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THE SPATIOTEMPORAL DYNAMICS OF EARLY ATTENTION PROCESSES: A HIGH-RESOLUTION ELECTROENCEPHALOGRAPHIC STUDY OF N2 SUBCOMPONENT SOURCES

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Abstract—The N2 subcomponents of event-related potentials are known to reflect early attentional processes. The anterior N2 may reflect conflict monitoring, whereas the posterior N2 may be involved in target detection. The aim of this study was to identify the brain areas involved in the generation of the N2 subcomponents, in order to define the spatiotemporal dynamics of these attentional processes. We recorded 128-channel electroencephalograms in 15 healthy controls performing a three-stimulus visual oddball task and identified standard-, distracter- and target-elicited N2 components. Individual N2 sources were localized using standardized-weighted-low-resolution-electromagnetic-tomography (swLORETA). Comparative analyses were performed with a non-parametric permutation technique. Common N2 generators were observed in the Brodmann area (BA) 24 of the anterior cingulate cortex (ACC). The posterior cingulate cortex and the central precuneus were more involved in distracter processing, whereas the anterior precuneus and BA 32 of the ACC were target-specific. In accordance with previous demonstration of the frontoparietal cortex's critical role in attentional processes, these new data shed light on the ACC's role in conflict monitoring and its interaction with other median and frontoparietal structures in early attentional processes.

Key words: swLORETA, cognitive event-related potentials, N2, attention, cognitive control, inhibition.

INTRODUCTION

Attention can be focused by relevant signals derived from task demands (i.e. target stimuli) or captured by salient properties of stimuli that are sometimes irrelevant for the task (i.e. distracter stimuli) (Kastner and Ungerleider, 2000). The attention processes were mostly investigated by late cognitive event-related potentials (ERPs), namely the P3. P3 subcomponents are thought to be generated by large fronto-parietal networks (Bledowski et al., 2004a,b; Bocquillon et al., 2011). Particularly, the dorsolateral prefrontal cortex (DLPF) is known to be involved in the generation of the P3 component, which reflects top–down processes as stimulus categorization and voluntary decision-making. The DLPF reportedly interacts with the anterior cingulate cortex (ACC) to fulfill this role (Devinsky et al., 1995; Barch et al., 2001). Although the ACC's functional role has been widely debated, the available evidence suggests that this structure is part of an executive attention supervisory system involved in the resolution of cognitive conflicts. The latter system may serve to evaluate the demand for cognitive control by monitoring the occurrence of conflict during information processing (Posner and Petersen, 1990; Braver et al., 2001). As suggested by the conflict-monitoring theory, the ACC's primary function may thus be to detect response conflict, whereas the DLPF cortex would implement top–down control of behavior (Barch et al., 2001), with the hypothesis that the ACC may play a role in an earlier time window. The ACC has indeed been identified as the main (but not the only one) putative generator of the N2 component of the ERP (see Table 1 for a review). N2 is the second, negative peak seen in the cognitive ERP. It usually occurs between 200 and 350 ms after a stimulus (Folstein and Van Petten, 2008) and was shown to be of value in monitoring processes such as cognitive control and inhibition (Donkers and Van Boxtel, 2004).

Several N2 subcomponents can be elicited by tasks requiring focused attention on stimuli, such as go/no-go or flanker tasks: a more anterior component with a frontocentral scalp distribution (also known as N2b) and a more posterior component (also called N2c)

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Abbreviations: ACC, anterior cingulate cortex; ANOVAs, analyses of variance; AP, anterior precuneus; BA, Brodmann area; CP, central precuneus; DLPF, dorsolateral prefrontal; EEG, electroencephalogram; EOG, electro-oculogram; ERN, error-related negativity; ERP, event-related potential; fMRI, functional magnetic resonance imaging; PCC, posterior cingulate cortex; RT, reaction time; swLORETA, standardized, weighted low-resolution electromagnetic tomography.

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Table 1. Identification or estimation of generators of N2 components (''no go'' N2, error-related negativity, novel-N2 and target N2) according to previous studies. Source localization methods are shown in bold, while other activation methods are given in italic type. BESA: brain electrical source analysis; (s)LORETA: (standard) low-resolution brain electromagnetic tomography; ICA: independent component analysis; SWARM: sLORETA-weighted accurate minimum norm method; er-fMRI: event-related functional magnetic resonance imaging; PET: positron emission tomography; EEG-fMRI: electroencephalography-functional magnetic resonance imaging.

Location	Investigational method	''no-go'' N200	Error-related negativity	Novel N200	Posterior target N200
Medial frontal lobe and anterior cingulate cortex	**Dipole modeling BESA**	**Van Veen and Carter (2002), Nieuwenhuis et al. (2003), Bekker et al. (2005), Jonkman et al. (2007), Ladouceur et al. (2007)**	**Dehaene et al. (1994), Dehaene (1996), Badgaiyan and Posner (1998), Holroyd et al. (1998), Nieuwenhuis et al. (2003), Ladouceur et al. (2007), Van Veen and Carter (2002)**		
	fMRI constrained BESA				**Crottaz-Herbette and Menon (2006)**
	Moving equivalent dipole		**Miltner et al. (2003)**		
	Minimum current estimates		**Helenius et al. (2010)**		
	LORETA	**Bokura et al. (2001)**			**Anderer et al. (2003)**
	sLORETA ICA	**Kropotov and Ponomarev (2009), Kropotov et al. (2011)**			
	SWARM	**Huster et al. (2010)**			**Huster et al. (2010)**
	er-fMRI	*Casey et al. (1997), Rubia et al. (1999, 2001), Braver et al. (2001), Menon et al. (2001)*	*Carter et al. (1998), Botvinick et al. (1999), Casey et al. (2000), Kiehl et al. (2000), Menon et al. (2001), Matthews et al. (2005), Chevrier et al. (2007)*	*Kiehl et al. (2001), Yamaguchi et al. (2004)*	*Braver et al. (2001), Kiehl et al. (2001), Yamaguchi et al. (2004), Crottaz-Herbette and Menon (2006)*
	PET	*Kawashima et al. (1996)*			
	lesion study		*Swick and Turken (2002), Stemmer et al. (2004)*		
	EEG/fMRI		*Debener et al. (2005)*		
Lateral frontal lobe superior, middle, inferior	**Dipole modeling BESA**				**Anllo-Vento et al. (1998)**
	Minimum current estimates		**Helenius et al. (2010)**		
	sLORETA ICA	**Kropotov and Ponomarev (2009), Kropotov et al. (2011)**			
	SWARM	**Huster et al. (2010)**			**Huster et al. (2010)**
	er-fMRI	*Konishi et al. (1999), Rubia et al. (1999, 2001), Menon et al. (2001), Chevrier et al. (2007), Matthews et al. (2005)*	*Carter et al. (1998), Kiehl et al. (2000)*	*Kirino et al. (2000), Kiehl et al. (2001), Yamaguchi et al. (2004)*	*Garavan et al. (1999), Kirino et al. (2000), Kiehl et al. (2001), Braver et al. (2001), Yamaguchi et al. (2004), Crottaz-Herbette and Menon (2006)*
	PET	*Kawashima et al. (1996)*			
Orbitofrontal	**LORETA**	**Casey et al. (1997), Bokura et al. (2001)**			
	er-fMRI		*Menon et al. (2001)*		
Prefrontal	Dipole modeling BESA		Ruchsow et al. (2002)		
	LORETA	Lavric et al. (2004)			Anderer et al. (2003)