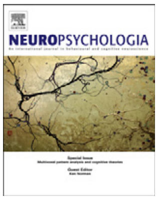
Neuropsychologia 50 (2012) 2303–2316

Contents lists available at SciVerse ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia



Crossing the hands disrupts tactile spatial attention but not motor attention: Evidence from event-related potentials

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ARTICLE INFO

Keywords:
Event-related brain potentials
Reference frames
Spatial attention
Unimanual movement preparation
Somatosensory processes

ABSTRACT

During covert shifts of tactile spatial attention both somatotopic and external reference frames are employed to encode hand location. When participants cross their hands these frames of references produce conflicting spatial codes which disrupt tactile attentional selectivity. Because attentional shifts are triggered not only in Attention tasks but also during covert movement preparation, the present study aimed at investigating the reference frame employed during such 'motor shifts of attention'. Event related brain potentials (ERPs) were recorded during a Motor task where a visual cue (S1) indicated the relevant hand for a manual movement prior to a tactile Go/Nogo stimulus (S2). For comparison, we ran a tactile Attention task where the same cue (S1) now indicated the relevant hand for a tactile discrimination (S2). Both tasks were performed under uncrossed and crossed hands conditions. In both Attention and Motor tasks similar lateralized components were observed following S1 presentation. Anterior and posterior ERP components indicative of covert attention shifts were exclusively guided by an external reference frame, while a later central negativity operated according to a somatotopic reference frame in both tasks. In the Motor task, this negativity reflected selective activation of the motor cortex in preparation for movement execution. In the Attention task, this component might reflect activity in the somatosensory cortex in preparation for the subsequent tactile discrimination. The presence of multiple and conflicting spatial codes resulted in disruption of tactile attentional selection in the Attention task where attentional modulations of tactile processing were delayed and attenuated with crossed hands as indicated by the analysis of ERPs elicited by S2. In contrast, attentional modulations of S2 processing in the Motor task were largely unaffected by the hand posture manipulation, suggesting that motor attention employs primarily one spatial coordinate system.

1. Introduction

Selective attention allows us to prioritize some stimuli over others. When, for example, the likely location of a forthcoming stimulus is known in advance, selective attention can be directed to the expected location allowing stimuli presented at that location (attended stimuli) to receive preferential processing relative to stimuli occurring at other locations (unattended stimuli). While most research has investigated the effects of directing attention to locations in our surroundings, a growing number of studies have now begun to unravel the behavioral effects and underlying brain mechanisms when orienting to one's own body. These studies have shown that spatial attention facilitates the speed and accuracy of responses to tactile stimuli when presented to the attended hand as compared to the unattended one (e.g., Sathian & Burton, 1991; Spence, Pavani, & Driver, 2000) and that it can lead to modulation of somatosensory ERPs at mid (i.e., P100 and N140 components) and longer latencies reflecting differential processing of stimuli at attended and unattended locations (e.g., Eimer & Forster, 2003; Forster & Eimer, 2004; García-Larrea, Lukaszewicz & Mauguire, 1995; Michie, Bearpark, Crawford & Glue, 1987; Van der Lubbe, Buitenweg, Boschker, Gerdes & Jongsma, 2011).

In cuing studies of endogenous tactile spatial attention, participants are required to encode the information delivered by a symbolic cue and to select the task relevant location on their own body accordingly, in order to process a forthcoming tactile stimulus. This spatial selection can be carried out according to multiple frames of reference. External frames of reference code the locations of tactile stimuli presented on the body surface relative to reference objects in the external environment. These

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http://dx.doi.org/10.1016/j.neuropsychologia.2012.05.034

external spatial codes are strictly dependent on the configuration or position of the body in external space. In contrast, anatomical reference frames encode the location of a tactile stimulus according to a somatotopic map where specific body locations are determined by the position of the stimulated cutaneous receptors on the skin and their representation on the cortical surface of the brain. Thus, anatomical codes are independent from the position of the body in external space. In principle, it is possible that either one of these reference frames or even both are used for the attentional selection of task-relevant locations on the body surface. This question has been investigated by asking participants to perform the same tactile Attention task under uncrossed and crossed hands conditions. External and anatomical codes are congruent when hands and arms are resting in their natural uncrossed position (i.e., left hand on the left side and right hand on the right side). In contrast, external and anatomical codes are incongruent when the hands and arms are crossed, because the left hand is now located on the right side of external space and vice versa. Typically, attentional modulations of somatosensory ERPs in response to tactile stimuli are delayed and attenuated with crossed as compared to uncrossed hands (Eardley & Van Velzen, 2011; Eimer, Cockburn, Smedley & Driver, 2001; Eimer, Forster & Van Velzen, 2003; Röder, Föcker, Hötting, & Spence, 2008). More specifically, attentional enhancements of the N140 component are typically absent, while later enhanced negativities are reduced with crossed than uncrossed hands (Eardley & Van Velzen, 2011; Eimer et al., 2001, 2003; Röder et al., 2008). The fact that spatial attention is disrupted with crossed hands indicates that both external and anatomical coordinates are involved in the spatial coding of tactile stimuli and that their conflicting spatial codes interfere with attentional selectivity.

Further support for the hypothesis that both external and anatomical frames of reference are employed to select relevant body locations in Attention tasks comes from ERP studies investigating the lateralized components measured in the interval between the onset of the symbolic cue and the subsequent target stimulus. Under uncrossed hands conditions, a negative deflection contralateral to the cued side was observed at anterior electrodes between 300 and 600 ms after cue onset (labeled 'anterior directing attention negativity', ADAN), and was followed by a relative positivity over posterior scalp sites contralateral to the cued side (late directing attention positivity, LDAP). The ADAN and LDAP components are usually interpreted as reflecting successive phases in the control of spatial orienting in anticipation of expected stimuli at cued locations (e.g., Eimer et al., 2003; Eimer, Forster, Fieger & Harbich, 2004; Eimer, Van Velzen & Driver, 2002). When participants performed the same Attention task with crossed hands, the anterior ADAN was delayed and characterized by a reversed polarity (Eardley & Van Velzen, 2011; Eimer et al., 2003). Because the cues indicated the side of space where the task-relevant hand was located (and not the relevant hand), the reversal of the ADAN in the crossed hands condition indicated that this component was elicited contralateral to the relevant hand rather than to the cued side of space, providing direct evidences that frontal areas responsible for the generation of this component operate according to an anatomical (somatotopic) frame of reference (Eardley & Van Velzen, 2011; Eimer et al., 2003). In contrast, little difference was found between the LDAP elicited in the tactile Attention task with uncrossed or crossed hands, suggesting that posterior processes indicated by the LDAP seem to be based on coordinates of external space (Eimer et al., 2003, 2004). These ERP findings indicate that both frames of reference are used by the orienting mechanisms that guide the attentional selection of a location on participants' body.

Shifts of attention able to modulate the processing of tactile stimuli can be observed not only in spatial Attention tasks, but also in purely Motor tasks, during the covert preparation of goal-directed motor responses. Behavioral studies have demonstrated superior performance for tactile events presented at intended saccade target locations, before the eyes begin to move (Rorden, Greene, Sasine, & Baylis, 2002; Juravle & Deubel, 2009). In addition, eye movement preparation enhances the perceptual processing of tactile stimuli presented at the destination of a saccadic eye movement, as indexed by the N140 component of the somatosensory event-related brain potential (Gherri & Eimer, 2008). A similar facilitation was found when participants were instructed to prepare a left or right manual movement (finger lift) and to detect tactile stimuli presented to the hand selected for the movement as compared to the opposite hand (Juravle & Deubel, 2009). Furthermore, the covert preparation of manual movements (Eimer, Forster, Van Velzen, & Prabhu, 2005; Forster & Eimer, 2007) resulted in spatially-specific modulations of early tactile processing. In these ERP studies a centrally presented symbolic cue instructed participants to prepare a finger lift with their left or right hand. Before movement execution (Go-Nogo stimulus presentation), a task irrelevant tactile probe was presented with equal probability to the left or right hand. N140 somatosensory ERP components elicited by these probes were enhanced when tactile stimuli were presented to the movement relevant hand as compared to ERPs elicited by stimuli to the opposite hand. The finding that spatially specific modulations of tactile processing were observed during covert movement preparation, even if participants had no incentive to direct their endogenous attention to the movement relevant hand, suggests that shifts of spatial attention are automatically elicited towards the movement-relevant hand during the preparation of a motor response (see also Gillmeister & Forster, 2012, for similar effects of hand movement preparation on tactile processing when the hands are located behind the back).

The observation that shifts of attention are triggered during movement preparation provides direct support for the premotor theory of attention (Rizzolatti, Riggio, & Sheliga, 1994). This theory postulates that the control of goal-directed movements and the control of spatial attention are closely linked, because they are implemented by shared brain circuits in the frontal and parietal lobes. More specifically, different brain circuits (pragmatic maps) are specialized for different types of movements (for eye movements, for hand movements etc.) and for different parts of space (Rizzolatti et al., 1994: Rizzolatti & Camarda, 1987). Shifts of attention are triggered whenever one of these pragmatic maps is activated but the planned movement is not overtly executed (Rizzolatti, Riggio, Dascola, & Umilta, 1987). Thus, spatial attention is the consequence of the activation of the same brain circuits that under different conditions would determine motor behavior.

The idea that a common network of cortical areas in the frontal and parietal lobes is involved in both spatial attention and movement preparation has received direct support from ERP studies in which the control mechanisms activated during covert shifts of attention and movement preparation were directly compared (e.g., Eimer, Van Velzen, Gherri & Press, 2007; Praamstra, Boutsen & Humphreys, 2005; Van der Lubbe, Neggers, Verleger & Kenemans, 2006). In these studies, participants were asked to covertly direct their attention (Attention task) or to covertly prepare a manual or a saccadic movement (Motor task) toward the side indicated by a cue presented at the beginning of each trial. Cue-locked ERP components were characterized by a similar pattern of activation over time with the anterior ADAN followed by the LDAP over posterior electrodes in both attention and Motor tasks, suggesting that not only similar brain areas were activated during these tasks but also that their temporal dynamics were very similar (Eimer et al., 2007; Mathews, Dean, & Sterr, 2006; Praamstra et al., 2005; Van der Lubbe et al., 2006).

Thus, consistent evidence indicates that largely overlapping cortical networks are activated during both covert shifts of spatial