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EEG dipole analysis of motor-priming foreperiod activity reveals separate sources for motor and spatial attention components

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Abstract

Objective: This study employed EEG source localisation procedures to study the contribution of motor preparatory and attentional processing to foreperiod activity in an S1–S2 motor priming task.
Methods: Behavioural and high-density event-related potential (ERP) data were recorded in an S1–S2 priming task where participants responded to S2 with a left or right-hand button press. S1 either provided information about response hand (informative) or ambiguous information (uninformative).
Results: Responses were significantly faster in informative trials compared with uninformative trials. Dipole source analysis of foreperiod lateralized ERPs revealed sources of motor preparatory activity in the dorsolateral premotor cortex (PMd) in line with previous work. In addition, two spatial attention components (ADAN, LDAP) were identified with generators in the PMd and occipitotemporal visual areas in the middle temporal (MT) region, respectively. Separation of motor-related and attentional PMd source locations was reliable along the rostral–caudal axis.
Conclusions: The presence of attentional components in a motor priming paradigm supports the premotor theory of attention which suggests a close link between attention and motor preparatory processes. Separation of components in the premotor cortex is in accord with a functional division of PMd into rostral (higher-order processing) and caudal (motor-related processing) areas as suggested by imaging work.
Significance: A prime for response preparation is a trigger for separate, but closely linked, attention-related activity in premotor areas.

Keywords: Event-related brain potentials; Source localisation; Movement preparation; LRP; ADAN; LDAP; BESA

1. Introduction

The S1–S2 motor priming paradigm (Rosenbaum and Kornblum, 1982) provides a framework for examining the experimental effects of prior warning that a particular response will shortly be required. S1 (prime) informs the participants about aspects of the upcoming movement (e.g. which hand to use) and S2 (response cue) subsequently cues the movement execution. Behaviourally, shorter reaction times (RT) are elicited in trials where the movement is correctly primed (valid trials) compared with incorrectly (invalid) or ambiguously primed trials (Rosenbaum and Kornblum, 1982). This RT advantage has been attributed in part to preparatory processing in cortical motor areas evidenced by event-related potential (ERP) (Leuthold and Jentzsch, 2002) and imaging studies (Dassonville et al., 1998; Deiber et al., 1996; Lee et al., 1999). More recently, lateralized ERP components typically associated with shifts in spatial attention have been found in response to an S1 (leftwards or rightwards pointing arrow) that primes for response with a particular hand (Eimer et al., 2005; Verleger et al., 2000; van der Lubbe et al., 2000). The presence of these components despite the absence of explicit attention shifts suggests that processes relating to attention and response preparation are closely linked. Here we used high-density EEG recorded in an S1–S2 motor priming task to study motor-related and attentional processing during the foreperiod.

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In the S1–S2 interval (the foreperiod) a rising cortical negativity is observed over centroparietal scalp locations. This was named the contingent negative variation (CNV) by Walter et al. (1964) to distinguish it from the similarly distributed readiness potential (RP) recorded prior to voluntary movements (Deecke et al., 1969). In addition to motor readiness, the CNV captures activity associated with stimulus processing and general expectancy as demonstrated by a clear CNV in an equivalent non-motor paradigm (Cui et al., 2000). The lateralized activity in the CNV can be calculated using the lateralized readiness potential (LRP) which takes advantage of the contralateral organization of the motor cortex to reveal activity associated with one particular response only. The LRP is calculated by subtracting ipsilateral from homologous contralateral sites in left and rightward trials and subsequently averaging subtracted waveforms (Coles, 1989). Dipole source analysis of the foreperiod LRP has revealed a lateral source anterior to the central sulcus interpreted as motor preparatory activity in the premotor cortex (PMC) (Leuthold and Jentzsch, 2002, 2001). This is in accord with imaging studies of motor preparation (Deiber et al., 1996), epicortical recordings (Matsumoto et al., 2003) and single-unit recordings in primates (Boussaoud, 2001).

The LRP calculation is not restricted to motor activity but reveals any lateralized activity associated with a left or rightward trial. As the term LRP is traditionally used to refer specifically to motor-related potentials, the generic term ERL (event-related lateralization) will hereafter be used. In studies where S1 covertly directs attention to the left or right hemifield, two ERL components have consistently been found (Eimer and Driver, 2001; Nobre et al., 2000; Praamstra et al., 2005). These components are referred to as ADAN (anterior directing-attention negativity) and LDAP (late directing-attention positivity). The ADAN is characterised by a frontocentral contralateral negativity ~300–600 ms post-S1 and the LDAP by an occipitotemporal contralateral positivity ~500–900 ms post-S1. Most recently, Praamstra et al. (2005) revealed sources for these components in the region of the lateral PMC (ADAN) and middle occipital gyrus (LDAP). The localisation of attentional ADAN activity in the premotor cortex, at first perhaps surprising, mirrors findings in imaging studies of spatial attention (Hopfinger et al., 2000; Rosen et al., 1999; Simon et al., 2002). These findings are consistent with the premotor theory of attention (Rizzolatti et al., 1987) which supposes that shared sensorimotor mechanisms underly shifts of attention and selection/programming of a motor response.

The ADAN and LDAP attentional ERP components have recently been observed in unimanual response tasks with central cues and no explicit shifts of attention (Eimer et al., 2005; Verleger et al., 2000). This presents an opportunity to utilise the Rosenbaum paradigm to separate the contribution of attentional and motor preparation activity to the foreperiod ERL within a single experiment. Unlike other imaging techniques, EEG provides the high temporal resolution required to distinguish activity in the millisecond range. The present study used dipole source analysis of high-density EEG to identify the time-course and source locations of attentional and motor preparatory ERL components.

2. Materials and methods

2.1. Subjects

Seven males and nine females (mean age 29.4, SD 9.9), all right-handed (mean handedness quotient 92.7, Oldfield, 1971), participated in a two-hour session. An hourly rate of £5 was paid for participation. The study had approval from the University of Surrey ethics committee and informed consent was taken prior to participation. All participants had normal or corrected-to-normal vision.

2.2. Experimental design

The study used a motor priming paradigm in which one of four prime stimuli (left ≪, right ≫, uninformative <> and no response ><) was followed by one of three response cues (left button press LH, right button press RH or no response NO). In the present study only the left, right and uninformative prime conditions were addressed. The left and right primes taken together are considered the informative condition. In the informative condition, the probability that the prime would correctly predict the upcoming response (valid trials) was 93% with invalid trials split evenly between the two alternative responses. The uninformative condition was not predictive and the chance of each response alternative occurring was equal (33%). The experiment was divided into eight blocks of 120 trials, which appeared in random order, observing the prime/response likelihoods as stated above. Stimulus presentation and experimental control were implemented using the Experimental Runtime System (ERTS) and EXKEY Logic (BeriSoft Cooperation; http://www.erts.de).

2.3. Stimuli

Primes consisted of two directional arrows and response cues of two letters (described above) displayed in white on a black background. Font size was controlled such that the two stimuli were the same size (1.15° wide by 0.92° tall). Participants sat at a viewing distance of 50 cm from a 19 in. screen. Stimuli were shown in the centre of the screen to prevent horizontal eye movements. Responses were executed with the left or right index finger, using the outer buttons of the standard EXKEY response pad.

2.4. Procedure

Data collection was conducted in an electrically shielded and sound attenuated room (2.5 × 3.5 m) that was dimly lit.