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Shifts of attention in the early blind: An ERP study of attentional control processes in the absence of visual spatial information

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Abstract

To investigate the role of visual spatial information in the control of spatial attention, event-related brain potentials (ERPs) were recorded during a tactile attention task for a group of totally blind participants who were either congenitally blind or had lost vision during infancy, and for an age-matched, sighted control group who performed the task in the dark. Participants had to shift attention to the left or right hand (as indicated by an auditory cue presented at the start of each trial) in order to detect infrequent tactile targets delivered to this hand. Effects of tactile attention on the processing of tactile events, as reflected by attentional modulations of somatosensory ERPs to tactile stimuli, were very similar for early blind and sighted participants, suggesting that the capacity to selectively process tactile information from one hand versus the other does not differ systematically between the blind and the sighted. ERPs measured during the cue–target interval revealed an anterior directing attention negativity (ADAN) that was present for the early blind group as well as for the sighted control group. In contrast, the subsequent posterior late direction attention negativity (LDAP) was absent in both groups. These results suggest that these two components reflect functionally distinct attentional control mechanisms which differ in their dependence on the availability of visually coded representations of external space.

Keywords: Attention; Blindness; Control; Touch; Event-related brain potential

1. Introduction

Covert shifts of spatial attention can affect the perceptual processing of stimuli that are located within the current focus of attention. Evidence for such attentional modulations of sensory processing has been provided by event-related brain potential (ERP) studies, which have demonstrated that amplitudes of early modality-specific ERP components are enhanced when visual (e.g., Mangun & Hillyard, 1991), auditory (e.g., Näätänen, 1982) or tactile (e.g., Michie, Bearpark, Crawford, & Glue, 1987) stimuli are presented at attended relative to unattended locations. In contrast, the covert attentional control processes that are elicited in anticipation of task-relevant stimuli at specific locations, and which are responsible for spatially specific effects of attention, have only recently become the object of experimental investigation. Such control processes can be studied by using fMRI or ERP measures of brain activity in response to attentional cues that direct attention to one side versus the other, prior to the presentation of any sensory events at attended versus unattended locations (see Corbetta & Shulman, 2002, for a review of fMRI evidence for attentional control circuits).

While most ERP studies have examined attentional control processes triggered during covert anticipatory shifts of visual spatial attention (e.g., Harter, Miller, Price, LaLonde, & Keyes, 1989; Yamaguchi, Tsuchiya, & Kobayashi, 1994; Hopf & Mangun, 2000; Nobre, Sebestyen, & Miniussi, 2000), some recent studies have now begun to look for ERP correlates of covert attentional orienting towards the anticipated side of relevant auditory or tactile events (Eimer, Van Velzen, & Driver, 2002; Eimer, Forster, & Van Velzen, 2003a; Eimer, Van Velzen, Forster, & Driver, 2003b; Eimer, Forster, Fieger, & Harbich, 2004; Eimer & Van Velzen, 2002). These experiments have uncovered two lateralised ERP components that are elicited during the cue–target interval and which are sensitive to the

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direction of a cued attentional shift. An enhanced negativity at frontal electrodes contralateral to the side of attentional shifts between 300 and 500 ms after cue onset ('anterior directing attention negativity', ADAN) was followed by an enhanced contralateral positivity at posterior electrodes ('late directing attention positivity', LDAP), which emerged during later phases of the cue–target interval. Interestingly, these effects were not just triggered during shifts of visual attention, but also when attention was directed towards anticipated task-relevant auditory or tactile events (e.g., Eimer et al., 2002).[1]

The functional interpretation of such lateralised ERP components that are elicited during covert attention shifts is currently under debate. Based on the observation that these components are very similar during attentional shifts towards task-relevant visual, auditory or tactile events, we have previously suggested (Eimer & Driver, 2001; Eimer et al., 2002) that they reflect the activity of multimodal attentional control processes, which determine the spatial parameters of attentional shifts in a supramodal fashion, regardless of sensory modality (see also Farah, Wong, Monheit, & Morrow, 1989, for similar arguments). While the ADAN may reflect processes within a multimodal 'anterior attention system' (Posner & Petersen, 1990), the posterior LDAP might be linked to the activation of posterior parietal areas, which are known to be involved both in the orienting of spatial attention (e.g., LaBerge, 1995) and in the integration of information from different sense modalities (e.g., Andersen, Snyder, Bradley, & Xing, 1997). In contrast, others (e.g., Harter et al., 1989) have argued that the posterior LDAP component reflects the spatially selective activation of modality-specific visual areas in anticipation of task-relevant visual events. This hypothesis might appear inconsistent with recent observations that this component is elicited not only when attention is allocated to the expected location of visual stimuli, but also during shifts of tactile or auditory attention (Eimer et al., 2002, 2003a; Eimer & Van Velzen, 2002; see also Green, Teder-Sälerjärvi, & McDonald, 2005), since there is no obvious reason to assume that visual areas should be selectively activated in anticipation of auditory or tactile events. However, if one assumes that the control of attentional shifts is generally dominated by visual spatial information, even when other modalities are task-relevant, the possibility that ADAN and/or LDAP might predominantly reflect visual attentional control becomes more plausible. Vision provides superior spatial acuity relative to hearing or touch, thus allowing for more precise tuning of spatial attention. In view of this, it could also be used to control shifts of attention to anticipated locations of auditory or tactile events. If visual information was used to guide the spatial selection of auditory or tactile stimuli, lateralised ERP components elicited during attentional shifts towards anticipated tactile or auditory events might primarily reflect shifts of attention within visual space, rather than the activity of a genuinely multimodal attentional control system.

On a more general level, the question under debate is which spatial reference frames are used when shifts of attention are programmed and executed. Attentional orienting might be based, primarily or exclusively, on visually mediated representations of external space, even when modalities other than vision are currently task-relevant. Alternatively, the control of spatial attention might be based on multiple frames of reference, including coordinates of visually represented external space, body-centred space, somatotopic space, or, in the case of genuinely supramodal attentional control, amodal spatial coordinates. Thus, it is clearly important to investigate whether the lateralised ERP components that are triggered during cued shifts of spatial attention (ADAN and LDAP) reflect attentional control processes that are based on a single shared spatial frame of reference, or whether these components are linked to separable control mechanisms that differ in terms of their spatial coordinates.

Some initial evidence for the latter hypothesis comes from previous ERP studies demonstrating dissociations between the ADAN and LDAP. In one experiment (Eimer et al., 2003a) participants directed attention to their left versus right hand (as indicated by a central precue on every trial), and ERPs were recorded during the cue–target interval under conditions where hands were either uncrossed or crossed. This manipulation of hand posture had a marked effect on the ADAN component. When considered in terms of the direction of attentional shifts in external space, the ADAN was delayed and reversed polarity with crossed relative to uncrossed hands, suggesting that the attentional control processes reflected by the ADAN may be primarily based on somatotopic spatial coordinates, and not on visually defined external space. In contrast, when considered in terms of external space, the LDAP component was completely unaffected by crossing the hands, thus indicating that the control processes reflected by this component operate primarily on the basis of representations of visually mediated external space. Another study (Eimer et al., 2004) supported these conclusions by demonstrating that when participants were cued to direct attention to the left or right hand for a tactile task, the distance between hands in external space modulated the LDAP (which was more pronounced when hands were wide apart), but left the ADAN component entirely unaffected.

One way to investigate the hypothesis that the LDAP (but not the ADAN) reflects the visually mediated control of attention shifts is to eliminate continuously available ambient visible sources of information about task-relevant stimulus locations. When visual spatial information about the visible positions of hands and arms, or the visible location of tactile and auditory stimulators, is eliminated either by blindfolding participants or by running an experiment in the dark, and visual cues are no longer available to aid and possibly dominate the spatial selection of tactile or auditory events, lateralised ERP components linked to attentional control based on coordinates of visual space should be absent, whereas components that are based on other non-visual spatial reference frames should remain unaffected.

[1] An earlier negative deflection at posterior electrodes contralateral to the direction of the induced attentional shift ('early directing attention negativity'), which was observed in some ERP studies (Harter et al., 1989; Nobre et al., 2000; Yamaguchi et al., 1994) is likely to be a lateralised visual response triggered by non-symmetrical visual cues (such as left-pointing and right-pointing arrows), rather than a genuine reflection of covert attentional control processes (see Van Velzen and Eimer, 2003, for supportive evidence).