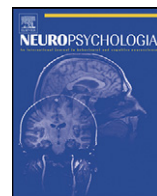




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Neural mechanisms of attentional shifts due to irrelevant spatial and numerical cues[☆]

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ABSTRACT

Studies of endogenous (cue-directed) attention have traditionally assumed that such shifts must be volitional. However, recent behavioural experiments have shown that participants make automatic endogenous shifts of attention when presented with symbolic cues that are systematically associated with particular spatial directions, such as arrows and numerals, even when such cues were not behaviourally relevant. Here we used event-related potentials (ERPs) to test whether these automatic shifts of attention use the same mechanisms as volitional shifts of attention. We presented participants with non-predictive (50% valid) task-irrelevant arrow and numeral cues while measuring cue- and target-locked ERPs. Although the cues were task-irrelevant, they elicited attention-related ERP components previously found in studies that used informative and/or task-relevant cues. These findings further substantiate the dissociation between endogenous and volitional attentional control, and suggest that the same fronto-parietal networks involved in volitional shifts of attention are also involved in reflexive endogenous shifts of attention.

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1. Introduction

The ability to selectively attend to spatial locations allows the brain to process the vast amount of information that it receives. Numerous studies have demonstrated the existence of two attentional systems in which attention can be controlled either *exogenously* (reflexively), by external stimuli in the environment, or *endogenously* (volitionally), by changes in an individual's goals and intentions (Posner, 1980; Posner & Dehaene, 1994). Studies of voluntary attention have traditionally used the spatial cueing paradigm, in which participants respond as quickly as possible to a peripheral target that is expected to appear in the direction indicated by a central symbolic orienting cue, such as an arrow (Posner, 1980). Targets appearing at the cued locations (valid condition) are generally detected faster than targets appearing away from the cued location (invalid condition). However, these studies traditionally

use more valid than invalid cues and instruct participants to direct their attention to the side indicated by the cue, on the assumption that symbolic cues can only give rise to volitional shifts of attention.

Recently, Hommel, Pratt, Colzato, and Godijn (2001) questioned this association between *endogenous* and *voluntary* attention using a cueing paradigm with non-predictive (50% valid) symbolic cues that have a consistent association with one side of space, such as arrows (leftward or rightward) and direction words ("left" or "right"). They found that these non-predictive cues automatically orient attention in the direction indicated. Subsequent studies have suggested that cuing effects traditionally measured with informative arrows involve a super-additive combination of automatic shifts due to the arrows and controlled shifts due to volitional orientation of attention (Ristic & Kingstone, 2006; Tipples, 2002).

Arabic numerals can also elicit automatic shifts of attention, further demonstrating that symbolic cues can cause reflexive shifts of visuospatial attention, and highlighting the dissociation between endogenous and voluntary attentional mechanisms (Casarotti, Michielin, Zorzi, & Umiltà, 2007; Fischer, Castel, Dodd, & Pratt, 2003; Galfano, Rusconi, & Umiltà, 2006; Ristic, Wright, & Kingstone, 2006). Western participants seem to represent numbers on a left to right oriented *mental number line* (for reviews, see Fias & Fischer, 2005; Hubbard, Piazza, Pinel, & Dehaene, 2005). For example, in the SNARC effect (Spatial Numerical Association of Response Codes

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effect; Dehaene, Bossini, & Giraux, 1993), reaction times in a parity judgment (odd/even) task are faster to smaller numbers with left-sided responses, and to larger numbers with right-sided responses. Fischer et al. (2003) found that subjects responded faster to targets presented in the left visual field when cued by smaller numerals (1/2), and to targets in the right visual field when cued by larger numerals (8/9), even though the cues were non-predictive and task-irrelevant. Similarly, Casarotti et al. (2007) showed that task-irrelevant numerals biased temporal order judgments, such that targets appearing in the hemifield congruent with the mental number line (small-left, large-right) were judged to appear earlier than targets in the incongruent hemifield. At a cortical level, the parietal lobe contains multiple regions involved in calculation and visuospatial processes (Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002), leading us to suggest that automatic associations between numbers and space emerge as the result of interactions between parietal regions involved in numerical and spatial processes (Dehaene, Piazza, Pinel, & Cohen, 2003; Hubbard et al., 2005).

The neural mechanisms that underlie these reflexive endogenous shifts of attention have not been extensively explored (although see Eimer, 1997; Hietanen, Leppanen, Nummenmaa, & Astikainen, 2008; Sato, Kochiyama, Uono, & Yoshikawa, 2009). One important method for investigating visuospatial attention is the use of event-related potentials (ERPs), which permit the observation of the time course of cognitive processes (for a review, see Luck, Woodman, & Vogel, 2000). Studies using the classic spatial cueing paradigm described above have reported three early cue-locked ERP components involved in voluntary shifts of attention (Harter, Miller, Price, Lalonde, & Keyes, 1989; Hopf & Mangun, 2000; Nobre, Sebestyen, & Miniussi, 2000; Talsma, Slagter, Nieuwenhuis, Hage, & Kok, 2005; Van der Stigchel, Heslenfeld, & Theeuwes, 2006). The “early directing attention negativity” (EDAN), a relative negativity appearing 200–400 ms after cue onset over contralateral posterior scalp sites, is thought to originate in parietal cortex and to reflect mechanisms of spatial orienting (but see Van Velzen & Eimer, 2003). The “anterior directing attention negativity” (ADAN), which appears over contralateral anterior scalp sites 300–500 ms after cue onset, is thought to reflect supramodal attentional control processes originating in frontal structures (e.g., Eimer, Van Velzen, & Driver, 2002), although recent research has suggested the presence of more than one generator (Green, Conder, & McDonald, 2008; Praamstra, Boutsen, & Humphreys, 2005). Finally, the “late directing attention positivity” (LDAP), a positive waveform arising over 500 ms after cue onset and following the EDAN and ADAN components, seems to reflect the biasing of excitability in visual sensory areas by supramodal top-down attentional control (Eimer et al., 2002; Harter et al., 1989), and is thought to be generated by occipital areas involved in endogenous spatial attention (Praamstra et al., 2005). As such, the EDAN, ADAN and LDAP are thought to reflect the actions of a fronto-parietal attentional network engaged in the control of spatial attention (Corbetta & Shulman, 2002; Posner & Petersen, 1990).

In the current study, we examined the EDAN and ADAN components described in previous studies of voluntary attention while participants performed a cueing task with non-predictive, task-irrelevant symbolic stimuli (arrows and numerals) to address two issues. First, we investigated whether these cues elicited similar attentional mechanisms as task-relevant cues by looking for the presence of similar electrophysiological signatures. Second, we explored whether numerical cues induce involuntary activation of spatial representations, by testing whether the EDAN and ADAN were elicited for both arrows and numerals. In particular, we expected that our non-informative cues would elicit the same attentional modulations that have been found for informative cues in the hemisphere contralateral to the direction associated with the

cue, indicating that small numbers and left arrows directed attention to the left, and that large numbers and right arrows directed attention to the right. Based on previous behavioural studies that have suggested that interactions between numbers and space begin only after numerical magnitude has been processed (e.g., Galfano et al., 2006), we also predicted that interactions between numerical magnitude and hemisphere would begin only after the P2p component, a positive component appearing between 200 and 260 ms over parietal sites, which has been shown to be linked to processing of numerical magnitude (Dehaene, 1996). Finally, we predicted that early ERP responses (P1 and N1 components) to the target stimuli would be enhanced when they appeared at a location congruent with that indicated by the cue, as seen in studies that have used informative cues (Hillyard, Vogel, & Luck, 1998; Luck et al., 2000). As predicted, we found that non-informative task-irrelevant arrows and numerical cues both elicited the EDAN and ADAN, and that these non-informative cues modulated ERP responses to the targets. The results of the current study also suggest that symbolic cues do not need to be task-relevant in order to elicit shifts of attention, and that similar visuospatial processes are elicited by both arrows and numbers, due to their overlearned associations with space.

2. Methods

2.1. Participants

We tested 20 French volunteers but excluded 5 from analysis because of excessive noise or artefacts (blinks, movement, etc.) during the recording (final group: 15 subjects, 4 females; mean age = 22.2, range = 20–29). All gave informed consent, were right handed and had normal or corrected to normal vision.

2.2. Experimental design and procedure

Participants were instructed to respond as quickly as possible to a peripheral target, which appeared in the left or right visual field with equal probability (see Fig. 1). Each trial started with a fixation point (Courier New 18 pt, 4 mm 0.2°) lasting 500 ms, followed by either a central arrow (2.4 cm wide × 2.2 cm high, 1.1° × 1.0°) or numeral (1, 2, 8 or 9; Courier New 18 pt, 2 cm × 1.3 cm, 0.9° × 0.6°) cue presented for 300 ms. After a variable delay (300, 400 or 500 ms) a white circle (diameter 1 cm, 0.4°) appeared for 100 ms at 4° (9.2 cm) eccentricity. Participants responded as quickly as possible after target presentation by pressing a response button with their dominant (right) hand. They were allowed 2 s from target onset to respond, followed by a 2 s interstimulus interval (ISI). All stimuli were white on a black background and were presented on a Dell Precision 19" flatscreen display (Model number 1907FP) display¹. Participants were seated in a comfortable chair and were instructed to maintain fixation and to minimize blinks and eye movements during stimulus presentation.

All participants completed 396 experimental trials, 36 of which were catch trials (i.e., no target appeared after the cue). There were 132 trials in the arrows cueing condition (1/3 of total trials, 60 target trials and 6 catch trials for each direction, left and right), and 264 trials in the numbers cueing condition (2/3 of total trials, 60 target trials and 6 catch trials for each digit 1, 2, 8 and 9) presented in random order. The experiment was divided into 12 blocks, each lasting approximately 4 min. There were 10 training trials at the beginning of the experiment, and 4 dummy trials at the beginning of each block that were not analysed. Subjects were explicitly told that the targets had a 50% probability of appearing on the left or right, independent of the cue and were not instructed to orient their attention in the direction indicated by the cue. In order to induce subjects to pay attention to the cue even though it was not relevant for the target detection task, subjects were required to answer questions concerning the cues they had seen in the previous block at the end of each block (e.g., “Did you see the number 1?” or “Did you see more arrows or numbers?”). The entire task lasted about 50 min.

¹ The temporal characteristics of LCD flatscreens have substantially improved in the past few years. According to the manufacturer's information, the 1907FP has a rise time (black-to-white) of 8 ms and an overall response time (black–white–black) of 20 ms. Independent testing of the gray-to-gray response time (PC World Magazine) using gray-to-gray confirms an average response time of 8 ms. Since our stimuli were white on a black background, we estimate that the delay between our event codes and full stimulus intensity was no more than 10–15 ms. Although this is still longer than response times attainable with CRTs, it is a constant factor in our experiments, and should not in any way systematically bias our findings.

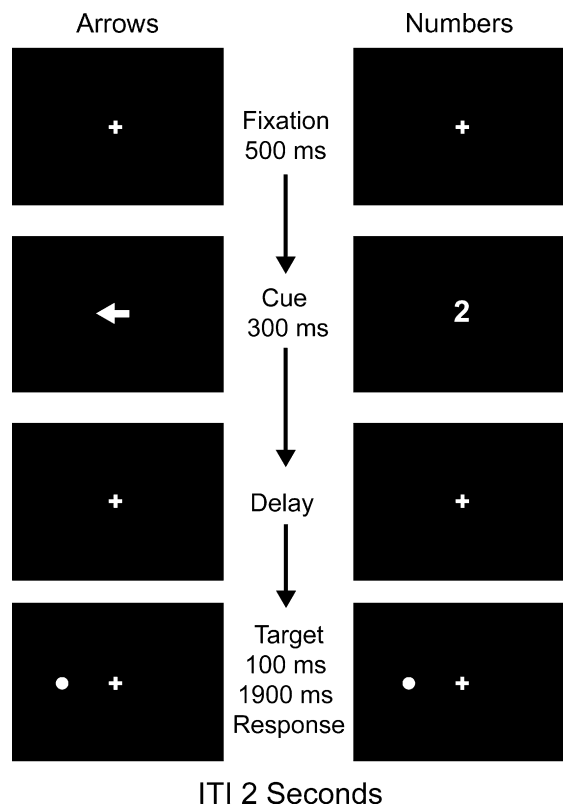


Fig. 1. Sequence of events. An arrow-cueing trial (on the left) and a numerical-cueing trial (on the right) are shown. After a fixation period lasting 500 ms, the cue was shown for 300 ms and followed by a variable delay which could last 300, 400 or 500 ms (cue–target onset asynchrony of 600, 700 or 800 ms). The target (100 ms) appeared either to the left or right of the fixation cross with equal probability, independent of the cue.

2.3. Data acquisition and analyses

We used a 256-channel Electrical Geodesics, Inc. (EGI) system for recording electroencephalogram (EEG) data. Electrodes were mounted on an elastic cap and were referenced to Cz with impedances maintained below 50 k Ω . EEG was recorded by a Net Amps 300 amplifier and EGI Netstation software. Continuous EEG was filtered with a 30 Hz low pass filter. After filtering, epochs locked to the cue onset (400 ms before and 600 ms after) and target onset (300 ms before and 600 ms after) were extracted. All epochs containing a blink or with more than 20% bad channels were rejected (threshold for rejection of blinks: 70 μ V averaged over 80 ms; bad channels: 100 μ V averaged over 100 ms, or 60 μ V averaged over 40 ms). Epochs with less than 20% bad channels were not excluded from analyses. We did not adopt any correction procedure for bad channels in these trials, as it can be difficult to know the extent to which correction procedures distort the results (e.g., Luck, 2005). However, all segments were visually inspected by the experimenter after the artefact rejection procedure in order to ensure that no bad segments were present for our main electrodes of interest. Only subjects with less than 30% rejected segments overall, and at least 30 good trials per condition were included in analyses. Epochs for each condition were averaged together, then data were re-referenced to an average reference corrected for polar average reference effect (PARE correction), and corrected to a 50 ms baseline.

Based on previous studies that have identified the EDAN over occipito-parietal electrodes (PO7/PO8, Van der Stigchel et al., 2006; or T5/T6 and PO3/PO4, Talsma et al., 2005), and the ADAN over central–frontal electrodes (F3/F4, Van der Stigchel et al., 2006; or F3/F4, F7/F8, C7/C8, C3/C4, Talsma et al., 2005), we defined three clusters of electrodes as our *a priori* regions of interest (ROIs): left and right occipital–parietal, central–parietal, and frontal ROIs. Electrodes for each ROI were averaged together. Finally, we performed a moving window analysis by stepping a 40 ms time window every 20 ms through all segments beginning at cue onset. For each time window, condition, and ROI, mean amplitudes were computed and analysed with a repeated measures ANOVA using hemisphere (left/right) and cue (left/right arrows or small/large numbers) as factors, separately for arrow-cueing and number-cueing conditions. Statistics were corrected using the Greenhouse–Geisser correction.

In order to assess the consequences of these attentional shifts on target processing, we also performed analyses on target-locked ERPs. We performed the same moving window analysis described above (40 ms windows every 20 ms) on mean amplitudes in our previously defined occipital–parietal and central–parietal

clusters to assess the P1 (80–140 ms) and N1 (160–220 ms) components, with Hemisphere (left/right), cue direction/magnitude and target position Congruency (congruent/incongruent), and Target Position (left/right) as factors. Stimuli presented at attended locations typically lead to a larger positivity approximately 100 ms after stimulus onset (P1 component) and a larger negativity approximately 200 ms after stimulus onset (N1 component) over the hemisphere contralateral to the visual stimulus than do stimuli presented at unattended locations (e.g., Hillyard et al., 1998; Luck et al., 2000). Based on previous experiments which found an enhancement of the P1 component for congruent trials in a number-cueing condition (Salillas, El Yagoubi, & Semenza, 2008) and N1 component for congruent trials in the arrow-cueing condition (e.g., Talsma et al., 2005), we expected that the amplitude of P1 and N1 components would be increased for targets contralateral to the shift of attention hypothesized for numbers and arrows, respectively.

3. Results

3.1. Behavioural results

Misses (less than 1% of trials) and reaction times faster than 100 ms or longer than 1000 ms were excluded from analyses, as well as all catch trials (false alarm rate less than 2% of trials). Repeated measures ANOVAs were then computed on reaction times with Cue Type (arrow/number), Cue Direction/Magnitude (for arrows: left/right; for numbers: small/large), and Target Position (left, right) as factors. Neither the Cue Direction/Magnitude \times Target Position interaction, nor the three-way interaction between Cue Type \times Cue Direction/Magnitude \times Target Position were significant ($F(1,14)=2.6$, $P=0.13$, and $F(1,14)=0.2$, $P=0.65$, respectively). The arrows and numbers conditions were then considered separately. For each condition, repeated measures ANOVAs were performed on reaction times with Cue Direction/Magnitude and Target Position as factors. There were no main effects for either the arrows and numbers condition. The Cue Direction/Magnitude \times Target Position interactions did not reach significance for arrows ($F(1,14)=1.2$, $P=0.3$), but approached significance for numbers ($F(1,14)=4.1$, $P=0.06$). Although these results are not significant, mean reaction times were faster when the target location was congruent with that indicated by the cue (i.e., to left-sided targets when previously cued by left arrows or small numbers, and to right-sided targets when cued by right arrows or large numbers; see Fig. 2).

Examination of the subjects' responses to the questions at the end of each block shows that they were correct on 93.5% of the questions that had a clear right or wrong answer (e.g., Did you see the number 1?). This high degree of accuracy indicates that the questions were indeed effective at inducing subjects to pay attention to the cues, despite the fact that subjects were informed that the cues were not informative about the location of the upcoming target.

3.2. Cue-locked ERP results

Fig. 3 shows the grand average ERPs for the arrow-cueing conditions (left/right arrows), and number-cueing conditions (small/large numbers) from left and right occipital–parietal, central–parietal, and frontal ROIs at cue onset.

3.2.1. Cue-locked ERPs: arrows condition

We observed a main effect of Hemisphere for arrows in the occipital–parietal and central–parietal ROIs in the early time windows (occipital–parietal: 100–220 ms and 300–360 ms, all $F_s(1,14)>4.7$, $P_s<0.05$; central–parietal: 80–200 ms, all $F_s(1,14)>5.4$, $P_s<0.05$), and later in the frontal ROIs (540–600 ms, all $F_s(1,14)>5.2$, $P_s<0.05$). A main effect of Cue Direction was only found at occipital–parietal sites in the 140–180 ms time window ($F(1,14)=5.5$, $P=0.03$). To examine attentional processes contralateral to the direction indicated by the cue (the EDAN and ADAN components) we then plotted the average ERPs for ipsilateral versus contralateral conditions (Fig. 4). We found significant Hemi-

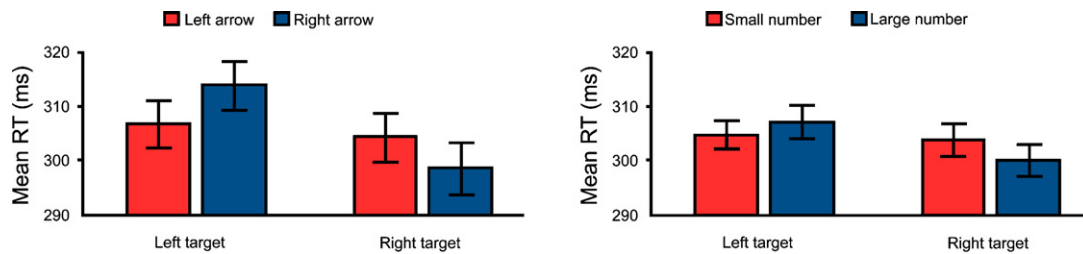


Fig. 2. Behavioural results. Mean reaction times are shown for arrow-cueing (on the left) and number-cueing (on the right) in function of the target position. Error bars indicate one SEM.

sphere \times Cue Direction interactions in each of our three different ROIs in different time windows. For the occipital–parietal ROI, waveforms over contralateral electrodes were significantly more negative for the 120–180, 260–300, 320–400, and 400–500 ms time windows (all $F_s(1,14) > 4.7$, $P_s < 0.05$; for all time windows, the range of the contralateral minus ipsilateral mean voltages was between -0.29 and $-0.63 \mu V$). Similarly, for central–parietal ROIs, waveforms over contralateral electrodes were significantly more negative for the 120–180, 320–400, and 400–480 ms time windows (all $F_s(1,14) > 5.9$, $P_s < 0.05$; for all time windows, the range of the contralateral minus ipsilateral mean voltages was between -0.42 and $-0.71 \mu V$), while for frontal sites the interaction was significant only in the later time windows between 340 and 460 ms (all $F_s(1,14) > 5.5$, $P_s < 0.05$; for all time windows, the range of the contralateral minus ipsilateral mean voltages was between -0.46

and $-0.62 \mu V$). Although the earliest Hemisphere \times Cue Direction interactions at occipital–parietal sites may reflect physical differences between leftward and rightward arrows, the later effects starting at 260 ms over posterior electrodes and starting at 340 ms over anterior electrodes are very similar to the EDAN and ADAN components described in literature.

3.2.2. Cue-locked ERPs: numbers condition

We observed a main effect of Hemisphere for numbers in all three ROIs in the early time windows (occipital–parietal: 100–180 ms, all $F_s(1,14) > 6.5$, $P_s < 0.05$; central–parietal 20–180 ms, all $F_s(1,14) > 7.2$, $P < 0.05$; frontal: 20–120 ms, all $F_s(1,14) > 4.6$, $P_s < 0.05$). We also found significant main effects of number magnitude on the P2p component (Dehaene, 1996) over occipital–parietal sites (120–180 ms, all $F_s(1,14) > 6.8$, $P_s < 0.05$,

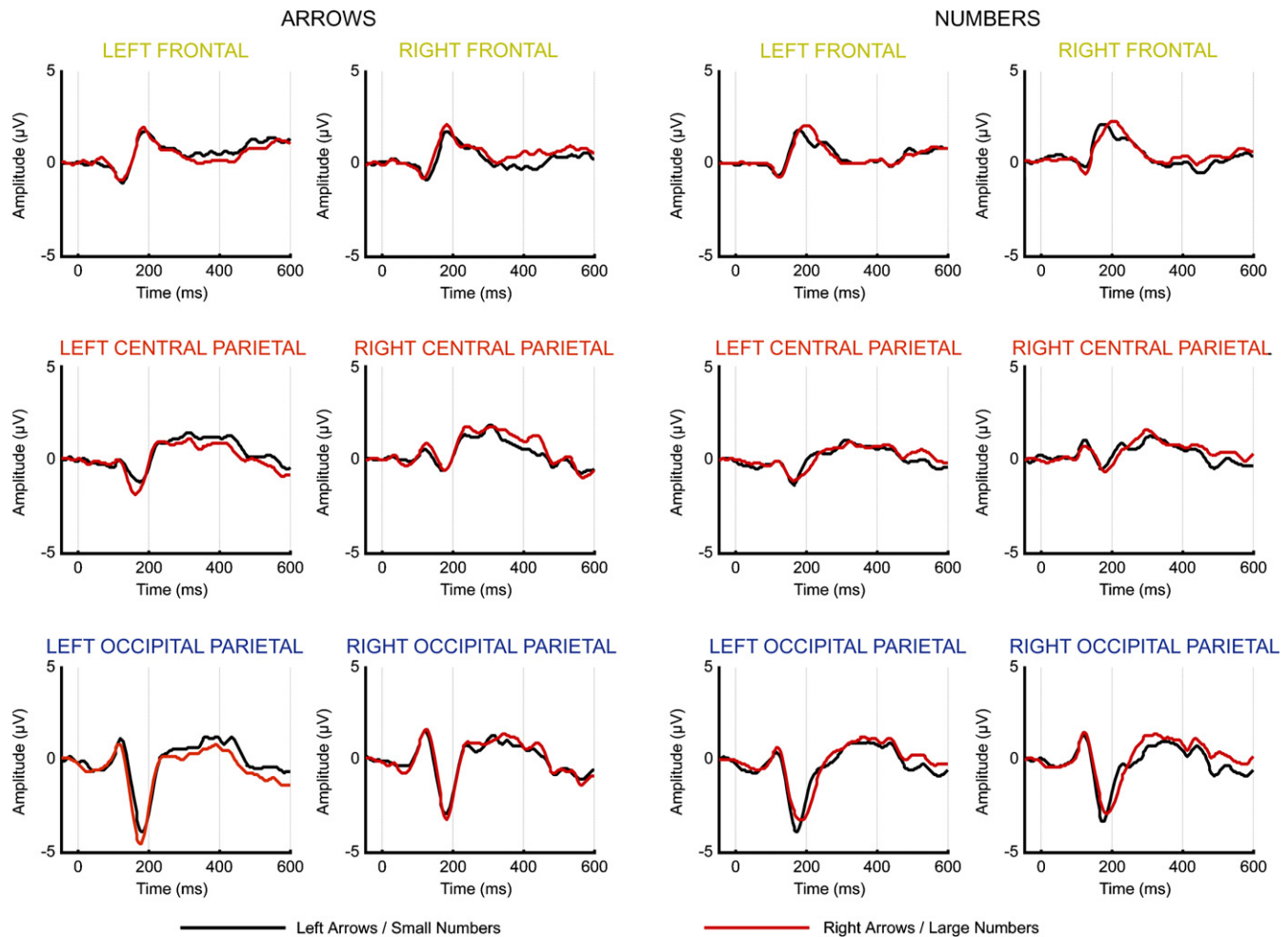


Fig. 3. Grand average cue-locked ERPs for arrow-cueing (on the left) and number-cueing (on the right), at three selected clusters of electrodes (left and right frontal, central–parietal, and occipital–parietal ROIs). Left arrows/small numbers cues are indicated by black lines and right arrows/large numbers cues by grey lines.

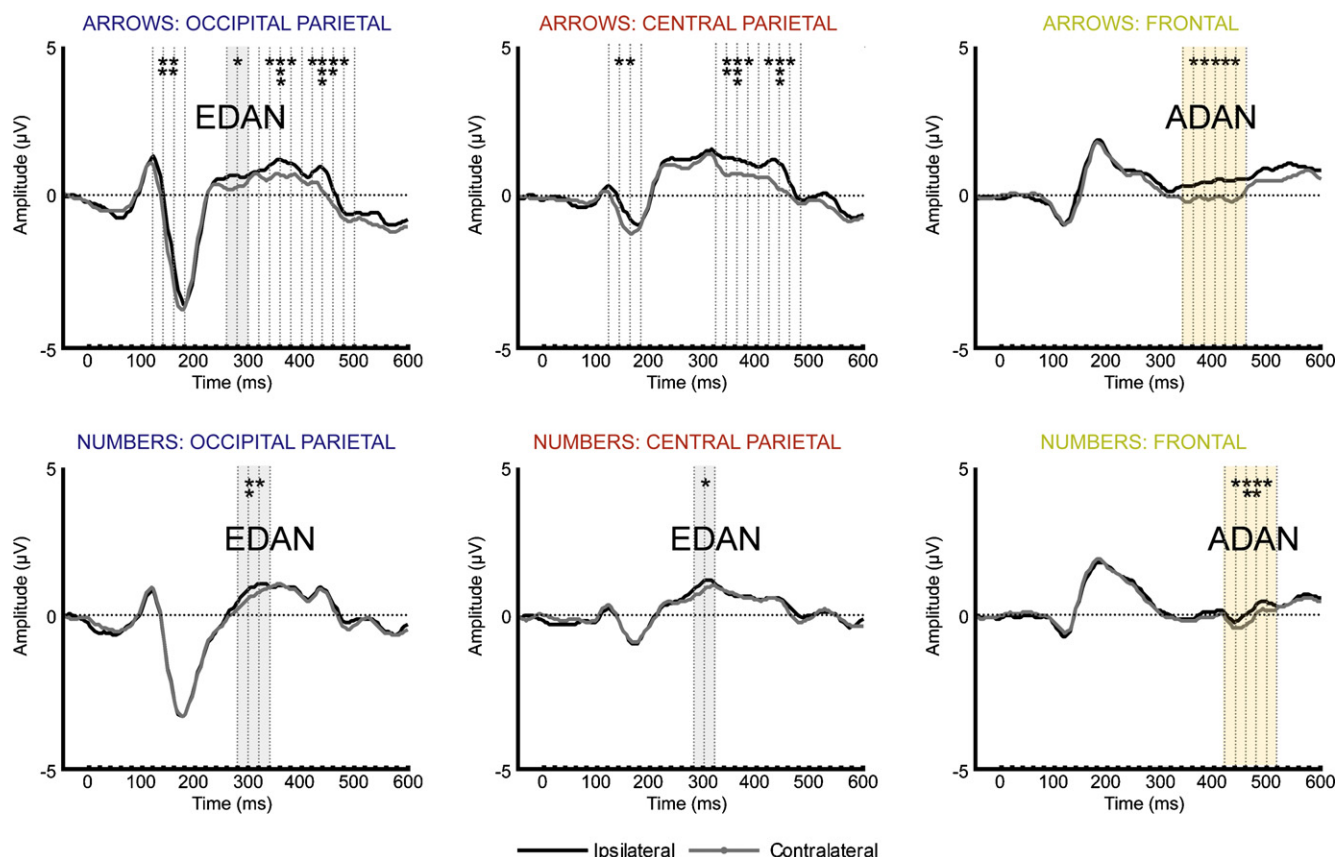


Fig. 4. Average cue-locked ERPs for ipsilateral (Left Hemisphere/Left Direction and Right Hemisphere/Right Direction, black line) versus contralateral (Left Hemisphere/Right Direction and Right Hemisphere/Left Direction, grey line) conditions for occipito-parietal, centro-parietal and frontal ROIs (from left to right, respectively). The upper row shows the arrow-cuing condition and the lower row the number-cuing condition. Stars are plotted vertically and indicate significant interactions between hemisphere and cue direction (or magnitude, for numbers) in 40 ms time windows.

180–240 ms, all $F_{s(1,14)} > 12.0$, $P_s < 0.005$, 260–300 ms, all $F_{s(1,14)} = 4.6$, $P_s < 0.05$, 460–600 ms, all $F_{s(1,14)} > 7.9$, $P_s < 0.05$, central-parietal sites (180–240 ms, all $F_{s(1,14)} > 13.6$, $P_s < 0.005$, 460–600 ms, $F_{s(1,14)} > 6.5$, $P_s < 0.05$), and frontal sites (140–180 ms, $F_{s(1,14)} = 9.0$, $P = 0.009$, 180–240 ms, all $F_{s(1,14)} > 20.5$, $P_s < 0.0005$, see Fig. 5). These results demonstrate that the numerical cues were processed up to a level where either numerical magnitude or number frequency (which is negatively correlated with magnitude) had an influence (Dehaene, 1996).

Most crucially for the purposes of our experiment, to determine whether attentional processes contralateral to the direction indicated by the cue (the EDAN and ADAN components) were also elicited with number cues, we plotted the average ERPs for ipsilateral (Left Hemisphere/Small Number and Right Hemisphere/Large Number) versus contralateral (Left Hemisphere/Large Number and Right Hemisphere/Small Number) conditions (Fig. 4). We found significant Hemisphere \times Cue Direction interactions in each of our three different ROIs in time windows similar to those observed for

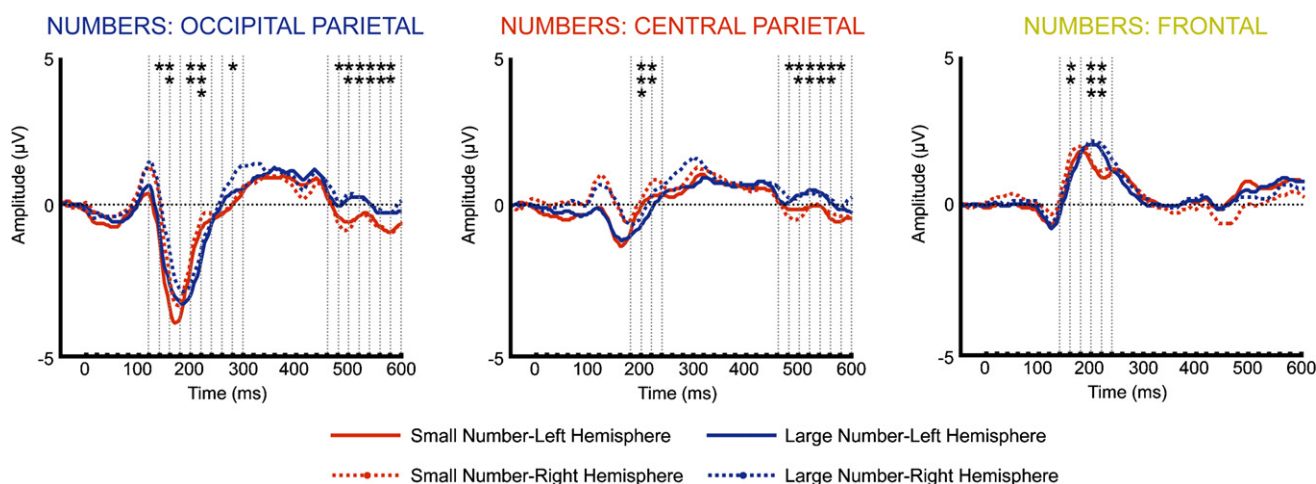


Fig. 5. Cue-locked ERPs elicited by numerical-cuing at occipital-parietal (on the left), central-parietal (central graph), and frontal (on the right) ROIs. Stars are plotted vertically and indicate significant main effects of Magnitude (small numbers versus large numbers) at particular 40 ms time windows.

arrow cues. For the occipital–parietal ROI, waveforms over contralateral electrodes were significantly more negative for all time windows between 280 and 340 ms (all $F_s(1,14) > 7.9$, $P_s < 0.05$; for all time windows, the range of the contralateral minus ipsilateral mean voltages was between -0.25 and $-0.29 \mu\text{V}$). Similarly, for central–parietal ROIs, waveforms over contralateral electrodes were significantly more negative for all time windows between 280 and 320 ms ($F(1,14) = 7.2$, $P = 0.018$; the contralateral minus ipsilateral mean voltages was $-0.24 \mu\text{V}$) while for frontal sites the interaction was significant only in the later time windows between 420 and 520 ms (all $F_s(1,14) > 4.8$, $P_s < 0.05$; for all time windows, the range of the contralateral minus ipsilateral mean voltages was between -0.23 and $-0.32 \mu\text{V}$). The Hemisphere \times Magnitude interactions starting at 280 ms over posterior and central electrodes and starting at 420 ms over anterior electrodes strongly mirrors the EDAN and ADAN effects observed for arrows.

3.3. Cue-locked ERPs: comparison of arrows and numbers conditions

We observed similar Hemisphere \times Cue Direction/Magnitude interactions for both arrows and numbers, consistent with previously reported EDAN and ADAN effects, suggesting that similar shifts of attention are elicited by arrows and numbers cues, even when they are task-irrelevant. However, inspection of the raw data (Fig. 4) suggests that these effects start earlier for arrows than for numbers (occipital–parietal sites: 260 ms vs. 280 ms; frontal sites: 340 ms vs. 420 ms). These differences suggest that the exact mechanisms whereby arrows and numbers elicit shifts of attention may also differ. However, such differences should be interpreted with caution, as it is well-known that direct comparison of stimuli with different physical features, which is unavoidably the case with our arrow and number cues, can lead to corresponding differences in the elicited ERPs. While this potential confound affects earlier components related to sensory processing more strongly than later cognitively related components (e.g., Luck, 2005), the effects may carry through even to late components. Given that the EDAN and ADAN effects occur after the P1 and N1 waveforms usually identified with the processing of physical stimulus features, the impact of physical differences on our attention-related components will be reduced but may not be entirely eliminated. The fact that the components are largely similar for the two cue types suggests that the differences we observe are not driven solely by these unavoidable low-level stimulus differences, but we cannot entirely exclude this possibility.

With these caveats in mind, we calculated an ANOVA with Cue Type (arrows, numbers), Time (40 ms time windows within temporal intervals of interest: occipital–parietal, 220–340 ms; central–parietal, 240–360 ms; frontal, 300–540 ms), Hemisphere (left, right) and Cue Direction/Magnitude (left/small, right/large) as factors in each of our three predefined ROIs. Temporal intervals of interest were defined for the three sites based on time intervals where the Hemisphere \times Cue Direction/Magnitude interaction was significant.

3.3.1. Cue-locked ERPs: arrows versus numbers at occipital–parietal ROIs

At occipital–parietal sites there was a significant effect of Time ($F(2,28) = 6.4$, $P = 0.009$) reflecting the recovery from the negative N1 peak. The Cue Type \times Time ($F(2,28) = 12.3$, $P = 0.001$) and Cue Type \times Time \times Cue Direction/Magnitude interactions ($F(2,28) = 7.0$, $P = 0.008$) were significant, indicating earlier baseline recovery for arrows than for numbers. Most importantly, the EDAN effect was present (Hemisphere \times Cue Direction interaction, $F(1,14) = 7.5$, $P = 0.016$) and did not differ in amplitude or time course between number and arrow cues (Cue Type \times Hemisphere \times Cue

Direction/Magnitude interaction, $F(1,14) = 0.090$, $P = 0.77$, and Cue Type \times Time \times Hemisphere \times Cue Direction/Magnitude interaction, $F(2,28) = 0.422$, $P = 0.656$).

3.3.2. Cue-locked ERPs: arrows versus numbers at central–parietal ROIs

Analyses at central–parietal sites revealed that arrows elicited more positive voltages than numbers (main effect of Cue Type, $F(1,14) = 7.3$, $P = 0.017$), with this difference decreasing as a function of time (Cue Type \times Time interaction, $F(2,28) = 5.3$, $P = 0.024$). We also find a significant Time \times Cue Direction/Magnitude interaction ($F(2,28) = 5.3$, $P = 0.018$). Crucially, the EDAN effect was present (Hemisphere \times Cue Direction/Magnitude interaction, $F(1,14) = 7.5$, $P = 0.016$) and did not differ for arrows and number cues (Cue Type \times Hemisphere \times Cue Direction interaction, $F(1,14) = 0.78$, $P = 0.39$). The Cue Type \times Time \times Hemisphere \times Cue Direction/Magnitude interaction was marginally significant ($F(2,28) = 2.7$, $P = 0.095$).

3.3.3. Cue-locked ERPs: arrows versus numbers at frontal ROIs

Analyses at frontal sites confirmed the presence of a significant ADAN effect (Hemisphere \times Cue Direction/Magnitude, $F(1,14) = 9.3$, $P = 0.009$). The Cue Type \times Time \times Hemisphere \times Cue Direction/Magnitude interaction approached significance ($F(5,70) = 2.3$, $P = 0.09$), consistent with the suggestion that the ADAN effect might start earlier for arrows than for numbers.

3.4. Target-locked ERP results

Fig. 6 shows the grand average ERPs for the congruent and incongruent conditions from left and right occipital–parietal and central–parietal ROIs at target onset, separately for arrows and numbers. We performed ANOVAs at occipital–parietal and central–parietal ROIs with Hemisphere (Left/Right), Congruency (Congruent: left arrows or small numbers followed by left targets and right arrows or large numbers followed by right targets), and Target Position (Left/Right) as factors at P1 (80–140 ms) and N1 (160–220 ms) time windows, separately for arrows and numbers.

3.4.1. Target-locked ERPs: arrows condition

A main effect of Hemisphere was found over central–parietal sites for all N1 time windows ($F_s(1,14) > 4.9$, $P_s < 0.05$), with more negative voltages over the left hemisphere than the right. The Hemisphere \times Target Position interaction was significant for the P1 and N1 components over both occipital–parietal and central–parietal sites (between 80 and 120 ms, $F_s(1,14) > 10.22$, $P < 0.01$; between 160 and 200 ms, $F(1,14) > 24.43$, $P < 0.001$); the P1 was more positive and N1 was more negative over the hemisphere contralateral to the target position, consistent with the standard contralateral distribution of these components. Although voltages were more negative at N1 time windows over occipital–parietal sites for congruent trials (mean voltage between 160 and 200 ms: congruent = $-0.57 \mu\text{V}$, incongruent = $-0.07 \mu\text{V}$; mean voltage between 180 and 220 ms: congruent = $-0.59 \mu\text{V}$, incongruent = $-0.11 \mu\text{V}$) this effect did not reach significance ($F_s(1,14) > 2.5$, $P_s > 0.1$). No other effects or interactions were significant.

3.4.2. Target-locked ERPs: numbers condition

Analyses of target-locked ERPs for the numbers condition revealed a main effect of Hemisphere over central–parietal sites for all time windows between 100 and 220 ms ($F_s(1,14) > 4.6$, $P_s < 0.05$), with more negative voltages over the left hemisphere, similar to the effect observed for arrows. Moreover, a significant main effect of Target Position was found over central–parietal sites for all time windows (P1: $F_s(1,14) > 6.64$, $P_s < 0.05$; N1: $F_s(1,14) > 5.05$, $P_s < 0.05$),

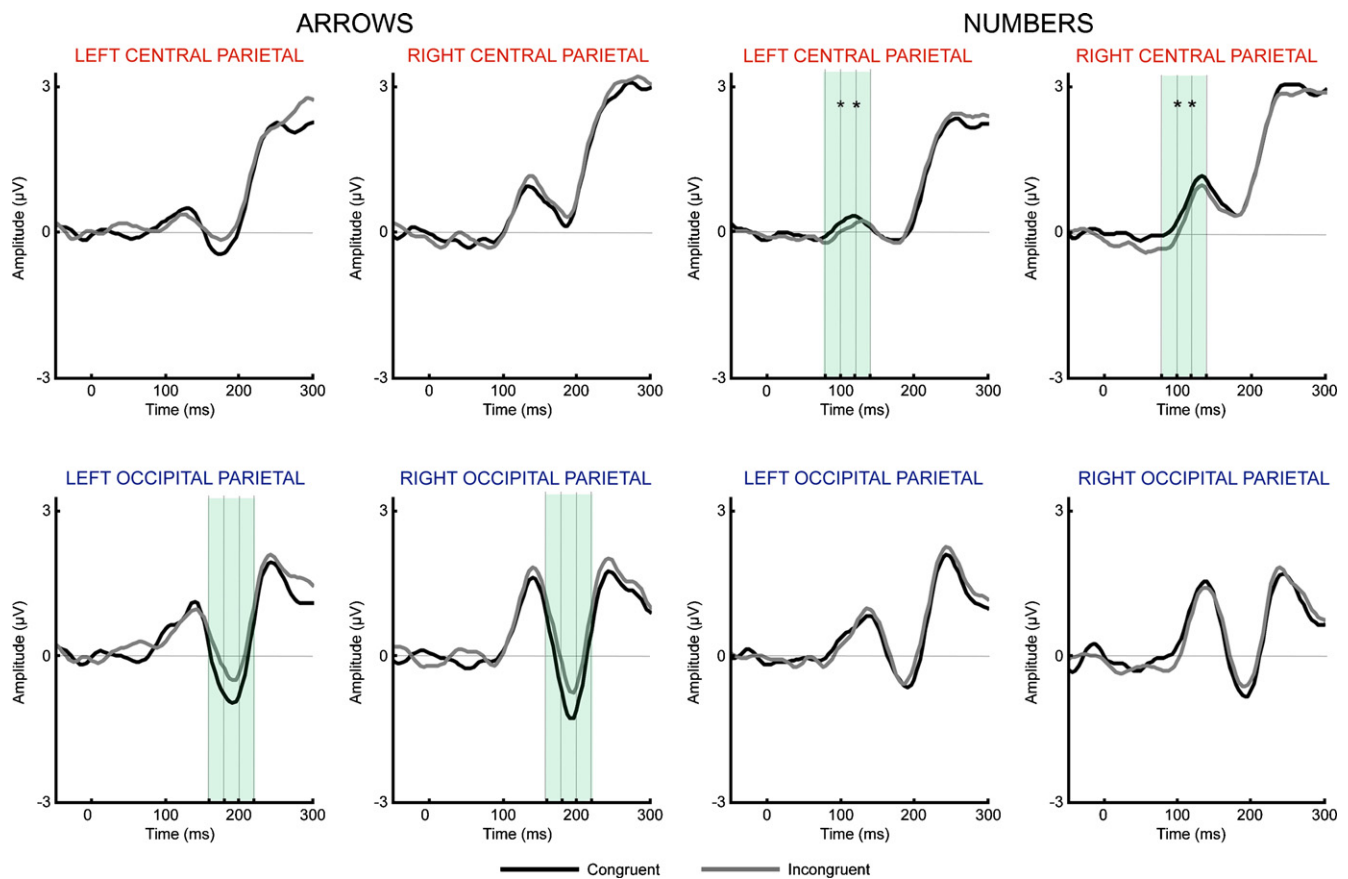


Fig. 6. Grand average target-locked ERPs for arrow-cuing (on the left) and number-cuing (on the right), at left and right central-parietal and occipital-parietal ROIs. Congruent conditions are indicated by black lines and incongruent conditions by grey lines. Relevant time windows at specific ROIs are highlighted. Stars indicate a significant main effect of congruency in 40 ms time windows.

indicating that voltages were always more positive for targets in the right visual field than for targets in the left visual field. As predicted, the P1 and N1 components were enhanced in the hemisphere contralateral to the target position, as revealed by the significant Hemisphere \times Target Position interaction at both occipital-parietal and central-parietal sites (between 80 and 120 ms, $F(1,14) > 6.17$, $P < 0.05$; between 160 and 200 ms, $F(1,14) > 26.26$, $P < 0.001$). Crucially, the main effect of Congruence was significant in all P1 time windows at central-parietal sites for number-cueing ($F(1,14) > 6.5$, $P_s < 0.03$), showing more positive voltages for congruent trials (mean voltage between 80 and 120 ms: congruent = $0.26 \mu\text{V}$, incongruent = $0.03 \mu\text{V}$; mean voltage between 100 and 140 ms: congruent = $0.54 \mu\text{V}$, incongruent = $0.38 \mu\text{V}$). No other effects or interactions were significant.

3.4.3. Correlation between target-locked ERPs and RTs

In order to test whether these ERP congruency effects were behaviourally relevant, we next correlated an index of the behavioural congruency effect ($RT_{\text{incongruent}} - RT_{\text{congruent}}$ for each cue type) and an index of the congruency effect observed for target-locked ERPs (voltage_{incongruent} – voltage_{congruent}) for each N1 time window at occipital-parietal sites for arrows, and for each P1 time window at central-parietal sites for numbers. In the behavioural index, positive values for RTs corresponded to faster RTs for congruent trials, while for the ERP index, positive values for the N1 component corresponded to enhanced voltages for congruent trials. Conversely, negative values for the P1 component corresponded to enhanced voltages for congruent trials. Based on previous studies (Harter et al., 1989; Talsma, Mulckhuyse, Slagter, & Theeuwes, 2007), we predicted a positive correlation between behavioural

facilitation and the N1 component, and a negative correlation between behavioural facilitation and the P1 component. We found a significant correlation between RTs and ERPs for arrows in the N1 time window between 160 and 200 ms ($\rho = 0.46$, $P < 0.05$, one-tailed), and for numbers in the P1 time window between 100 and 140 ms ($\rho = -0.49$, $P < 0.05$, one-tailed).

Examination of the scatter plots show that our behavioural and ERP indices varied continuously across their range, with no evidence of a discontinuity. These results argue against the possibility that our effects reflect a mix of two samples of subjects, those who completely ignored the cues, and those who treated them as 100% informative, despite being told that they were non-informative. Finally, there is no correlation between the behavioural indices for arrows and numbers ($\rho = 0.00$). Since both cue types were randomly intermixed, this further argues against the idea that individual subjects were adopting a consistent strategy of treating the cues as informative.

4. Discussion and conclusions

The present study aimed to investigate the time course of the orienting shifts induced by non-informative symbolic cues with spatial meaning such as arrows and numbers by exploring electrophysiological activity during a simple detection task. Our results are consistent with previous behavioural studies that find symbolic cues with spatial meaning can elicit automatic endogenous shifts of attention. Consistent with these previous studies reporting spatial attentional biases for non-predictive arrows (e.g., Hommel et al., 2001) and numbers (e.g., Fischer et al., 2003), in the present experiment responses were faster for congruent trials (i.e., when the

target appeared in the location associated with the preceding cue). However, the behavioural effect was not significant for arrows and only approached significance for numbers. One possible reason for the lack of a significant behavioural effect, especially in the arrow condition, could be that we used relatively long SOAs (600–800 ms) in order to examine the full time course of the orienting of attention without interference from target-evoked ERPs. It is important to consider that cueing effects for arrows and numbers have been shown to have different behavioural time courses. Although shifts of attention with non-predictive arrows have been observed also at longer SOAs (e.g., 1000 ms in Experiment 1 of [Hommel et al., 2001](#)), studies which investigated attentional orienting induced by non-predictive arrows show the effect starting at earlier SOAs (e.g., [Ristic & Kingstone, 2006](#)), whereas shifts of attention induced by numbers have been found at longer SOAs (e.g., [Fischer et al., 2003](#)). Additionally, [Bonato, Priftis, Marenzi, and Zorzi \(2009\)](#) recently showed that cueing effects with non-predictive arrows were more consistent at shorter SOAs (200 and 350 ms) than at longer SOAs (550–800 ms). It is therefore possible that by the time the target appeared, the cueing effect induced by arrows had almost completely decayed away. Moreover, it has been shown that the effects of numerical cues are stronger when the cues are task-relevant ([Casarotti et al., 2007](#)). Our cues were task-irrelevant, which may also have reduced the behavioural cueing effect.

The most important result of this study was that negative deflections were found over the hemisphere contralateral to the hypothesized direction of shifts of attention for both arrows and number cues. These contralateral negativities followed the same time course as the EDAN and the ADAN components described in literature as markers of spatial attention shifts (e.g., [Harter et al., 1989](#); [Nobre et al., 2000](#); [Talsma et al., 2005](#); [Van der Stigchel et al., 2006](#)). The EDAN and ADAN effects were significant for both arrows and numbers at occipito-parietal ROIs and at frontal ROIs, respectively, in overlapping time windows (EDAN: 280–300 ms and ADAN: 420–460 ms both for arrows and numbers). These results provide evidence of the attentional shifts induced by non-predictive symbolic cues with a spatial meaning (see also [Hietanen et al., 2008](#); [Salillas et al., 2008](#)), and suggest similar orienting mechanisms for spatial and numerical cueing.

Previous studies of attention have used non-predictive, but task-relevant, arrow cues to demonstrate the existence of ERP components related to voluntary shifts of visuo-spatial attention (EDAN and ADAN; [Hopf & Mangun, 2000](#)). However, studies using arrow cues may confound shifts of attention due to space-related cues with perceptually triggered asymmetric processing of the cues themselves ([Van Velzen & Eimer, 2003](#)). Here we rule out this interpretation by showing that numerals can generate the same attention-related ERP components as arrows. Unlike for arrows, the association between numbers and space arises only from semantic-level associations. Indeed, we found interactions between hemisphere and cue direction at earlier perceptual processing stages (cue-locked P1–N1) only for arrow cues, but not for numbers.

[Hietanen et al. \(2008\)](#) recently also showed that non-informative, task-irrelevant arrows elicited EDAN and ADAN components. However, gaze cues, which elicited behaviourally similar cuing effects, did not elicit similar ERPs, suggesting different cortical mechanisms for arrow and gaze cues. In contrast, we find that numerical cues also elicit the EDAN and ADAN components, suggesting common mechanisms for shifts of attention elicited by arrows and numbers. Our findings of similar attentional cue-locked ERPs for arrow and number cues at occipital-parietal and frontal sites are consistent with recent fMRI results ([Sato et al., 2009](#)) showing analogous patterns of activations for different non-predictive attention-triggering stimuli (eyes, hands, arrows) at temporal, parietal and frontal sites. Sato et al. also find increased activation in

the superior temporal sulcus region in the automatic orienting of attention regardless of the cue type.

In fact, the EDAN and ADAN effects we found both for arrows and numbers had slightly different localisations and latencies for the two cue types, although these differences did not reach significance. In particular, the EDAN effect is significant at central-parietal electrodes between 280 and 320 ms for numbers but not for arrows, probably reflecting an earlier involvement of parietal areas for attentional spatial processing induced by numbers. Interestingly, a sustained contralateral negativity after 320 ms extended up to 500 ms at posterior and central sites for arrows but not for numbers. Studies reporting EDAN and ADAN have usually interpreted the entire contralateral negativity observed between about 200–400 ms at posterior sites as a unique EDAN component, and the contralateral negativity at centro-parietal sites (or “ipsilateral relative positivity”, [Nobre et al., 2000](#)) as representing a mix of the EDAN and ADAN effects reflecting the shift of attentional processes from posterior to anterior areas. Nevertheless, the present results suggest that posterior contralateral negativities between 200 and 500 ms induced by arrows may reflect a series of different attentional subcomponents, the last ones possibly generated by cognitive processes which are specific for directional cues with explicit spatial meaning such as arrows.

The similar patterns of ERP components found here with arrows and numerical cues provide additional evidence that numbers automatically evoke associations with space ([Hubbard et al., 2005](#); [Knops, Thirion, Hubbard, Michel, & Dehaene, 2009](#)). Indeed, previous studies found that attention is directed to the side of space indicated by a numerical cue ([Casarotti et al., 2007](#); [Fischer et al., 2003](#); [Galfano et al., 2006](#); [Ristic et al., 2006](#)), with small numbers associated to the left part of the space and large numbers to the right. Moreover, these behavioural studies have suggested that numerical magnitude must be processed before evoking spatial associations. The present study is consistent with, but goes beyond the inferences from behavioural studies, by directly showing that the modulation of the P2p, which reflects semantic number processing, occurred prior to the interactions between numerical magnitude and hemisphere, which reflect shifts of attention induced by number cues. The involvement of parietal areas in numerical processing replicates earlier ERP and fMRI studies showing modulation of parietal regions during semantic processing of numbers (for a review, see [Dehaene et al., 2003](#)). Most crucially, we find that the activation of a spatial representation for numbers occurs within approximately 280 ms after the onset of the number, shortly after the semantic meaning of the digit is first accessed ([Dehaene, 1996](#)), in line with the behavioural results.

The shift of attention induced by the spatial meaning of numbers was also confirmed by the significant enhancement of P1 component at central-parietal sites for congruent trials (i.e., small numbers followed by left targets and large numbers followed by right targets). Using a similar cuing paradigm, [Salillas et al. \(2008\)](#) also showed that ERPs locked to target onset were modulated by numerical magnitude, such that the P100 and P300 components contralateral to the target were stronger when a left-sided target was cued by 1 and 2, and when a right-sided target was cued by numbers 8 and 9. Whereas the examination of ERPs elicited by target stimuli permits the study of the effects of attention, focusing on ERPs elicited by cues permits an examination of the mechanisms involved in shifts of attention. In this sense, the attention shifts elicited following numerical cues observed in the present study are in line with the findings by [Salillas et al. \(2008\)](#), and furthermore bear directly on the mechanism by which numbers induce this spatial biasing effect.

Finally, the current study was not able to systematically investigate the LDAP component. Although the LDAP generally begins

approximately 500 ms after cue onset (Eimer et al., 2002; Harter et al., 1989), other studies reported an LDAP as early as 400 ms after cue onset (Harter et al., 1989 for left hemisphere activations; Hopf & Mangun, 2000; Praamstra et al., 2005). As we ended our recording epoch with the earliest onset of the target (600 ms after cue onset), we cannot say whether we were simply unable to observe the LDAP component in the present experiment as a consequence of the cue–target intervals used, or whether other reasons are responsible for this finding. The LDAP component has been proposed to reflect modulation of baseline activity in visual–sensory areas (Harter et al., 1989). However, studies observing the LDAP for stimuli in different sensory modalities (visual, auditory and tactile, see Eimer et al., 2002) have suggested that this component may be involved in different top-down attentional processes, and in particular in the control of spatial orienting. All studies observing the LDAP component to date have used voluntary spatial paradigms. Given that in the present study no LDAP was observed using non-predictive cues, it is possible that this component is more related to voluntary attention shifts in response to informative cues, and not evoked by non-predictive spatial cues². Further ERP studies directly comparing voluntary and non-voluntary cues would provide a deeper understanding of different endogenous processes.

In conclusion, this study provides further electrophysiological evidence that the same processes involved in volitional–endogenous shifts of attention are also elicited by symbolic cues with overlearned spatial associations, showing that even task-irrelevant arrows and numbers can elicit the same pattern of ERP components that have previously been observed for task-relevant cues. Additionally, we suggest that both behavioural attentional orienting effects and ERP components observed using informative central cues may reflect combinations of volitional and reflexive mechanisms (see Eimer, 1997; Ristic et al., 2006). Finally, our results are consistent with a growing body of literature suggesting that brain imaging methods, including fMRI and EEG, may be more sensitive than behavioural methods for detecting complex cognitive mechanisms such as shifts of attention elicited by non-predictive cues (Fink, Marshall, Weiss, Toni, & Zilles, 2002; Thiel, Zilles, & Fink, 2005, for a review, see Wilkinson & Halligan, 2004).

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