%; $F(1,13) = 16.3$, $P < 0.01$). Similarly, a significantly higher percentage of false alarms were made to degraded than to intact targets (4.4% vs. 0.3%, $F(1,13) = 16.8$, $P < 0.001$). None of the statistical terms involving the factor Cue Type were significant, suggesting that the effects of this factor were mainly expressed in the speed of responding.

3.2. Electrophysiological data

3.2.1. Attention-directing cues: left vs. right

Differences between left and right attention-directing cues consisted of an enlargement of the P1 and N1 components over occipito-temporal brain areas contralateral to the direction indicated by the cue (see Fig. 3a). These effects were presumably caused by physical differences between left-pointing and right-pointing arrows [30][1]. More importantly, attention-directing cues were associated with a sustained negativity contralateral to the cue direction, extending from about 250–400 ms after cue onset and most pronounced at electrodes near the junction of occipital, temporal, and parietal cortex (see Fig. 3b). The time course of this EDAN effect was statistically tested by evaluating the signals at electrodes T5 and T6 between 200 and 900 ms after cue onset. ANOVAs revealed significant interactions between Hemisphere (left or right) and Cue Direction (left or right) between 260 and 380 ms after cue onset (all F values$(1,13) > 15.0$, P values < 0.01).

Between about 300 and 500 ms after cue onset, a negative difference (ADAN) between left and right attention-directing cue ERPs was visible at lateral anterior electrodes. This effect was tested statistically by computing mean amplitudes in consecutive 20-ms time windows at electrodes F3 and F4 and submitting these to ANOVAs with within-subject factors Hemisphere and Cue Direction. The ADAN was reflected in a significant interaction between these two factors between 340 and 400 ms after cue onset (F values$(1,13) > 5.2$, P values < 0.05), suggesting that an

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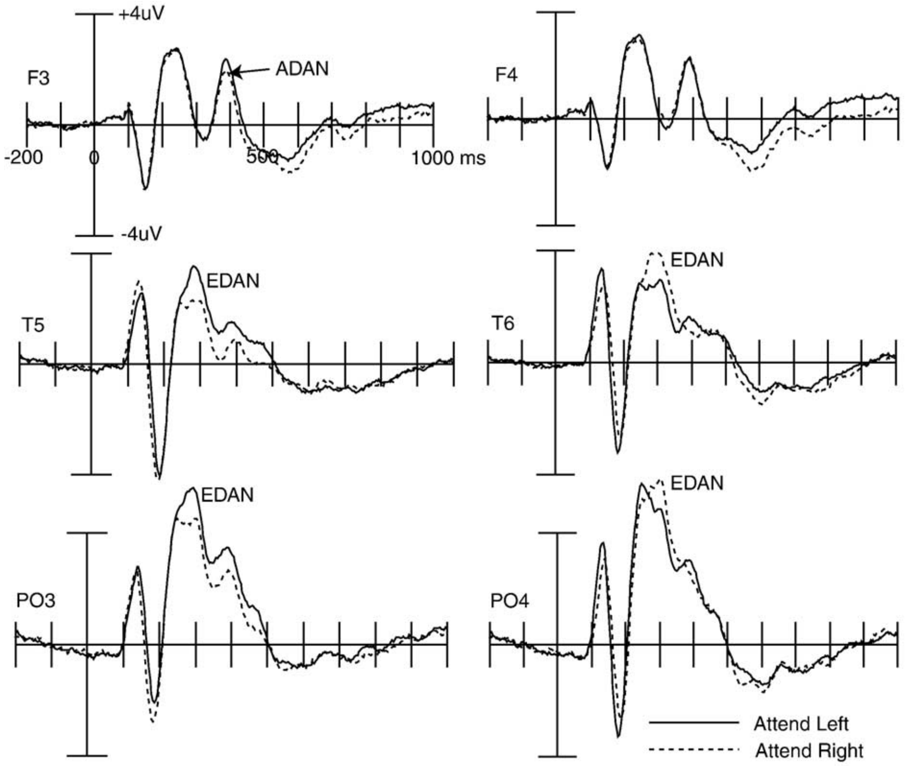
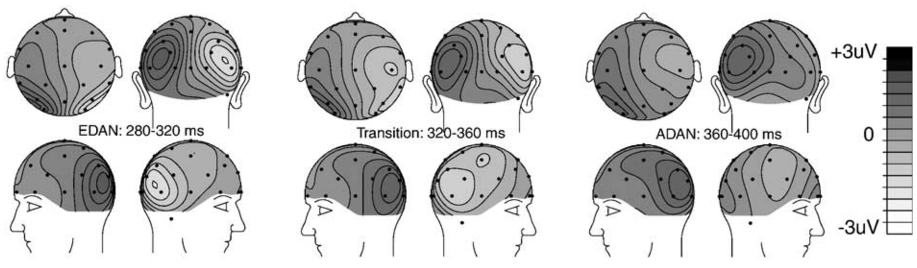
[1] Because early differences between the ERP waveforms associated with left and right attention-directing cues and non-informative cues may reflect physical differences between the cues, we limit the discussion of the results to latencies >200 ms following the cue (cf. [30]).



a) Left vs. Right Attention-Directing Cues



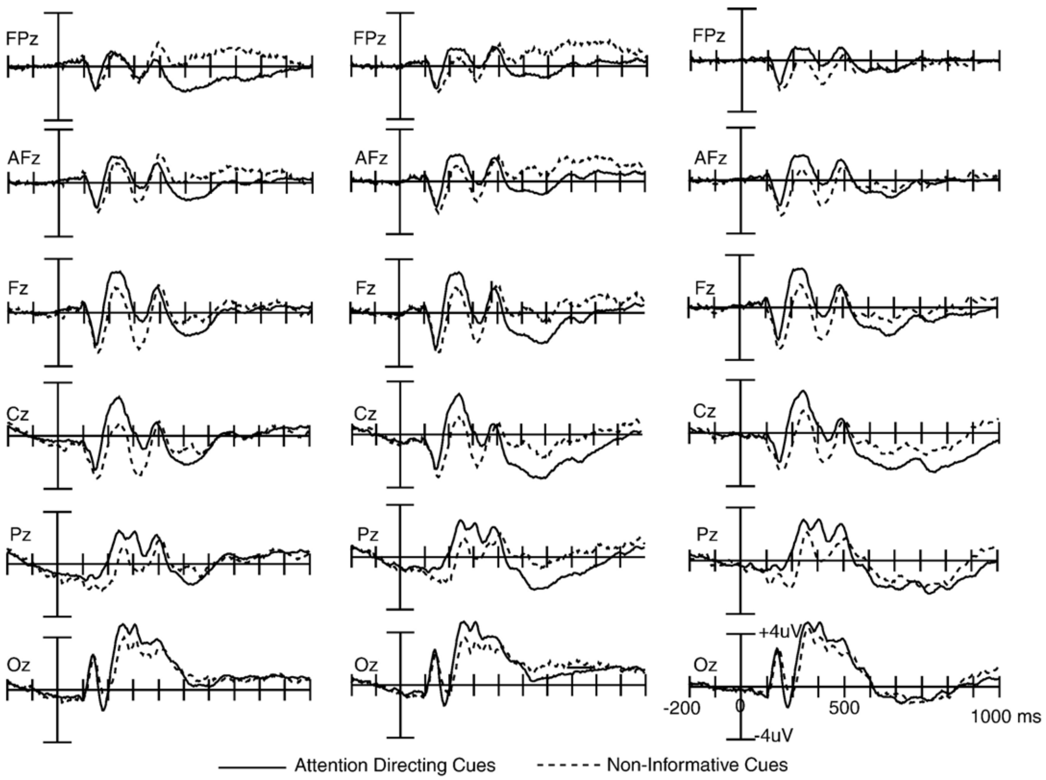
b) Scalp Topographies of the EDAN and ADAN Effects

Fig. 3. (a) ERP waveforms elicited at lateral frontal (F3, F4), and left and right temporal (T5, T6) and posterior (PO3, PO4) electrodes by cues directing attention to the left or right side. Time = 0 ms indicates the cue onset. (b) Scalp topography of the attention-directing effects. Shown here are the early directing attention negativity (EDAN; 280–320 ms following the cue), a transitional period during which the anterior directing attention negativity (ADAN) emerges (320–360 ms), and finally the time window in which both effects are present. These topographies were obtained by subtracting left from right attention-directing cue ERPs.

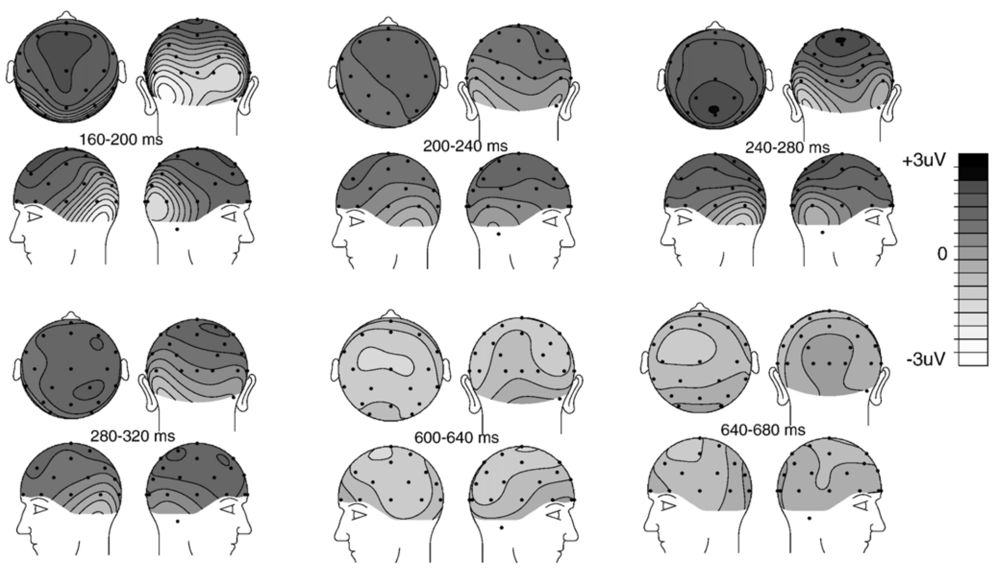
additional anterior effect followed the EDAN by about 40 ms (see Fig. 3b). No LDAP effects were found in the present dataset, which is probably due to the use of short cue–stimulus intervals.

3.2.2. *Attention-directing vs. non-informative cues*

The difference in ERP activity between attention-directing and non-informative cues was analyzed by collapsing the ERPs to left and right attention-directing cues and contrasting the resulting waveform with the ERP waveform associated with non-informative cues. Figs. 4a–c reveal an effect of directing attention between about 160 and 400 ms following the onset of the imperative stimulus: The ERP waveform associated with attention-directing cues was positively enhanced compared to the waveform associated with non-informative cues. During this time interval, the distribution of the effect shifted from fronto-central to more posterior electrodes. After about 450 ms, the two waveforms inverted in polarity and at around the same latency, the attention-directing effect also reversed. The attention-directing effect was statistically tested by conducting ANOVAs with within-subject factors Cue Type (attention-directing vs. non-informative) and Electrode (AFz, Fz, Cz, F3, F4, C3, and C4). This analysis revealed significant effects of Cue Type between 100 and 380 ms after stimulus onset (*F* values(1,13) > 5.9, *P* values < 0.05),



a) Short Cue-Stimulus Interval b) Intermediate Cue-Stimulus Interval c) Long Cue-Stimulus Interval



d) Scalp Topographies Based on the Long Cue-stimulus Interval in 40 ms Bins

Fig. 4. ERP waveforms elicited at midline electrodes by attention-directing cues and non-informative cues. (a) ERPs based on trials with short cue–stimulus intervals (SOA 200–400 ms). (b) ERPs based on trials with intermediate cue–stimulus intervals (SOA 400–600 ms). (c) ERPs based on trials with long cue–stimulus intervals (SOA 600–800 ms). (d) Scalp topographies of the difference waveform (attention-directing minus non-informative; based on long cue–stimulus intervals) in 40 ms bins at latencies 160–320 ms, for the early positive enhancement, and 600–680 ms, corresponding with but slightly extending the late negativity.

indicating that attention-directing cues elicited significantly more positive fronto-central ERP activity than non-informative cues. The reversed effect did not become significant (F values$(1,13) < 2.5$, P values > 0.1).

In order to more clearly evaluate attention-directing processes late in the cue–stimulus interval, we conducted a similar analysis, now focusing specifically on trials with a long cue–stimulus interval (600–800 ms). As can be seen in Figs. 4a–c, the waveforms for the three subsets of the trials were similar. Perhaps, the clearest difference concerned the increased negativity for attention-directing trials at longer latencies (> 500 ms), which was more pronounced and extended longer with increasing cue–stimulus interval durations. ANOVAs indicated that the attention-directing waveform was significantly more positive than the non-informative waveform between 80 and 360 ms following cue onset (F values(1,13) > 4.7, P values < 0.05) and significantly more negative between 600 and 660 ms (F values(1,13) > 5.1, P values < 0.05). As Fig. 4c illustrates, the early positive enhancement shifted from a fronto-central to a more posterior distribution. The subsequent negativity was characterized by a more centrally distributed scalp distribution.

To evaluate whether the duration of attention-directing processes would vary with the length of the cue–stimulus interval, we investigated the interaction between Cue Type (attention-directing vs. non-informative) and Cue–stimulus Interval (short, intermediate, or long). Fig. 5 illustrates the attention-directing effect by plotting difference waves, obtained by subtracting ERPs elicited by non-informative cues from ERPs elicited by attention-directing cues, separately for short (200–400 ms), intermediate (400–600 ms), and long (600–800 ms) cue–stimulus intervals. Starting around 400 ms after cue onset, the difference waveforms showed a negative-going trend that was initially similar for the short, intermediate, and long cue–stimulus intervals. Around 500 ms after cue onset, the attention-directing difference wave for the short cue–stimulus interval returned to baseline, whereas the waveforms associated with the intermediate and long cue–stimulus intervals remained negatively displaced. Although this pattern is consistent with the notion that attention relaxation is dependent on the moment of stimulus presentation, the interaction between Cue Type and Cue–stimulus Interval (at electrodes F3, F4, C3, and C4) failed to reach significance (F values(1,13) < 1.2, P values > 0.1).

3.2.3. ERPs elicited by imperative stimuli

In a final set of analyses, we computed the ERPs elicited by imperative stimuli. This was done separately for stimuli preceded by valid, invalid, and non-informative cues, but collapsing across target and non-target stimuli, and degraded and intact stimuli. The ADJAR procedure was used to remove the overlapping cue-related activity from the stimulus-locked ERP waveforms. The resulting waveforms, shown in Fig. 6a, can be summarized as follows. First, the amplitudes of both the P1 and N1 components increased with the validity of the cue (P1: $F(2,26) = 13.9$, $P < 0.01$, N1: $F(2,26) = 8.2$, $P < 0.005$). This ERP signature indicates that participants shifted their attention in response to the attention-directing cues [17,50], corroborating the cuing effect in the behavioral results and supporting an important assumption of our research. Second, post-hoc comparisons indicated that the P1 amplitude for invalidly cued imperative stimuli differed significantly from that for validly cued stimuli (F(1,13 $= 7.0$, $P < 0.05$) and that for non-

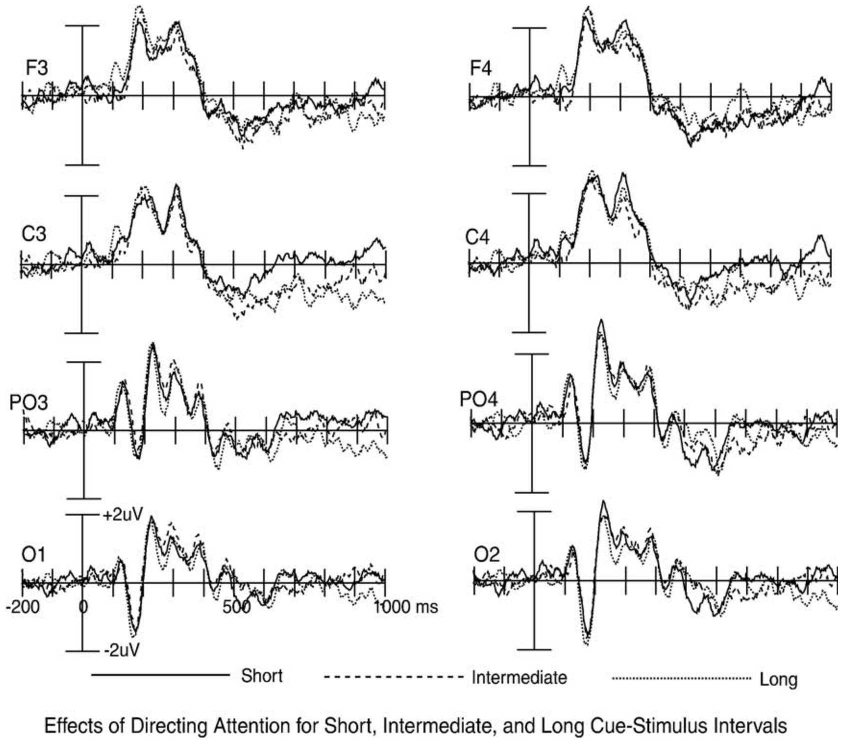
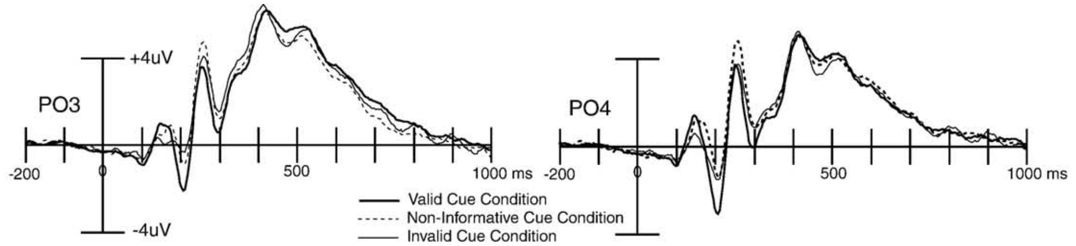
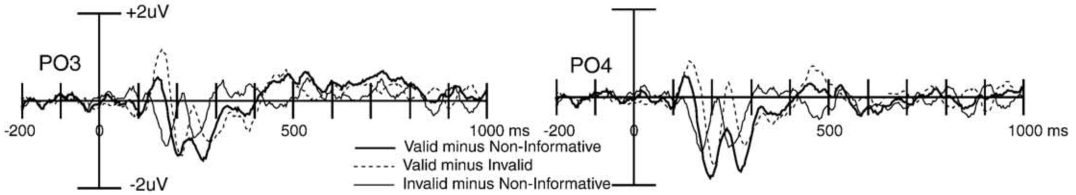


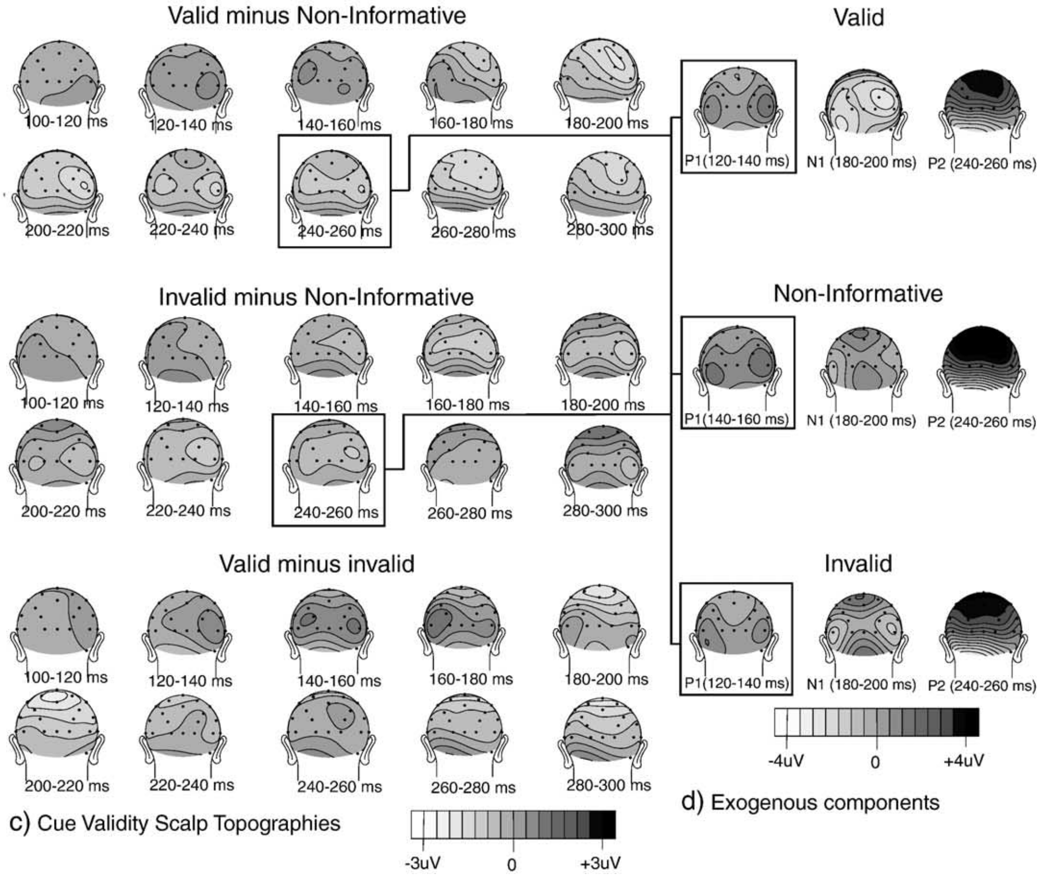
Fig. 5. ERP difference waveforms (attention-directing cues minus non-informative cues) computed for left and right frontal, central, and posterior electrodes and plotted separately for short, intermediate, and long cue–stimulus intervals. See text for further details.



a) Imperative Stimulus ERPs



b) Difference waves



c) Cue Validity Scalp Topographies

d) Exogenous components

Fig. 6. (a) ERP waveforms elicited by imperative stimuli that were preceded by valid, non-informative, and invalid cues. (b) Difference waves. (c) Scalp topographies of the cuing effects. The topographies of the P2 effect (240–260 ms; see text) are boxed. Because the large-amplitude P2s elicited on non-informative cue trials were subtracted from the smaller P2s elicited on valid and invalid cue trials, the scalp topography of the P2 is depicted as a negativity here. (d) Scalp topographies of the exogenous P1, N1, and P2 components elicited by the imperative stimuli. Note that the scalp topography of the P2 effect bears a strong resemblance to that of the exogenous P1 components.

informatively cued stimuli ($F(1,13) = 6.2$, $P < 0.05$). The P1 amplitudes for validly and non-informatively cued stimuli did not differ from each other ($F(1,13) < 1$). For the N1, a qualitatively different pattern of results was found. The N1 for validly cued stimuli was larger than the N1s for non-informatively cued stimuli ($F(1,13) = 12.6$, $P < 0.005$) and invalidly cued stimuli ($F(1,13) = 7.7$, $P < 0.02$), which did not reliably differ from each other ($F(1,13) = 2.7$, $P > 0.1$).

Finally, non-informatively cued stimuli were characterized by a large P2 effect, peaking between 240 and 260 ms and largest over temporo–parieto–occipital scalp regions (see Figs. 6b and c). An ANOVA of P2 amplitude with within-subject factors Electrode (PO3 vs. PO4) and Cue Type (valid, non-informative, or invalid) indicated a significant effect of Cue Type ($F(2,26) = 6.3$, $P < 0.02$). This P2 effect was somewhat more pronounced over the right hemisphere (i.e., PO4), as reflected by a marginally significant interaction between Electrode and Cue Type ($F(2,26) = 3.1$, $P = 0.07$). Post hoc comparisons indicated that the P2 for non-informatively cued stimuli was larger than the P2 for validly cued stimuli ($F(1,13) = 8.8$, $P < 0.02$) and the P2 for invalidly cued stimuli ($F(1,13) = 12.9$, $P < 0.005$) and that the latter two conditions did not reliably differ ($F(1,13) < 1$). Thus, the largest P2 effect was associated with the condition in which attention could not be directed in advance of the stimuli. Interestingly, the scalp topography of this P2 effect was similar to that of the exogenous P1 components observed in the (non-difference wave) ERP waveforms elicited by the imperative stimuli (see Figs. 6c and d).

4. Discussion

In the present study, we used a spatial cuing paradigm to investigate the electrophysiological correlates of shifting, maintaining, and relaxing visuospatial attention. Compared to previous ERP studies, we used relatively short intervals between cues and imperative stimuli to discourage participants from delaying the shift of attention toward the location of the upcoming imperative stimulus. In an initial analysis, comparing ERPs associated with left and right attention-directing cues, we replicated previous findings of an EDAN, an early negativity over posterior scalp regions contralateral to the location indicated by the cue [14,36], as well as a small ADAN effect, which was found mainly over right frontal areas. Although the ADAN started somewhat later than the EDAN, these two effects partially overlapped in time with the more posteriorly distributed EDAN preceding the ADAN. This result is similar to what has previously been described in the literature [5,18]. However, the inclusion of non-informative cues in the task design allowed us to obtain a better estimate of the full temporal pattern of attentional orienting by comparing the average brain activity elicited by left and right attention-directing cues with brain activity elicited by non-informative cues. Furthermore, the ERPs associated with attention-directing and non-informative cues were compared for three different cue–stimulus interval ranges: short (200–400 ms), intermediate (400–600 ms), and long (600–800 ms).

The main results from these analyses can be summarized as follows. First, the ERPs elicited by attention-directing cues were characterized by a broad fronto-central positivity lasting from around 160 to 400 ms after cue onset. This early positive enhancement of the ERP was observed for all three cue–stimulus intervals. Second, around 450–500 ms following the cue, the early positivity was followed by a centrally distributed sustained negativity that was most pronounced for long and, to a somewhat lesser degree, for intermediate cue–stimulus intervals but absent for short cue–stimulus intervals. As will be discussed below, the early positivity and subsequent sustained negativity may correspond with two distinct aspects of attentional orienting: shifting attention to a new location and maintaining attention focused on the location indicated by the cue. Finally, we observed an enhancement of the P2 component elicited by imperative stimuli that were preceded by non-informative cues. These three principal findings will now be discussed in turn.

4.1. Early positive enhancement

Brain activity specifically linked to directing attention to spatial position was identified starting at about 160 ms following the cue. This initial ERP effect consisted of a positivity that was broadly distributed over fronto-central and parietal recording sites (see Fig. 4). The broad scalp distribution of this effect is consistent with the involvement of a distributed network of brain areas in the control and orienting of attention. In line with this, recent studies using the high spatial resolution of fMRI have implicated a network of frontal and parietal regions in the top–down control of spatial attention [4,19,22]. The present results suggest that, when subjects must orient attention as rapidly as possible, (parts of) this network might be engaged within 200 ms after presentation of the cue. The use of arrow symbols as cues might have further facilitated a rapid orientation of attention because this type of symbol is well learned [41,46]. Previous studies comparing ERPs elicited by attention-directing cues and non-informative cues have observed a similar early positive enhancement associated with the shifting of attention. However, in these studies, the enhancement had a more posterior scalp distribution [30,53] or occurred somewhat later in time [53]. Since both of these studies used longer cue–stimulus intervals, it is possible that subjects in these studies were slower at shifting their attention than was necessary in the current study, which may have reduced the demands on anterior areas involved in initiating attention shifts [34]. Future ERP studies may help clarify these apparent discrepancies.

The scalp distribution of the early positivity was clearly more complex than the scalp distribution of the EDAN and ADAN. This illustrates our argument that non-informative cues can be helpful as a control condition for isolating brain activity related to shifting attention and that, by comparing conditions in which attention is directed to the left and right, attention-directing processes that are not lateralized with respect to the cued location are cancelled out. Nonetheless, as discussed extensively in [21], caution is warranted when interpreting comparisons including a non-informative cue condition. For example, it is hard to determine the strategy that participants employ when presented with a non-informative cue. It is generally assumed that participants adopt a passive strategy and follow the instruction to refrain from shifting attention. Yet, although the behavioral data are consistent with this assumption (as discussed below), we cannot rule out the alternative possibility that (some) participants engaged in a more active strategy of dividing their attention between the two peripheral imperative stimulus locations. To the extent that participants used this 'active' strategy, this will have weakened our contrast between brain activity following attention-directing cues and brain activity following non-informative cues. Another aspect of our non-informative cues is that they occurred less frequently (20%) compared to left-pointing (40%) and right-pointing (40%) attention-directing cues. It is unclear whether the relative novelty of the non-informative cues may have affected their processing. In any case, the ERPs associated with non-informative cues did not show an enhanced amplitude of the frontal P3 component, which is typically observed for stimuli that are experienced as novel or highly deviant (reviewed in [11]).

4.2. Late sustained negativity

The early positivity resolved as negative-going potentials between 450 and 500 ms post-cue that were initially maximal over fronto-central and later over central electrode sites (see Fig. 4b). Interestingly, the scalp topography of this late fronto-central negativity strongly resembles that of the 'contingent negative variation' (CNV; [49]). This slow wave negativity is considered to be a reflection of anticipating a forthcoming imperative stimulus (early CNV) and of motor preparation (late CNV; see [47] for a review). More recent studies have also reported negative slow wave activity related to various cognitive processes involving either preparation or maintenance of information in working memory [23,42]. Although CNV activity is typically observed with longer and fixed intervals, similarities between CNV activity and slow attention-directing potentials have been noted before in the literature [6,53]. Mangun [30] as well as two preliminary ERP studies [43,52] have shown similar differences in late sustained fronto-central negativity between attention-directing and reference cues. The fronto-central negativity observed in these studies and the present study may thus reflect processes specific to the attentional orienting conditions, involved in preparing the system for appropriate task performance, such as maintaining the attentional focus at the specified location. Finally, we did not find solid evidence for the hypothesis that attention-directing brain activity would return to baseline levels immediately after the presentation of the imperative stimulus. It is possible that attention relaxation occurs but is not as tightly locked to stimulus presentation as we expected. The variability in the latency of this process might be too large relative to the differences between the short, intermediate, and long cue–stimulus intervals, resulting in insufficient power to detect the expected effect.

4.3. Stimulus-related ERP components

Analysis of the ERP waveforms elicited by imperative stimuli revealed an enhancement of the posterior P1 and N1 associated with validly cued imperative stimuli, consistent with the assumption that participants shifted their attention successfully in response to the cues [17,50]. Furthermore, a more detailed analysis of the P1 and N1 confirmed earlier observations that the P1 appears to be mainly sensitive to the costs associated with invalid cues, whereas the N1 appears to be mainly sensitive to the benefits associated with valid cues [28,30].

Following the N1, the stimulus-related ERPs showed a posterior P2 component that was larger for non-informative cue trials than for valid and invalid cue trials. It is unlikely that this P2 effect reflects the modulatory influence of selective attention: in contrast to the N1 and P1 [17], the P2 was of similar amplitude for valid and invalid cue trials, suggesting instead that the P2 effect reflects a difference in processing of stimuli preceded by attention-directing cues and stimuli preceded by non-informative cues. A possible functional explanation of the larger P2 for non-informative cue trials is that it reflects a relatively late rise in activation in visual areas associated with the processing of the imperative stimulus. This explanation appears consistent with the response times on non-informative cue trials, which were slow and insensitive to cue–stimulus interval, leading non-informative trials to be even slower than invalid cue trials in some conditions. This pattern of response times suggests that non-informative cues had a reduced general alerting effect [21] or led participants to engage a passive strategy. As a consequence, on non-informative cue trials, visual areas may have been less primed during the cue–stimulus interval, leading to a delayed attentional modulation in visual areas once the stimulus was presented. The possibility that the large P2 effect on non-informative cue trials reflects this late modulation of activity in visual areas is consistent with earlier reports that the amplitude of the posterior P2 is sensitive to attention [8,20]. Finally, the similarities in scalp topography between the P2 effect elicited by non-informatively cued imperative stimuli and the exogenous P1 components further support the conclusion that the P2 effect is largely generated in visual brain areas and thus reflects a relatively late (re)activation of visual brain areas in this condition.

4.4. Summary and conclusions

The present findings indicate that a rich succession of neural processes supports attentional orienting to a position in space. First, following the decoding of cue information, a process occurs by which the focus of attention is directed, as signaled by a broad positivity over fronto-central and parietal scalp regions. This may reflect initial commands that subsequently prepare specific cortical regions for upcoming task-relevant information. This subsequent preparatory state is reflected by a sustained negativity, which can be observed from around 500 ms onwards over fronto-central recording sites. Regions involved in this preparatory state may include both visual areas involved in processing information at the cued location and frontal and parietal brain areas involved in the maintenance of the attentional set. Finally, imperative stimuli preceded by non-informative cues elicited larger posterior P2 components than imperative stimuli preceded by attention-directing cues. This suggests that the reduced general alerting effect of non-informative cues resulted in a delay of top–down attentional modulation in visual areas associated with imperative stimulus processing.

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