

Manual response preparation disrupts spatial attention: An electrophysiological investigation of links between action and attention

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ABSTRACT

Previous behavioural and neuroscience studies have shown that the systems involved in the control of attention and action are functionally and anatomically linked. We used behavioural and event-related brain potential measures to investigate whether such links are mandatory or merely optional. Cues presented at the start of each trial instructed participants to shift attention to the left or right side and to simultaneously prepare to a finger movement with their left or right hand. In different trials, cues were followed by a central Go signal, requiring execution of the prepared manual response (motor task), or by a peripheral visual stimulus, which required a target–non-target discrimination only when presented on the cued side (attention task). Lateralised ERP components indicative of covert attention shifts were found when attention and action were directed to the same side (same side condition), but not when attention and action were directed to opposite sides (opposite sides condition). Likewise, effects of spatial attention on the processing of peripheral visual stimuli were present only when attention and action were directed to the same side, but not in the opposite sides condition. These results demonstrate that preparing a manual response on one side severely disrupts the attentional selection of visual stimuli on the other side, and suggest that it is not possible to simultaneously direct attention and action to different locations in space. They support the hypothesis that the control of spatial attention and action are implemented by shared brain circuits, and are therefore linked in a mandatory fashion.

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1. Introduction

The selection of perceptual objects and the selection of motor responses have traditionally been regarded as separate processes that take place sequentially. Attentional mechanisms are responsible for the selective processing and representation of currently task-relevant sensory information, and are followed by motor control mechanisms that implement the selection, programming, and execution of specific motor responses. Recent findings have challenged such simple serial models of sensorimotor control by demonstrating that far from being functionally, temporally, and anatomically distinct, the selection of sensory information and the selection of motor responses often take place in parallel, and may even be implemented by the same neural mechanisms.

Neurophysiological studies in primates have demonstrated that cortical areas involved in eye movement control, such as the lateral intraparietal area (LIP e.g., Andersen, Essick, & Siegel, 1987; Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975;

Robinson, Goldberg, & Stanton, 1978) and the frontal eye field (FEF, e.g., Bizzi, 1968; Bruce & Goldberg, 1985) are activated not only during the execution of a saccadic eye movement, but also during purely attentional tasks in the absence of saccades (Bushnell, Goldberg, & Robinson, 1981; Colby, Duhamel, & Goldberg, 1996; Robinson, Bowman, & Kertzman, 1995; Schall, Morel, King, & Bullier, 1995; Steinmetz, Connor, Constantinidis, & McLaughlin, 1994). Microstimulation of the FEF usually evokes eye movements (Robinson & Fuchs, 1969), but can also facilitate performance in attentional tasks (e.g. Moore & Fallah, 2001, 2004). This suggests a substantial overlap of brain areas involved in the control of eye movements and spatial attention, and neuroimaging studies with human participants have found converging evidence for this assumption (Astafiev et al., 2003; Beauchamp, Petit, Ellmore, Ingeholm, & Haxby, 2001; Corbetta, 1998; Nobre, Gitelman, Dias, & Mesulam, 2000a; Perry & Zeki, 2000). Further support for the hypothesis that an overlapping network of areas is involved in the control of eye movement and spatial attention was obtained in recent event-related brain potential (ERP) studies which found similar electrophysiological correlates of covert saccade preparation and covert shifts of attention (Eimer, Van Velzen, Gherri, & Press, 2007; Van der Lubbe, Neggers, Verleger, & Kenemans, 2006;

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Van der Stigchel, Heslenfeld, & Theeuwes, 2006; Wauschkuhn et al., 2008;).

Such links between eye movement preparation and the attentional selection of perceptual objects are explicitly predicted by the premotor theory of attention, which postulates that processes involved in the control of selective spatial attention and of spatially directed motor responses are implemented by common neural substrates (Rizzolatti, 1983; Rizzolatti & Camarda, 1987; Rizzolatti, Riggio, & Sheliga, 1994). When these shared control structures are activated to direct action toward a specific location in space, they will also direct spatial attention to that location. Covert shifts of spatial attention occur whenever such motor programs are activated, even if the response is not overtly executed (Rizzolatti, Riggio, Dascola, & Umiltà, 1987). Although this theory was originally formulated to explain links between attention and eye movements, it was successively generalized to include different types of movements. The anatomical organization of the brain suggests the presence of several parieto-frontal circuits (e.g. Fadiga, Fogassi, Gallese, & Rizzolatti, 2000; Luppino & Rizzolatti, 2000; Matelli & Luppino, 2001; Rizzolatti, Luppino, & Matelli, 1998) that are responsible for sensorimotor transformations, each dedicated to a specific movement (e.g. saccadic eye movements, reaching or grasping movements).

Support for the premotor theory of attention comes from behavioural studies where participants had to prepare and execute a goal-directed motor response (a saccade or a manual reaching movement) towards a target location on the left or right side, and to detect or identify a visual target that was randomly presented in close proximity to the movement target location or at a different position in the visual field. Performance was better for visual events at the target location for an upcoming eye movement (Deubel & Schneider, 1996, 2003; Hoffman & Subramaniam, 1995; Kowler, Anderson, Doshier, & Blaser, 1995) or manual response (Deubel & Schneider, 2003, 2004; Deubel, Schneider, & Paprotta, 1998; Tipper, Lortie, & Baylis, 1992), as would be expected if response preparation triggers attentional shifts towards response target locations (see also Kitadono & Humphreys, 2007, 2009, for recent neuropsychological evidence that response preparation toward the left or right side affects the pattern of spatial deficits in extinction and neglect). This was also demonstrated in recent ERP studies where participants prepared a left or right saccade (e.g. Eimer et al., 2007) or a left or right manual movement (e.g. Baldauf & Deubel, 2009; Eimer & Van Velzen, 2006; Eimer, Van Velzen, Gherri, & Press, 2006), and task-irrelevant visual probe stimuli were presented prior to response execution. Visual N1 components were enhanced for probes that appeared close to the movement target location, and these effects were similar to the effects previously observed as a result of covert shifts of spatial attention (e.g., Eason, 1981; Eimer, 1994; Mangun & Hillyard, 1991).

According to the premotor theory of attention, shifts of attention are an immediate and inevitable consequence of spatially directed response preparation. This hypothesis is supported by behavioural experiments where participants had to prepare a saccade or reaching movement to the left or right side, and to simultaneously shift their attention to a peripheral location in preparation for an upcoming visual discrimination task. Visual discrimination performance was consistently better when the target locations for the motor and attention tasks coincided, relative to a condition when they were in opposite hemifields (Deubel & Schneider, 1996, 2003; Deubel et al., 1998; Hoffman & Subramaniam, 1995; Kowler et al., 1995; Shepherd, Findlay, & Hockey, 1986), as would be expected if response preparation and selective attention are linked in an obligatory fashion.

However, there is also some evidence which suggests that such links between response preparation and attention are not entirely unaffected by top-down strategic factors. Kowler et al. (1995, Exp.

4) investigated how performance is affected by prioritizing either the speed of saccadic responses or the accuracy of perceptual discriminations via instructions. They found that attention can to some degree be directed away from saccade target locations with little or no costs for saccade latencies, indicating that there may be some degree of independence between these two domains. More recently, Montagnini and Castet (2007) studied whether advance information about the likely location of a perceptual target can modulate the effects of saccade preparation on perceptual discrimination. In their experiments, saccade target location was indicated by a cue, while targets for a visual orientation discrimination task were either presented at the saccade target location or in the opposite hemifield. In some blocks, visual targets appeared at the saccade target location on 75% of all trials, and on the opposite side on the remaining 25%, while in other blocks, these probabilities were reversed. If links between saccade preparation and attention were completely mandatory, perceptual performance benefits for stimuli at saccade target locations should be unaffected by this probability manipulation. However, these benefits were in fact much larger in blocks where perceptual targets were more likely to appear at saccade target locations. This suggests that some component of spatial attention may be independent of saccade preparation, and can be directed away from the target location for an upcoming saccade towards the expected location of a perceptual target. In summary, previous studies that compared behavioural performance when the target locations for a motor and an attentional task either coincided or were on opposite sides have not yet conclusively answered the question whether response preparation and spatial attention are linked in a mandatory fashion or are at least partially independent. The present study is the first to address this issue by using ERP markers of attention. Given their good temporal resolution, ERPs can provide new insights into how response preparation affects the distribution of attention in visual space and the attentional processing of visual stimuli. For example, attentional modulations of early sensory-specific visual ERP components such as the P1 and N1 are interpreted as reflecting the spatially selective processing of visual stimuli at early sensory-perceptual stages (e.g., Mangun & Hillyard, 1991). A demonstration that such ERP effects are attenuated or even abolished under conditions where the target locations for the attentional task and a concurrent motor task are on opposite sides would not only provide new evidence that links between spatial attention and response preparation are obligatory, but would also show that such obligatory links affect early perceptual stages of visual processing.

If the mechanisms involved in spatial attention and response preparation are inevitably linked, it should be impossible to direct visual attention to one side while simultaneously preparing a manual response or eye movement on the opposite side. In contrast, if such links are optional, perceptual and response selection processes may be decoupled if this is required by the specific demands of an experimental task. These two hypotheses were tested in an experiment where participants had to shift their attention to the left or right side (attention task), and to simultaneously prepare a finger lift with their left or right hand (motor task), as indicated by cues presented at the start of each trial. On half of all trials, cues instructed participants to prepare a movement with one hand and to direct attention to the side where this hand was located (same side condition). On the other half of trials, the cued direction of an attentional shift and the cued response hand were in different hemifields (opposite sides condition). Cue stimuli (S1) were followed after a 1400 ms interval by a second stimulus (S2). On one third of all trials, S2 was a Go signal presented at fixation (the letter 'G'), indicating that the motor task had to be executed with the cued hand. On all other trials, S2 was a peripheral visual stimulus (a brief illumination of an LED) that was presented on the left or right side close to the left or right hand (see Fig. 1). Participants had to

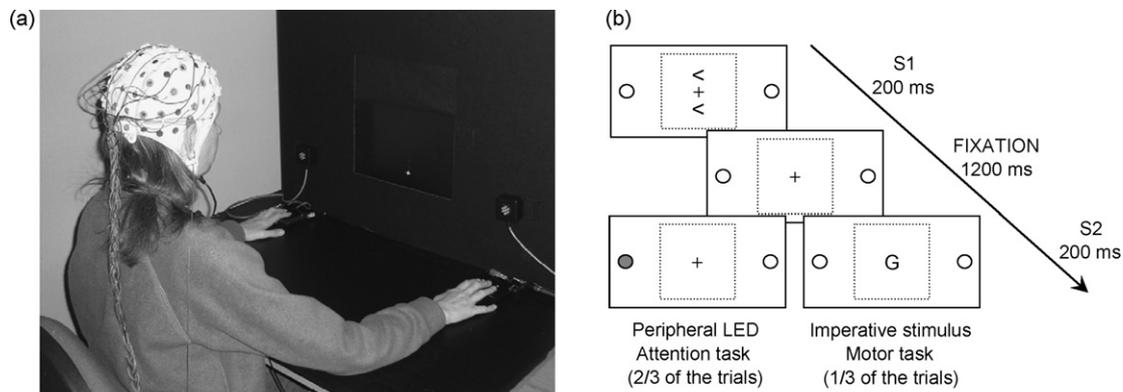


Fig. 1. (A) Stimulus set-up used in this study. Participants were seated in front of a black cardboard. The monitor was positioned behind the panel and was visible through a hole in the cardboard. The centrally presented cue (S1) and S2 for the motor task (go stimulus, the letter 'G') were shown on the monitor, while the peripheral S2 for the attention task (target and non-target visual stimuli) was presented via one of two LED ensembles mounted on the panel. Participants' hands were positioned on the left and right side, aligned with the left and right LED, with their index fingers placed on two infra-red response keys used to collect RTs for the motor task. Vocal responses for the attention task were recorded via a head-mounted microphone. (B) Schematic illustration of the time course of events on single trials in the attention and motor tasks. Circles on the left and right represent LEDs, and dashed squares represent the computer screen.

detect and respond to infrequent targets ('gap' stimuli) when these appeared on the side that was cued for the attention task, but could ignore peripheral visual stimuli when they were presented on the opposite uncued side.

In contrast to most previous behavioural studies of links between attention and response preparation, which investigated how preparing goal-directed manual reaching movements or saccades affects visual discrimination performance (see above), the manual response required in the present experiment was a simple finger lift, which required the selection of the left or right hand, but no additional specification of a movement goal location in visual space. Previous ERP research (e.g., Eimer & Van Velzen, 2006) has demonstrated that under these conditions, visual attention shifts towards the task-relevant hand are still triggered during covert manual response preparation. Given its simplicity, the motor task imposed only minimal demands on response programming. For the concurrent attention task, a target–non-target discrimination was only required when peripheral stimuli were presented on the cued side, while stimuli on the opposite side could be completely ignored, in order to ensure that participants had a strong incentive to fully focus visual-spatial attention on the cued side. This combination of a very simple spatial motor task and an attentional task that encouraged a strong attentional focus on one side was chosen to maximize the chances of obtaining evidence for optional, rather than mandatory, effects of manual response preparation on spatial attention. The critical question was how the preparation of a left or right manual response would affect the spatial selection of target locations for the attention task (which were located near to the left or right hand) in the same side and opposite sides conditions. If links between manual response preparation and spatial attention are obligatory, preparing a manual response on the side opposite to the direction of a cued attentional shift should disrupt attentional processes, resulting in performance costs in the attention task in the opposite sides condition relative to the same side condition, as well as in systematic differences in ERP markers of spatial attention between these two task conditions. If these links are merely optional, at least for the case of simple manual responses, performance in the attention task, and ERP correlates of spatially selective attentional processing, should be very similar in both tasks.

Two sets of ERP analyses were conducted to identify differences in attentional processing between the same side and opposite sides conditions. First, ERPs triggered during the S1–S2 interval were measured for cues instructing participants to direct attention to

the left versus right side, separately for the same side and opposite sides condition. Shifts of spatial attention are known to be associated with lateralised ERP components that can be observed in the cue–target interval of attentional cueing tasks (e.g., Harter, Miller, Price, LaLonde, & Keyes, 1989; Hopf & Mangun, 2000; Nobre, Sebestyen, & Miniussi, 2000b; Yamaguchi, Tsuchiya, & Kobayashi, 1994). Between 300 and 600 ms after cue onset, a negative deflection contralateral to the cued attentional shift is triggered at anterior electrodes (anterior directing attention negativity, ADAN), and is followed by a relative positivity over posterior scalp sites contralateral to the cued side (late directing attention positivity, LDAP). These two components are supposed to reflect brain activity within frontal and posterior areas of the fronto-parietal attentional control network. They have also been observed during saccade and manual response preparation (Eimer & Van Velzen, 2006; Eimer, Forster, Van Velzen, & Prabhu, 2005; Eimer et al., 2006, 2007; Mathews, Dean, & Sterr, 2006; Praamstra, Boutsen, & Humphreys, 2005; Van der Lubbe et al., 2000; Wauschkuhn, Wascher, & Verleger, 1997; see also Gherri, Van Velzen, & Eimer, 2007, 2009), in line with the hypothesis that attention shifts are triggered during response programming. Given these previous findings, ADAN and LDAP components should also be elicited in the same side condition where the spatial parameters for attention and response selection were congruent. The critical new question was whether these components would also be triggered during cued attentional shifts in the opposite sides condition where a manual response was simultaneously prepared on the other side. If links between spatial attention and response preparation are mandatory, response preparation should interfere with attentional orienting in this condition, resulting in attenuated or possibly even entirely absent ADAN and LDAP components.

The second analysis focused on ERPs to lateral visual non-target stimuli (S2), and compared ERPs for stimuli on the side that was cued for the attention task, and on the opposite unattended side. In the same side condition, attentional modulations of visual ERP components similar to those observed in earlier studies of visual-spatial attention (e.g., Mangun & Hillyard, 1991) should be observed, indicating that attention was focused on the cued side. The critical question was whether such attentional modulations would remain to be present in the opposite sides condition. If links between attention and action are optional, so that spatial attention and movement preparation can be directed to opposite locations without mutual interference when required by task instructions, attentional modulations of ERPs to lateral visual stimuli should be similar in the same

and opposite sides conditions. In contrast, if links between attention and action are mandatory and cannot be spatially dissociated, spatially specific attentional ERP modulations should be reduced or possibly even entirely absent in the opposite sides condition.

2. Method

2.1. Participants

Fourteen paid volunteers took part in the experiment. Four were excluded because of poor fixation in the S1–S2 interval (see below), and 10 participants remained in the sample (5 females and 5 males; 23–34 years old; average age: 27.7 years). All were right-handed and had normal or corrected-to-normal vision. The experiment was performed in compliance with relevant institutional guidelines, in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki, and was approved by the Birkbeck School of Psychology ethics committee.

2.2. Stimuli and procedure

Subjects were seated in a dimly lit sound attenuated cabin facing a black cardboard panel (60 × 90 cm) at a viewing distance of 60 cm. A 20 × 20 cm hole located in the centre of the panel allowed participants to see the computer monitor placed behind it (see Fig. 1). Two LED ensembles were mounted on the panel. They were located 30 cm to the left and right of the centre of the panel and were horizontally aligned with the centre of the screen at an angle of about 30° below eye level. These LED ensembles consisted of six segments arranged in a circle plus one central segment. The angular size of each LED was 0.65°, the diameter of the circle was 2.4°. Participants' hands were positioned on the left and right side, with index fingers located 30 cm to the left and right of the body midline over two infra-red response keys. The position of the hands was vertically aligned with the LEDs position.

Each trial started with the presentation of a visual cue (S1) consisting of two arrows ('<' or '>'), one presented 0.5° above and one 0.5° below the fixation cross (200 ms duration). The direction of the top arrow indicated the relevant side (left or right) for the attention task, and the direction of the bottom arrow indicated the relevant side (left or right) for the motor task. Arrow cues pointed to the same side (same side condition) or to opposite sides (opposite sides condition) on half of all trials, respectively. Each cue was followed after a 1200 ms interval by a second visual stimulus (S2). In one third of all trials, S2 was a visual Go stimulus for the motor task (the letter 'G') replacing the central fixation cross at the screen centre for 200 ms. In the remaining two thirds of trials, S2 was a peripheral visual stimulus consisting of a 200 ms illumination of one of the two LED ensembles. These stimuli were either continuous or contained a 50 ms gap that started 75 ms after stimulus onset.

Participants' task during the S1–S2 interval was to maintain central fixation, to shift their attention to the side indicated by the top arrow, and to simultaneously prepare to lift the finger that was indicated by the bottom arrow. When the letter 'G' was presented (motor task), they had to lift the index finger of the cued hand as fast as possible. When a peripheral visual stimulus was presented instead (attention task), had to respond vocally by saying 'yes' whenever a gap (target) stimulus was presented on the attended side. No vocal response was required to continuous (non-target) stimuli on the attended side, and to all visual stimuli on the unattended side, which could be completely ignored. For the motor task, manual reaction times (RTs) were measured via an infra-red response system consisting of a transmitter and receiver LED located on either side of the middle segment of the left and right index fingers in the resting position. A response was registered when an index finger was lifted, allowing the light beam of the transmitter LED to reach the receiver LED. For the attention task, voice onset times were measured with a voice key.

Twelve blocks of 72 trials each were run. On 24 trials per block, the Go stimulus for the motor task was presented as S2, which was preceded with equal probability by one of the four cue types (both arrows pointing to the left or right side; top arrow pointing to the left and bottom arrow to the right, or vice versa). On 48 trials per block, a single peripheral visual stimulus was presented as S2. On 24 trials, this stimulus appeared on the side cued for the attention task, and thus required a target–non-target discrimination. Four gap targets and 20 non-targets were presented on the attended side in every block. In the remaining 24 trials, peripheral stimuli (four gap and 20 non-gap stimuli) were presented on the side uncued for the attention task, and could thus be ignored. These trial probabilities were chosen to ensure that participants had to execute of the cued manual response and to perform an attentional target–non-target discrimination on the cued side equally often in each block. Prior the start of the experiment, each participant completed one training block that was identical to the subsequent experimental blocks.

2.3. EEG recording and data analyses

The EEG was DC-recorded with a lowpass of 40 Hz and a digitization rate of 500 Hz from 23 Ag–AgCl electrodes (Fpz, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3, Pz, P4, P8, PO7, PO8 and Oz) relative to a left earlobe reference. EEG was digitally re-referenced to the average of the left and right earlobe. Horizontal eye movements (HEOG) were measured bipolarly from a pair of electrodes placed at the outer canthi of the eyes. All electrode impedances were kept below 5 kΩ.

Trials with eyeblinks (voltage at Fpz exceeding ±60 μV), horizontal eye movements (voltage at HEOG exceeding ±30 μV), or other artefacts (voltage at any site exceeding ±80 μV) were excluded prior to data analysis, as were trials with response errors. The average rate of excluded trials was 28% across all participants. To detect small systematic deviations of eye position, which would indicate residual tendencies to move the eyes towards the location cued for the attention task, averaged HEOG waveform obtained in the 1000 ms interval following cue onset in response to cues directing attention to the left versus right side (separately for the same side and different sides condition) were examined for each participant. Four showed residual HEOG deviations exceeding ±3.5 μV and were excluded from further analyses.

Statistical analyses were conducted on the basis of ERP mean amplitudes obtained within predefined measurement windows. Separate analyses were run for ERPs elicited by cues (S1) and by peripheral visual non-targets (S2). ERPs following central cues were averaged relative to a 100 ms pre-cue baseline for the 1000 ms following cue onset. Separate averages were computed for all four different types of cues (attention and motor cues both left or both right; attention cue left and motor cue right, or vice versa), collapsed all different types of S2. ERP mean amplitudes were analysed with repeated measures ANOVAs, and separate analyses were conducted for lateral anterior and posterior electrode sites. These analyses included the factors condition (same side vs. opposite sides indicated by the attention and the motor cues), laterality (electrode ipsilateral vs. contralateral to the side indicated by the attention cue), electrode site (F7/8 vs. F3/4 vs. FC5/6, for the anterior analysis; PO7/8 vs. P3/4 vs. P7/8, for the posterior analysis), and recording hemisphere (left vs. right). In these analyses, the presence of anterior and posterior lateralised ERP components (ADAN, LDAP) will be reflected by significant main effects of the factor laterality. As in our earlier studies (e.g. Eimer et al., 2005, 2007), these analyses were based on mean amplitudes obtained within two successive post-cue latency windows between 350 and 550 ms (where the ADAN was previously observed) and between 600 and 900 ms (where the LDAP component was found).

ERPs triggered by peripheral visual non-target stimuli (S2) were computed relative to a 100 ms pre-S2 baseline for 400 ms after S2 onset. Separate averages were computed for all combinations of condition (same vs. opposite sides), attended side (left vs. right) and stimulus location (left vs. right). Mean amplitudes were computed within latency windows centred on the peak amplitudes of visual P1 and N1 components (110–140 ms post-stimulus and 150–190 ms post-stimulus, respectively), and for a longer-latency post-stimulus window (250–350 ms). These mean amplitude values were analysed with repeated measures ANOVAs, separately for midline electrodes (Fz, Cz, Pz), and for lateral anterior (F7/8, F3/4, FC5/6), central (C3/4, T7/8, CP5/6), and posterior sites (PO7/8, P3/4, P7/8). Analyses included the factors condition (same vs. opposite sides), spatial attention (stimulus presented on the attended vs. unattended side), stimulus side (left vs. right), electrode site (defined as above) and hemisphere (left vs. right, for lateral electrodes only). Only effects and interactions that involve the experimental factors of interest are reported, excluding ERP effects due trivially to stimulus laterality.

For the motor task, RTs for correct manual responses and error rates were analysed in separate repeated measures ANOVA for the factors condition (same side vs. opposite sides) and response hand (left vs. right). For the attention task, vocal RTs to targets on the cued side and error rates were analysed for the factors condition and stimulus side (left vs. right). For all analyses, Greenhouse–Geisser adjustments to the degrees of freedom were applied where appropriate.

3. Results

3.1. Behavioural performance

3.1.1. Motor task

Correct manual responses were faster in the same side condition as compared to the opposite sides condition (564 ms vs. 618 ms; $F(1,9) = 10.9, p < 0.009$). Right-hand responses were faster than left-hand responses (571 ms vs. 610 ms; $F(1,9) = 10.5, p < 0.010$), but there was no interaction between condition and hand ($F(1,9) < 1$). Trials with manual RTs faster than 200 ms or slower than 1200 ms (0.2% and 0.9% of all trials, respectively) were excluded from this analysis. Choice errors (responses with the uncued hand) occurred more frequently in the opposite sides condition than in the same side condition (4.2% vs. 1.8%; $F(1,9) = 12.2, p < 0.007$). Participants failed to respond on 1.8% of all Go trials.

3.1.2. Attention task

Vocal RTs to target stimuli on the cued side were faster in the same side condition than in the opposite sides condition (831 ms vs. 889 ms; $F(1,9) = 9.5, p < 0.013$). There was no main effect of target side ($F(1,9) < 1$), and no significant interaction between condition and target side ($F(1,9) = 3.5, p = 0.094$). Trials where vocal responses to cued targets were slower than 1200 ms (3.7% of these trials)

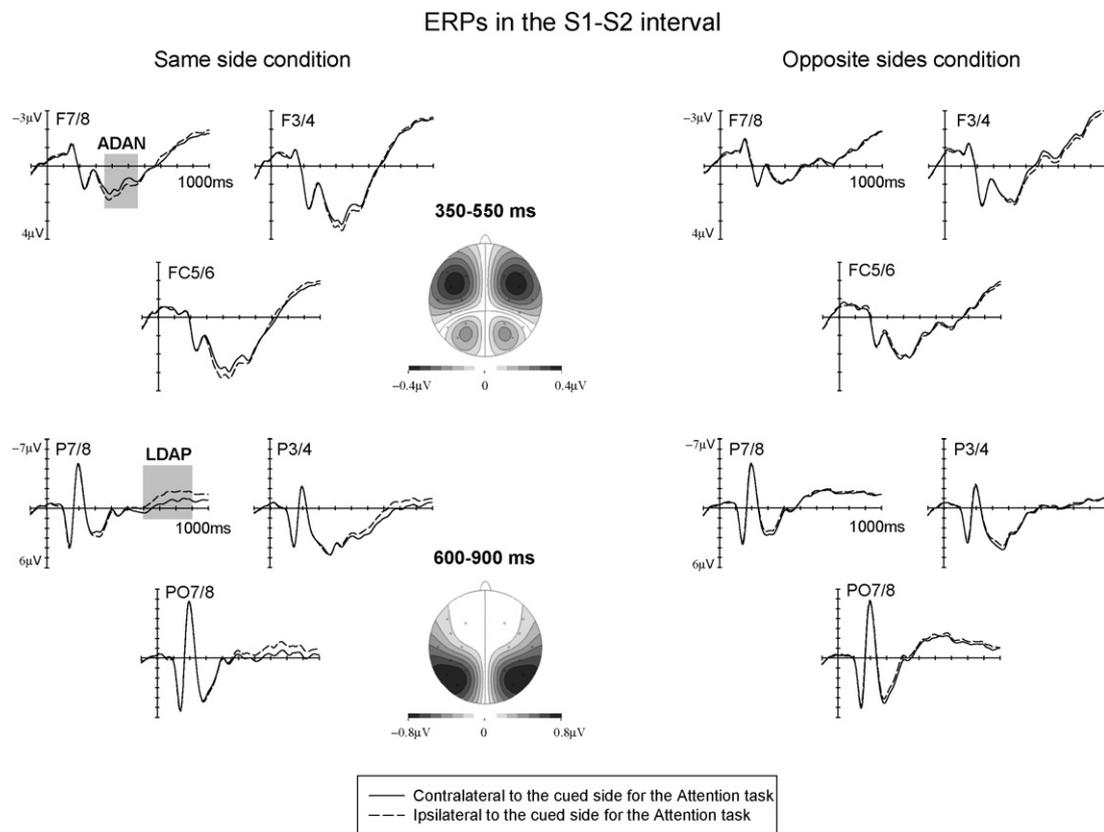


Fig. 2. Grand-averaged ERPs elicited in the 1000 ms interval following cue onset at lateral anterior and posterior electrode pairs ipsilateral (dashed lines) and contralateral (solid lines) to the cued side for the attention task. In the same side condition (left panels) the cued side for the attention task corresponded to the cued side for the motor task. In the opposite sides condition (right panels) the cued side for the attention task corresponded to the uncued side for the motor task and vice versa. The measurement windows used to compute ADAN (350–550 ms after cue onset) and LDAP components (600–900 ms after cue onset) are marked with boxes. The scalp distribution of the ADAN and LDAP components in the same side condition are shown in topographic maps that represent differences between brain activity observed over hemisphere ipsi- and contralateral to the cued side for the attention task. They were constructed by spherical splines interpolation (see Perrin, Pernier, Bertrand, & Echallier, 1989) after mirroring the difference waveforms to obtain symmetrical but inverse amplitude values for both hemispheres. Amplitudes range between -0.4 and $0.4 \mu\text{V}$ for the 350–550 ms interval and between -0.8 and $0.8 \mu\text{V}$ for the 600–900 ms interval.

were excluded from this analysis. False alarms to targets (gap stimuli) presented on the uncued side occurred more frequently in the opposite sides condition than in the same side condition (7.3% vs. 1.7%; $F(1,9) = 7.1, p < 0.026$). Participants failed to respond to targets on the cued side on 6.8% of these trials, and the false alarm rate to peripheral non-targets was less than 1%.

3.2. Lateralised ERP components in the S1–S2 interval

Fig. 2 shows ERPs elicited in the 1000 ms following cue onset at lateral anterior and posterior electrodes ipsilateral and contralateral to the side of a cued attention shift, separately for the same side condition (left panels) and the opposite sides condition (right panels). In the same side condition, an anterior directing attention negativity (ADAN) emerged between 350 and 500 ms after cue onset at anterior electrode pairs, and was followed by the posterior late directing attention positivity (LDAP). To visualize the scalp distribution of these ADAN and LDAP component in the same side condition, Fig. 2 includes topographic maps of the difference between ipsilateral and contralateral brain activity, plotted separately for the 350–550 ms post-cue interval (where the ADAN was triggered at anterior electrode sites), and for the 600–900 ms post-cue time window (where the posterior LDAP was present). In marked contrast to the same side condition, no ADAN and LDAP components seemed to be present in the opposite sides condition (Fig. 2, right panels).

These informal observations were confirmed by statistical analyses. In the 350–550 ms post-cue time interval, a main effect of laterality ($F(1,9) = 6.4, p < 0.032$), reflecting the presence of the

ADAN, was accompanied by the laterality \times condition interaction ($F(1,9) = 5.5, p < 0.044$). Follow-up analyses conducted separately for both conditions revealed the presence of a significant ADAN in the same side condition ($F(1,9) = 42.8, p < 0.001$). In contrast, no significant effect of laterality was observed in the opposite sides condition ($F(1,9) < 1$). In the 600–900 ms interval, the presence of the LDAP was reflected by a main effect of laterality at lateral posterior electrode sites ($F(1,9) = 16.2, p < 0.003$). Again, an interaction between condition and laterality was observed ($F(1,9) = 17.4, p < 0.002$). Follow-up analyses confirmed the presence of a reliable LDAP in the same side condition ($F(1,9) = 37.6, p < 0.001$), whereas no significant effect of laterality was observed in the opposite side condition ($F(1,9) = 1.3, p < 0.29$). No reliable main effects of laterality, or interactions between laterality and condition were observed in the 350–550 ms time window at lateral posterior electrodes, or in the 600–900 ms time window at lateral anterior electrodes. In addition to these lateralised ERP modulations, there were also significant main effects of condition during the 350–550 ms interval at anterior electrodes ($F(1,9) = 23.6, p < 0.001$), and during the 600–900 ms time window at posterior sites ($F(1,9) = 5.2, p < 0.05$), as ERPs in the opposite sides condition were generally more negative than ERPs in the same side condition (see Fig. 2).

3.3. ERPs elicited in response to peripheral visual non-target stimuli

Fig. 3 shows visual ERPs triggered by peripheral visual non-targets in the 400 ms after S2 onset in the same side condition

ERPs elicited by visual non target stimuli

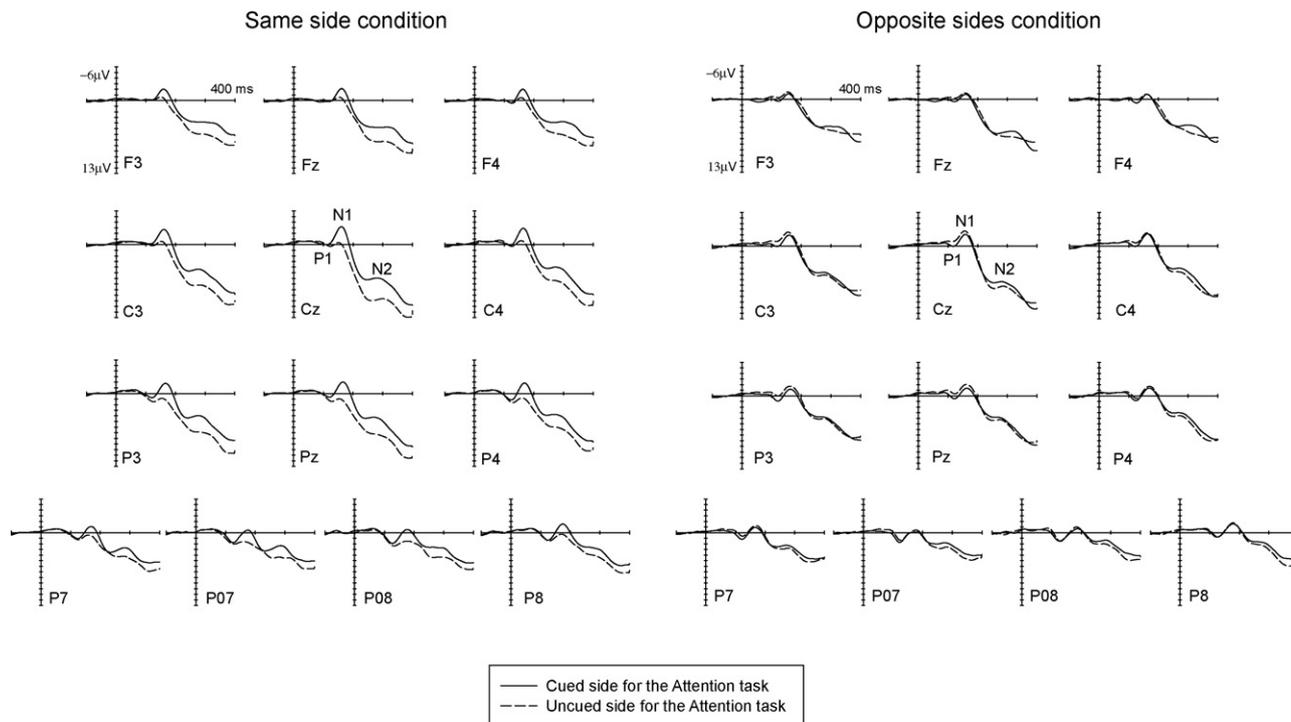


Fig. 3. Grand-averaged visual ERPs elicited by peripheral visual non-target stimuli delivered 1400 ms after cue onset, shown separately for the same side condition (left panels) and the opposite sides condition (right panels). Solid lines show ERPs triggered by visual stimuli presented on the cued side for the attention task (which was the cued side for the motor task in the same side condition and the uncued side for the motor task in the opposite sides condition), while dashed lines show ERPs elicited by visual stimuli presented on the uncued side for the attention task (which was the uncued side for the motor task in the same side condition and the cued side for the motor task in the opposite sides condition).

(left panels) and the opposite sides condition (right panels), shown separately for stimuli presented on the side that was cued for the attention task, and stimuli on the opposite unattended side. In the same side condition, visual stimuli presented on the attended side were close to the cued response hand for the motor task. In the opposite sides condition, the cued response hand was located close to visual stimuli on the opposite uncued side. Attentional enhancements of N1 amplitudes and a subsequent sustained attentional negativity were present in the same side condition (Fig. 3, left panel). In contrast, no attentional N1 modulation, and a strongly reduced later sustained negativity was observed in the opposite sides condition (Fig. 3, right panel).

No significant effects of spatial attention (all $F(1,9) < 2.2$, all $p > 0.175$) or spatial attention \times condition interactions (all $F(1,9) < 3.2$, all $p > 0.1$) were observed for the P1 time window (110–140 ms after S2 onset) at any of the electrode sites. In contrast, main effects of spatial attention were present in the N1 measurement window (150–190 ms post-stimulus) at central and posterior electrodes (all $F(1,9) > 8.1$, all $p < 0.019$). Critically, significant condition \times spatial attention interactions were present at all electrode sites (all $F(1,9) > 11.9$, all $p < 0.007$), demonstrating that the side of the cued motor response had a strong impact on attentional N1 modulations. Follow-up analyses conducted separately for both conditions confirmed that N1 components were reliably larger in response to attended visual stimuli at all electrode sites in the same side condition (all $F(1,9) > 10.1$, all $p < 0.011$), whereas no such effects were present in the opposite sides condition (all $F(1,9) < 1$). Although significant spatial attention \times electrode site interactions were observed in the same side condition at all lateral anterior, central, and posterior electrodes, as well as at midline sites (all $F(2,18) > 9.3$, all $p < 0.007$), follow-up analyses conducted separately

for individual electrodes confirmed that spatial attention effects in this condition were reliable at all recording sites (all $F(1,9) > 5.4$, all $p < 0.045$).

In the subsequent longer-latency analysis window (250–350 ms post-stimulus), main effects of spatial attention were obtained at anterior, central, midline, and posterior electrode sites (all $F(1,9) > 6.0$, all $p < 0.037$), indicative of a sustained attentional negativity in this time range (see Fig. 3). Similar to the N1 time window, interactions between condition and spatial attention were found at central, midline and posterior electrodes (all $F(1,9) > 5.0$, all $p < 0.05$), again reflecting the impact of manual response preparation on attentional ERP modulations. Follow-up analyses conducted separately for the two conditions confirmed reliable spatial attention effects in the same side condition at all electrode sites (all $F(1,9) > 8.6$, all $p < 0.017$). In contrast, even though Fig. 3 suggests a small sustained attentional negativity in the opposite sides condition, there were no reliable attention effects at any electrode site in this condition (all $F(1,9) < 2.2$, all $p > 0.18$). Significant spatial attention \times electrode site interactions were present in the same side condition at lateral anterior, central, and posterior electrodes (all $F(2,18) > 6.8$, all $p < 0.021$), but follow-up analyses conducted separately for individual electrodes confirmed that spatial attention effects in this condition were reliable at all recording sites (all $F(1,9) > 6.8$, all $p < 0.028$).

4. Discussion

Previous research has shown that the mechanisms involved in the attentional selection of perceptual events and of motor responses are functionally linked, and are implemented by partially overlapping brain systems. The present experiment investigated

whether such links are mandatory or merely optional by studying how the side of manual response preparation affects the concurrent attentional selection of visual stimuli in the left or right hemifield. Participants were cued to prepare a left or right finger lift while simultaneously shifting their visual attention to the left or right side. Cues were followed by imperative stimuli that required the execution of the prepared hand movement (motor task), or by a peripheral visual stimulus that required a target–non-target discrimination when it was presented on the attended side (attention task). In half of all trials, the same side was relevant for the motor and attention task, while in the other half, cues directed attention and action to opposite sides.

Behavioural performance in the attention and motor tasks was worse in the opposite sides as compared to the same side condition, with slower RTs and higher error rates on trials where attention and response preparation were spatially dissociated in both tasks. This is in line with previous behavioural studies (Deubel et al., 1998; Hoffman & Subramaniam, 1995; Kowler et al., 1995; Shepherd et al., 1986) that demonstrated inferior discrimination performance for visual stimuli that appeared contralateral to a current manual or eye movement target location, as compared to stimuli that coincided with a planned action. Whereas participants had to execute both the attention and the motor task on each trial in these studies, only one of these tasks had to be performed in the present experiment, thus eliminating dual-task interference effects on response execution. In spite of this fact, performance in the attention and the motor task was still impaired in the opposite sides condition relative to the same side condition, in line with the existence of strong links between spatial attention and spatially directed manual response preparation.

The ERP results obtained in this experiment provide new information about the nature of these links, and indicate that they may be obligatory rather than merely optional. In the same side condition, where the side cued for the attention task coincided with the side cued for the motor task, the predicted ERP correlates of visual-spatial attention were obtained. In the cue-target interval, lateralised ERP components sensitive to the direction of a cued attentional shift (ADAN, LDAP) were clearly present, and similar in terms of their latencies and topographies to the components observed in previous ERP studies of cued spatial attention (e.g., Harter et al., 1989; Hopf & Mangun, 2000; Yamaguchi et al., 1994). In addition, subsequent peripheral visual non-target stimuli on the attended side triggered larger N1 components and a longer-latency sustained attentional negativity, again analogous to previous ERP investigations of cued visual-spatial attention (e.g., Eimer, 1994; Mangun & Hillyard, 1991). These observations confirm that in the same side condition, attention was directed to the side signalled by the cue, which resulted in spatially selective enhanced processing of visual stimuli that were presented on this side, relative to visual events on the opposite unattended side.

The critical new question was whether similar attentional ERP effects would also be observed in the opposite sides condition, where participants prepared a manual response contralateral to the side cued for the attention task. If spatial links between manual response preparation and attention are *optional*, it should be possible to direct attention and action to different locations in space when task instructions explicitly require them to be spatially decoupled. In this case, lateralised ERP components in the cue-target interval associated with the orienting of attention, and subsequent attentional modulations of ERPs to lateral visual events at attended versus unattended locations should be similar in the same side and in the opposite sides condition. In contrast, if spatial links between manual response preparation and spatial attention are *mandatory*, it should be difficult if not impossible to direct attention to one side while simultaneously preparing a motor response on the other side, and this should be reflected by systematic differ-

ences in attentional ERP effects between the same side and opposite sides condition (see Eimer, 1999, for an ERP study that applied an analogous logic to the study of crossmodal links in spatial attention). The ERP results observed in the opposite sides condition provide clear-cut support for mandatory links between response preparation and attention. In the cue-target interval, no ADAN and LDAP components were triggered at all, in marked contrast to the results observed for the same side condition (Fig. 2). In addition, no attentional enhancements of visual N1 components were present for peripheral visual non-target stimuli in the opposite sides condition, and no reliable sustained attentional negativity was elicited, which again differs markedly from the pattern of results observed in the same side condition (Fig. 3). The observation that the side where a manual response was prepared had a systematic impact on attentional modulations of the N1 component elicited between 150 and 190 ms after stimulus onset provides strong evidence that response preparation can affect the spatially selective processing of visual stimuli at relatively early sensory-perceptual stages.

The absence of ADAN and LDAP components in the opposite sides condition suggests that no shifts of spatial attention towards the side cued for the attention task were triggered at all on trials where participants had to concurrently prepare a manual response on the opposite side. Alternatively, it is possible that shifts of spatial attention in opposite directions were triggered simultaneously by the cues for the attention and for the motor task, resulting in lateralised ADAN and LDAP components of opposite polarity that cancelled each other out (see below). In either case, the absence of ADAN and LDAP components in the opposite sides condition strongly suggests that shifts of attention towards the side relevant for the attention task were severely disrupted when a manual response was concurrently prepared on the opposite side, as would be expected if attention and response preparation were linked in a mandatory fashion. This conclusion is further supported by the absence of any attentional modulations of ERPs to peripheral visual non-target stimuli in the opposite sides condition, demonstrating that the spatially selective visual processing enhancements observed in the same side condition were eliminated when a movement was simultaneously prepared on the opposite side of space.

It should be noted that the effects of spatial attention observed in this study, as well as the modulation of these effects by manual response preparation reflect differences of visual-perceptual processing between attended and unattended visual hemifields. Such differences can only provide only relatively coarse measures of the distribution of spatial attention and of response preparation effects on attentional processing. It would therefore be important to investigate in future studies with combined behavioural and ERP measures how the preparation of manual responses or eye movements modulates the focus of spatial attention for different locations within the same hemifield.

Overall, the ERP results obtained in this study provide unequivocal evidence that shifts of visuo-spatial attention towards cued task-relevant locations are disrupted by the concurrent preparation of a movement directed to the opposite side of space. It is remarkable that even the preparation of an elementary movement such as a finger lift appears to interfere with the control of endogenous spatial attention up to the point that ERP markers of selective attentional processes were effectively eliminated. As mentioned above, these effects of manual response preparation on attention can be interpreted in two different ways. On the one hand, the cues for the motor and the attention task may both have independently triggered shifts of attention, which cancelled each other out in the opposite sides condition. According to the premotor theory of attention (Rizzolatti et al., 1994), activation of each brain circuit responsible for a specific sensorimotor transformation (e.g. for eye movement, for hand movement etc.) will direct both action and attention in space. Given the strict func-

tional association between eye movement and visual attention, covert visuo-spatial attention shifts are assumed to be linked to the activation of oculomotor programs. It is thus conceivable that two distinct sensorimotor circuits were activated in the present experiment, one for eye movements and one for hand movements, eliciting independent shifts of attention. In this case, ERP correlates of leftward versus rightward attentional shifts and subsequent spatially selective attentional processing would cancel each other out in the opposite sides condition. An alternative possibility is that a single domain-general sensorimotor circuit is responsible for determining the spatial parameters for manual responses and attention shifts. In this case, it should not be possible to simultaneously activate spatially incongruent locations for the attention and motor task, and no shifts of attention should have been elicited at all in the opposite sides condition.

Even though these two alternative scenarios make slightly different assumptions about the nature of the sensorimotor circuits involved in the control of selective attention and action, both assume strong and mandatory links between attention and response preparation. The current results provide new evidence for this hypothesis by demonstrating that the preparation of a simple manual response on one side severely disrupts the attentional selection of task-relevant visual stimuli on the other side. The fact that attention and action cannot be spatially dissociated even when this is required by task instructions clearly indicates that the links underlying these domains are not merely optional, and points to the existence of a unitary sensorimotor system that controls the selection of spatial response parameters as well as the attentional selection of perceptual objects.

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