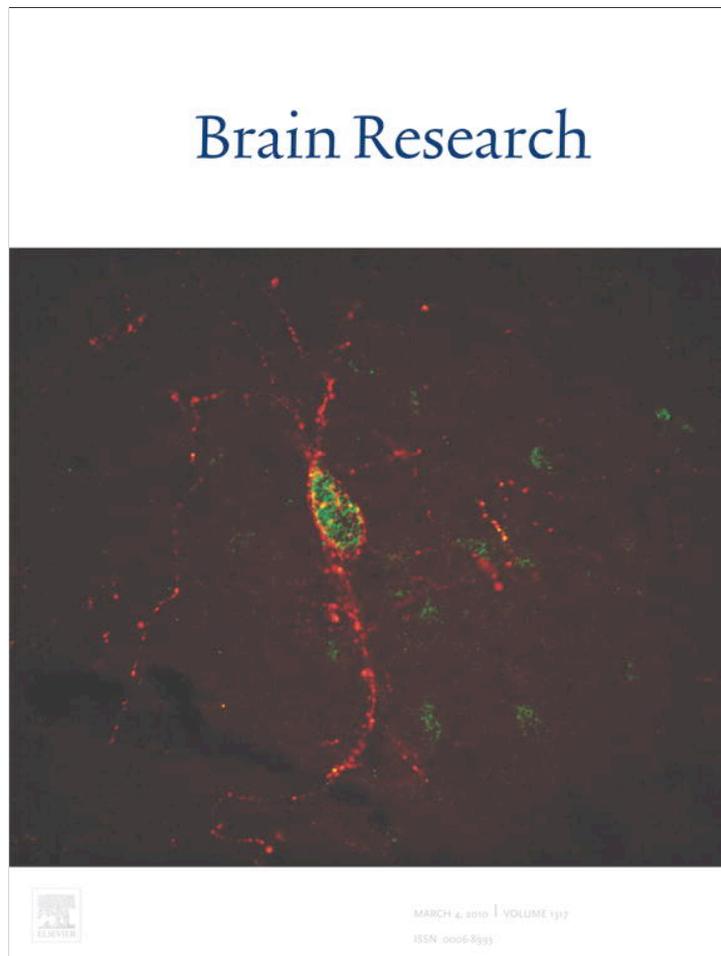


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RESEARCH

Research Report

An early parietal ERP component of the frontoparietal system: EDAN ≠ N2pc

Peter Praamstra^{a,b,*}, Dimitrios Kourtis^{a,c}

^aBehavioural Brain Sciences Centre, School of Psychology, University of Birmingham, UK

^bDepartment of Neurology, Queen Elizabeth Hospital, University of Birmingham, UK

^cDonders Institute for Brain, Cognition and Behaviour, Radboud University, Nijmegen, The Netherlands

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ABSTRACT

Directing spatial attention or manual response selection by means of arrow cues elicits a characteristic sequence of lateralized ERP components. Van Velzen and Eimer (2003) proposed that one of these components, the EDAN (early directing-attention negativity) is not related to the control of spatial attention but is instead an N2pc in disguise, related to the visual processing of arrow cues. While this proposal seems widely accepted, it has never been evaluated whether the hitherto not well-determined scalp distribution of the EDAN matches the well-established scalp distribution of the N2pc. This paper reviews evidence from earlier published work supporting a parietal distribution of the EDAN. This strongly argues against the proposed identification with the N2pc. The EDAN may instead reflect early parietal activity within the frontoparietal network, preceding the frontal activation represented in the anterior directing-attention negativity (ADAN).

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1. Introduction

Directing visual attention across space, in the context of attentional cuing tasks, is known to elicit several different lateralized ERP components in the interval between an attention-directing cue and a later presented target. Harter and co-workers (Harter et al., 1989) identified and labeled the EDAN (early directing-attention negativity) and LDAP (late directing-attention positivity) components. While the EDAN and LDAP both have a posterior scalp distribution, a frontally distributed lateralization, probably first observed by Eimer (1993) (see also Hopf and Mangun, 2000; Nobre et al., 2000), is now known as ADAN (anterior directing-attention negativity). In view of its latency and scalp distribution, and because cuing tasks often use arrows as attention-directing cues,

researchers have realized that the EDAN may be related not to the control of spatial attention, but instead due to physical differences between left- and right-pointing cues. Van Velzen and Eimer (2003) addressed this possibility and provided evidence that, while not due to physical differences per se, the EDAN may be related to visual selection of the arrow head. Selection of a part of a multi-element display evokes an N2pc component with a negative polarity over the hemisphere contralateral to the selected stimulus element. Because, however small an arrow is, its head will typically be in the hemifield to which the cue directs attention, the EDAN could reflect an N2pc in disguise. Van Velzen and Eimer (2003) evaluated this hypothesis by constructing left-right symmetrical arrow stimuli with the relevant arrow head either in the hemifield congruent to the indicated direction of

* Corresponding author. Behavioural Brain Sciences Centre, University of Birmingham, Birmingham B15 2TT, UK. Fax: +44 121 414 4897. E-mail address: p.praamstra@bham.ac.uk (P. Praamstra).

attention or in the incongruent field. They found a lateralization as a function of the arrow head location rather than the arrow head direction, supporting the proposed identity of EDAN and N2pc.

Although the identification of EDAN and N2pc seems widely accepted, the data are by no means conclusive. Firstly, the visuospatial selection between two arrow heads in Van Velzen and Eimer's (2003) experiment is not necessarily a process also occurring when a single arrow is presented as cue. Secondly, it has never been evaluated whether the hitherto not well-determined scalp distribution of the EDAN matches the well-established lateral occipital scalp distribution of the N2pc. A re-evaluation of the question whether the EDAN can be identified with the N2pc is not trivial. The EDAN has been suggested to reflect an early step in endogenous control processes that guide spatial selective attention in anticipation of an impending stimulus (Harter et al., 1989; Hopf and Mangun, 2000). The functional role of the N2pc, on the other hand, is the visual-attentional selection between multiple concurrent stimuli (Luck and Hillyard, 1994). EEG studies on the control of spatial attention would give up a potentially relevant marker of spatial attentional control if they adopted the practice, initiated by Van Velzen and Eimer (2003), of subtracting out early cue-induced lateralizations. Against this background, the present report reviews evidence from earlier work in which we found a parietal distribution of the EDAN, which is difficult to reconcile with the proposed identity of EDAN and N2pc.

2. Results

Reported results are confined to what is relevant here. Results relating to the original goal of the experiments are reported in Praamstra et al. (2009).

2.1. Component morphology and scalp distribution

Lateralized potentials of Experiment 1 are represented in Fig. 1. The waveforms on the left emphasize ADAN, LRP, EDAN and LDAP components, respectively, and were obtained by pooling the signals from four neighboring electrodes located at the scalp maximum of the respective components. Of main interest here is the EDAN, derived from electrode pairs P3/4, P5/6, PPO5h/6h, and CPP5h/6h. The EDAN was quantified in the time window 250–300 ms and differed from baseline in each of the conditions ($T's > 5.3$, $P's < 0.001$). As is clear from the figure, EDAN amplitude was not influenced by the physical differences between 1-, 2-, and 3-arrow cues ($F(1.5, 22.9) < 1$), providing an argument against the concern that the EDAN could be caused by the physical asymmetry inherent in the arrow form. By contrast, physical differences between the cue types did appear to have an effect at occipital sites in an earlier time window coincident with the visual N1 component, caused by more pronounced N1 amplitude asymmetry when the cue consisted of more arrows. This was confirmed by measurements taken at electrode pair PO7/8 in a time window of 160–185 ms ($F(1.8, 27.5) = 10.3$, $P < 0.001$) (see Fig. 1).

Scalp distributions of lateralized potentials in Experiment 2 were identical to those in Experiment 1, as evident from the

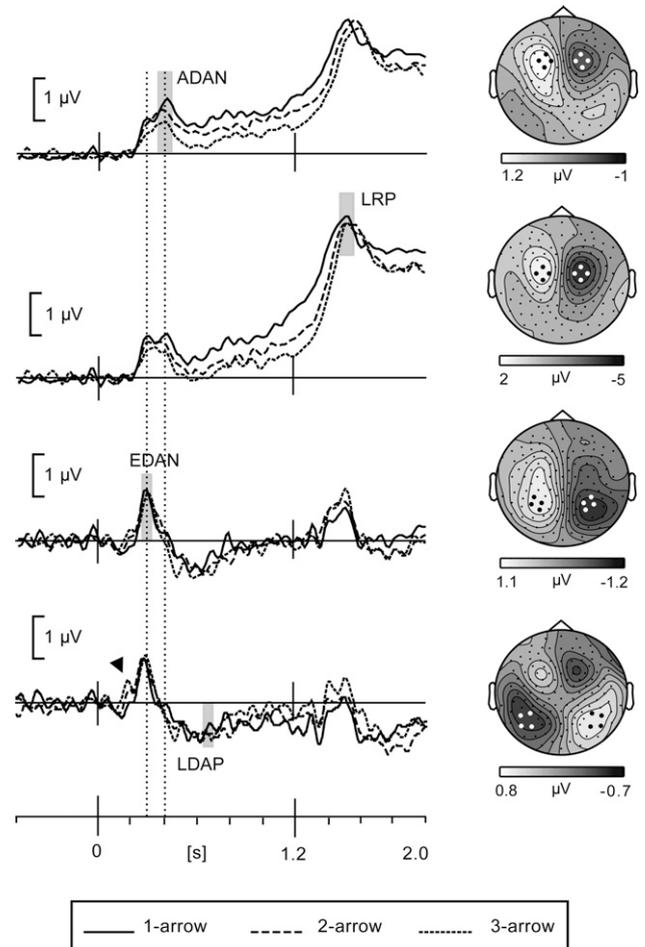


Fig. 1 – From top to bottom: lateralized potentials measured from frontal electrode group (ADAN), frontocentral electrode pool (LRP), parietal electrode pool (EDAN), and occipitoparietal electrodes (LDAP). The displayed waveforms are averaged across all participants of Experiment 1 and represent the mean activity across four electrodes, selected on the basis of the scalp topography of the component. The gray bars correspond to the latency of scalp topographies, which were produced by subtracting left and right hand movement conditions and based on data averaged across 1-, 2-, and 3-arrow conditions. Note the identical EDAN amplitude across conditions. The arrow head preceding the EDAN indicates a difference between conditions attributed to physical stimulus differences between conditions. The vertical dashed lines emphasize the overlap of EDAN with the ADAN. Note that the scalp topographies of the lateralized potentials are created by subtracting left- and right-hand movement conditions.

identical scalp maxima (see Fig. 2). The amplitude of the EDAN was significantly different from zero for each of the conditions ($T's > 6.4$, $P's < 0.001$). There was a tendency towards a lower amplitude for the 2-arrow-w condition compared to the 2-arrow-s and 3-arrow conditions, but this difference did not reach significance ($F(2.0, 29.4) = 3.16$, $P > 0.05$).

The scalp topographies of lateralized components in Figs. 1 and 2 are represented on the basis of a subtraction of left-

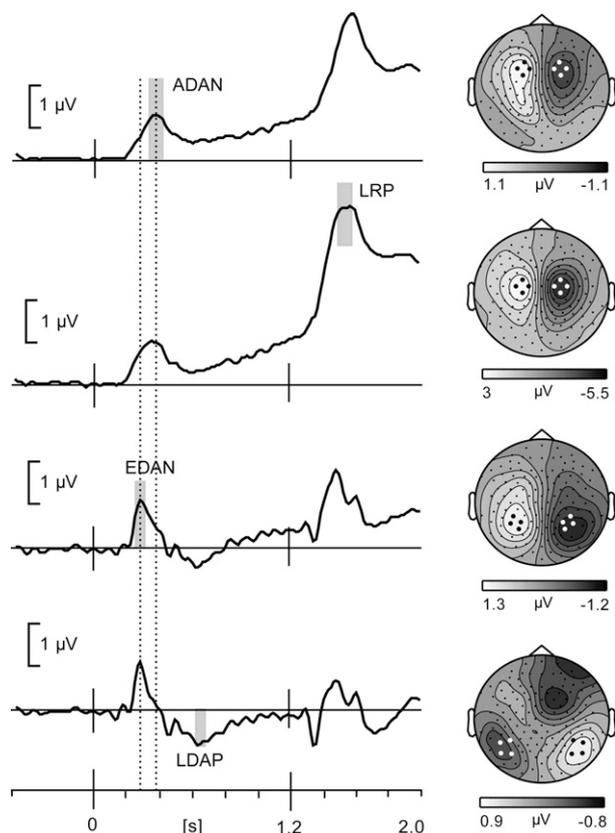


Fig. 2 – Same as **Fig. 1** for data of **Experiment 2**, collapsed across conditions. Note the identical scalp distributions compared to **Experiment 1**.

and right cue conditions. An advantage of this representation relative to the more common representation based on (polarity-inverted) duplication of lateralized potentials over both hemispheres (Praamstra et al., 1996), is that it enables an evaluation of interhemispheric differences in the contribution to the lateralized potentials (Oostenvelde et al., 2003). In terms of amplitude, left and right hemisphere make roughly equal contributions to the ADAN and EDAN, while the right hemisphere appears to contribute more than the left to the LRP at the time of the response. This paradoxical result is almost certainly due to the left motor cortex being involved in ipsi- as well as contralateral hand movements. In terms of distribution, there is a pleasing symmetry of the ADAN and LRP. There is some asymmetry of the EDAN, more so in Experiment 1 than in Experiment 2, perhaps due to the left hemisphere leading the right in an activation that moves from parietal to frontal areas. Judged from EDAN and ADAN peak latencies, there is a latency difference between parietal and frontal activation of ~ 100 ms. To have an objective measure of this latency difference, we measured peak latencies of EDAN and ADAN in the 1-arrow condition of Experiment 1 and in the 2-arrow-s condition of Experiment 2, i.e. the conditions with the highest ADAN amplitude. This produced (mean \pm SD) values of 276 ± 27 ms and 399 ± 41 ms (Experiment 1) and 274 ± 25 ms and 388 ± 42 ms (Experiment 2) for the EDAN and ADAN. Especially in the data of Experiment 1 the EDAN can be seen to partly overlap with the ADAN, a

feature also noted in earlier reports (Hopf and Mangun, 2000; Talsma et al., 2005). The ADAN shows a scalp maximum at electrode pairs FFC3h/4h, FC1/2, FC3/4, and FCC3h/4h while the LRP at peak latency has its maximum amplitude at more posterior sites CCP3h/4h, C1/2, C3/4, and FCC3h/4h. This difference in distribution along the anterior–posterior axis is consistent with their presumed generation in premotor and primary motor cortex.

2.2. Source reconstruction

Dipole source analysis was applied to the data of Experiment 2, collapsed over all conditions, separately for each cue side (left or right). Lateralized potentials were subsequently obtained by means of subtracting left-cue and right-cue data sets. Given the good symmetry of scalp distributions of EDAN, ADAN, and LDAP (Fig. 3), each of these components was modeled with a dipole pair constrained to symmetrical locations in left and right hemisphere (Praamstra et al., 1996). Given the opposite polarity of signals over left and right hemisphere, dipole source orientations were anti-symmetrical. The time windows in which the components were fitted were 250–325 ms (EDAN), 325–425 ms (ADAN), 550–700 ms (LDAP). Effects of modeling the components in isolation versus in the presence of sources for the other components were minimal, except for the LDAP, whose sources assumed a location near the supratemporal plane when the EDAN was not accounted for by parietal sources. The goodness-of-fit for the integral source model in the EDAN time window was 98%. Importantly, the fit changed very little (to 95%) when the LDAP sources were switched off, in spite of the fact that the latter sources, in the occipito-temporal cortex, showed a small deflection coincident with the EDAN. The fit was 95% in the ADAN time window and 89% in the time range of the LDAP. Across the entire window 250–700 ms, the goodness-of-fit was 93%.

The Talairach–Tournoux coordinates of the dipole source locations for the ADAN were $X=\pm 30$, $Y=-9$, $Z=43$, corresponding with an origin in the lateral premotor cortex. The EDAN sources were located at $X=\pm 22$, $Y=-72$, $Z=22$, in the parietal cortex (precuneus). Sources for the LDAP were located at $X=\pm 50$, $Y=-45$, $Z=-26$ at the ventral surface of the temporal lobe. The results from a dipole source reconstruction of the data of Experiment 1 were virtually identical, with sources localized to the same structures and model fit within a comparable range.

The dipole source reconstruction demonstrates that lateralized activity in the time window of the directing-attention potentials can be plausibly accounted for by the known components EDAN, ADAN, and LDAP. The analysis resolves the temporal overlap between these components, and renders it unlikely that there is significant overlap by an as yet unidentified source or component. The main value of the source analysis is spatial–temporal decomposition rather than localization of sources. It is nonetheless relevant to note that the movement execution-related LRP, modeled in the window 1400–1525 ms, provided an anatomical reference. Being the highest amplitude signal and known to originate in M1, it yielded sources exactly in the hand motor knob of the precentral gyrus ($X=\pm 30$, $Y=-24$, $Z=50$).

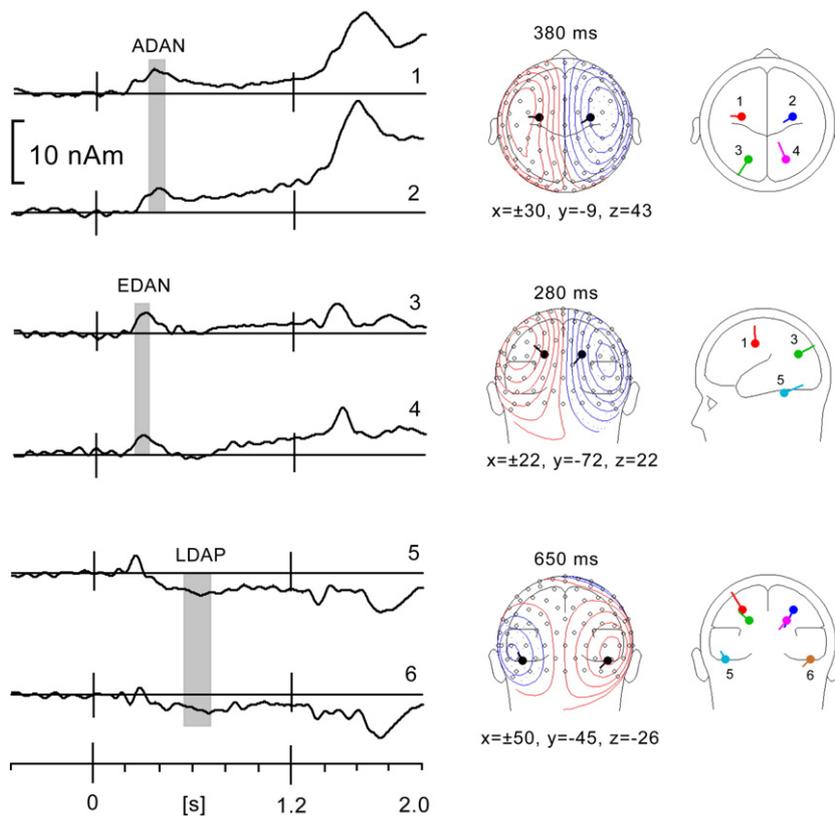


Fig. 3 – Dipole source waveforms, representing the time course of source activities, for ADAN, EDAN, and LDAP (left). Scalp distributions of these components at the indicated latencies, with superimposed dipoles (middle). Schematic head model with dipole locations (right). Isopotential lines are spaced at 0.2 μ V.

2.3. Review of N2pc scalp distribution

Since the here reported EDAN data were not collected with N2pc data for comparison, we reviewed the scalp distribution of the N2pc reported in 87 available publications between 1994 and 2009 (see Supplementary Material). The results are summarized in Table 1. They show that in 56/87 (64%) of studies electrodes PO7/8 or P7/8 showed the highest N2pc amplitude. This is consistent with the frequently cited occipitotemporal scalp distribution of this component. By

contrast, electrodes included in our EDAN electrode pool (P3/4, P5/6, CPP5h/6h, PPO5h/6h) were never identified as yielding the highest N2pc amplitude. One, or in one instance two electrodes of the EDAN pool, however, were included in N2pc electrode pools in 9/87 (10%) of studies. These pools broadly covered occipital, occipitotemporal, and occipitoparietal scalp, and even included electrodes PO7/8 and/or P7/8 in all but one report. Taken together, these data indicate that no N2pc scalp distributions have been reported that coincide with the EDAN distribution reported here.

Table 1 – Summary of N2pc scalp distribution.

N2pc of maximal amplitude at single electrode			N2pc of equal amplitude at 2 or 3 electrode sites		N2pc analysed by pooling waveforms from 3 to 6 electrodes
PO7/8	P7/8	PPO9h/10h PO3/4 PO5/6 O1/2	PO7/8,P7/8 PO7/8,PO3/4 P7/8,PO9/10 P7/8,PO5/6 P7/8,PO3/4	PO7/8,P7/8,O1/2 PO7/8,PO3/4,O1/2 P7/8,PO3/4,O1/2	PO7/8,P7/8,P5/6 P7/8,O1/2,P3/4 O1/2,PO5/6,P5/6 O1/2,P7/8,PO7/8,P3/4 O1/2,PO3h/4h,PO5h/6h,PPO3h/4h PO7/8,PO3h/4h,PO5h/6h,PPO5h/6h PO7/8,5/6,3/4,P7/8,5/6,3/4 PO7/8,PO3/4,O1/2,P7/8,P5/6
43	13	7	6	8	10

Summary of N2pc scalp distribution information in publications from 1994 to 2009. Numbers refer to number of publications (from a total of $n=87$). The highlighted electrodes in the third column are electrodes used to quantify the EDAN in the present paper. A list of the publications is available as Supplementary Material.

3. Discussion

The N2pc component has a well-established scalp distribution over occipitotemporal areas and has indeed its origin in the occipitotemporal cortex according to convergent evidence from EEG, MEG and fMRI (Hopf et al., 2000, 2002, 2004, 2006; Praamstra and Oostenveld, 2003).¹ The present data describe a parietal scalp distribution of the EDAN that distinguishes it from the N2pc. The non-identity of N2pc and EDAN scalp distributions argues against the proposed identification of the EDAN with the N2pc by Van Velzen and Eimer (2003), and suggests an interpretation of the EDAN as a component associated with executive control of spatial attention and motor intention by the frontoparietal network.

High-resolution sampling of the scalp distribution of the EDAN is vital to evaluate the claim of Van Velzen and Eimer (2003) that the EDAN is the same component as the N2pc. This is because their evidence is based on the use of ambiguous multi-element arrow head stimuli whose directional information can only be extracted by means of a visual selection operation already known to elicit the N2pc. Hence, their findings do not necessarily generalize to the processing of conventional arrow stimuli. The EDAN=N2pc position appears to be supported, however, by a recent study that failed to find an early posterior contralateral negativity following the spatial cue (Woodman et al., 2009). This was attributed to the use of central cues (letters) instead of inherently asymmetrical arrow cues, thus avoiding a cue configuration that might elicit an N2pc. While supporting the identity of EDAN and N2pc, the finding represents a null-result that might have a different explanation, a possibility that is underlined by the fact that no ADAN component was elicited either. Important in this context, in functional imaging studies the activation of the frontoparietal attention network by spatial cues is by no means dependent on the use of arrow cues (e.g., Giesbrecht et al., 2003).²

Our identification of a parietal origin of the EDAN is certainly not at odds with the earliest descriptions of its scalp distribution based on recordings with few electrodes (Harter et al., 1989; Yamaguchi et al., 1994) and some more recent studies with better spatial sampling (Hopf and Mangun, 2000; Talsma et al., 2005; Van der Lubbe et al., 2005). However, there are also studies reporting a more occipitotemporal distribution (Nobre et al., 2000; Van der Lubbe et al., 2006; Van der Stigchel et al., 2006; Wauschkuhn et al., 1997). Possible factors that may account for the differences between studies are (i) the generally low amplitude and low signal-to-noise

ratio of lateralized potentials, (ii) the susceptibility of lateralized potentials to misalignment of 'homologous' electrodes, distorting their distribution, (iii) attenuation of the EDAN by the LDAP. It is fair to say that the present data, in comparison to previous reports, show a very robust EDAN with a fairly symmetrical scalp distribution, both contributing to an optimal assessment of its distribution. In favor of the present data is also the fact that the more established ADAN and LRP components demonstrate, consistent across two experiments, a scalp distribution that agrees with current views on their origin in premotor and motor cortex, respectively.

A possible argument against our data having any bearing on the claimed identity of EDAN and N2pc is that they were obtained in a movement cuing task rather than an attentional cuing task. While the task difference must not be ignored, this is not a compelling argument. From the considerable body of published ADAN, LDAP and EDAN data to date, no consistent differences have emerged between data sets acquired in movement and spatial attention tasks. Accordingly, the 'attention-directing' components are regarded as associated with frontoparietal circuits involved in the deployment of spatial attention and spatial aspects of response selection (Eimer et al., 2005; Gherri et al., 2007, 2009; Kranczioch et al., 2009; Mathews et al., 2006; Praamstra et al., 2005; Verleger et al., 2000).³

The assumed association of lateralized attention-directing ERP components with the frontoparietal attention network, defined primarily by neuroimaging evidence (Corbetta and Shulman, 2002), does not imply that there is an exact match between components identified on the basis of functional-anatomy and ERP components. The frontocentral scalp distribution of the ADAN makes this component a plausible EEG correlate of the frontal activation within the frontoparietal system (Nobre et al., 2000; Praamstra et al., 2005; Verleger et al., 2000). However, there was thus far no candidate (lateralized) ERP component matching the parietal activation, although some investigators have attempted to assimilate the LDAP into this role (Eimer et al., 2002; Gherri et al., 2007; Macaluso et al., 2003; Van der Lubbe et al., 2006). This absence may be due to the fact that subtractions of attend-left and attend-right conditions subtract out spatially non-specific attentional control activity within the frontoparietal network, as argued in several recent studies (Grent-'t-Jong and Woldorff, 2007; McDonald and Green, 2008; Praamstra et al., 2005; Talsma et al., 2005). Comparing instead attend-left/right conditions against a neutral cue condition, some of these studies have indeed identified parietal activity in a time window preceding the ADAN, either in time-domain analyses (Praamstra et al., 2005; Talsma et al., 2005) or time-frequency analyses of oscillatory activity (Green and McDonald, 2008). The present data provide convergent evidence for parietal EEG

¹ We acknowledge that Hopf et al. (2000) raised the possibility of a small parietal contribution to the N2pc, early in its time course (180–200ms). This possibility was suggested by their MEG data, but not evident in their concomitantly recorded EEG data. The observation has not been reproduced in subsequent MEG studies from this group. We further note that the latency is earlier (~100ms) than the parietal EDAN reported here.

² We do not want to rule out that spatial cues in the form of arrows have properties that make it more likely that attention-directing potentials are elicited than with symbolic cues that are less overlearned. This is relevant to recent behavioral work pointing to a special status of arrow cues (cf. Hommel et al., 2001).

³ McDonald and Green (2008) represent a dissenting view, based on (i) work on auditory spatial attention failing to elicit an ADAN (Green et al., 2005) and (ii) the presumed identification of multiple sources for the ADAN, possibly mapping to attention- and response-related processes (Green et al., 2008). Against the first point see Seiss et al. (2007). The second point is weakened by indeterminate source locations and by the fact that lateralized potentials were collapsed over both hemispheres for modeling (cf. Oostenveld et al., 2003).

activity preceding the ADAN, now in the form of the lateralized EDAN component, thus establishing a better match between EEG and imaging manifestations of the frontoparietal network.

In conclusion, the posterior parietal scalp distribution of the EDAN does not support an identification of EDAN and N2pc. It is suggested, therefore, that the EDAN deserves a rehabilitation as ‘attention-directing’ component associated with the frontoparietal network. In combination, the ADAN and EDAN provide unique information on the temporal dynamics of frontoparietal activation, matching the existing evidence from other EEG indices (Green and McDonald, 2008; Praamstra et al., 2005). Located in frontal and parietal cortex, no claims regarding the exact origin of these components are made here. Based on the existence of multiple parietofrontal circuits (Burnod et al., 1999; Wise et al., 1997) it is conceivable that their distribution is influenced by task factors, e.g. whether subjects covertly attend, look, or point to a location. To establish such a sensitivity would require very high recording standards, but would make these components even more valuable for the investigation of frontoparietal function.

4. Experimental procedures

The methods are here described in shortened form. For a full description we refer to Praamstra et al. (2009).

4.1. Participants

We report on data of two experiments. Experiment 1 had 16 participants (9 male; age 30 ± 6 years), 14 of whom were right-handed (by self-report). Experiment 2 had 16 participants (11 male; age 35 ± 7 years), all right-handed. All had normal or corrected-to-normal vision. Data of five further participants (two for Experiment 1 and three for Experiment 2) were excluded because of excessive artifacts. All participants provided their informed consent and the study had been approved by the South Birmingham Research Ethics Committee.

4.2. Procedure and stimuli

The experimental paradigm was a cued choice-response task with stimuli presented on a computer screen and responses made by pointing movements with the index finger. In Experiment 1, three cue conditions provided prior information on the pointing direction indicated by the subsequently presented response signal. In the full information “1-arrow” condition, a single arrow presented at fixation indicated the correct pointing target. In the “2-arrow” partial information condition, a pair of arrows indicated two possible adjacent targets. In the “3-arrow” partial information condition, three arrows indicated three possible adjacent targets. The 1, 2, or 3-arrow cue stimulus was followed by a response stimulus which specified the target by means of a single arrow of the same shape and size as the cue arrows. The six possible pointing targets were arranged on a circle and were permanently displayed on the computer screen (see Fig. 4). Responses were made by sliding the index finger from a

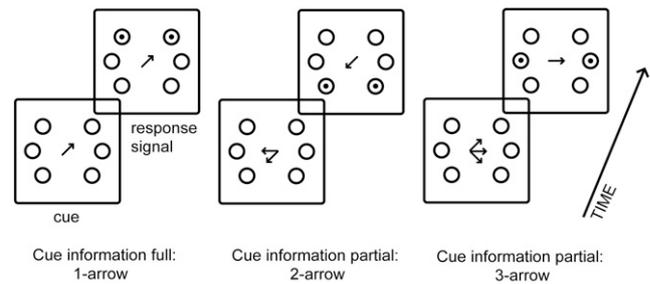


Fig. 4 – Sample cue and response stimuli used in Experiment 1. The delay period between cue and response signal was 1.2 s.

central home position to a peripheral target position on a flat surface in front of the participant. The left hand responded to targets on the left and the right hand to targets on the right.

Experiment 2 differed from Experiment 1 in using two different 2-choice conditions, i.e., a “2-arrow-s(mall)” condition and a “2-arrow-w(ide)” condition. In the former condition, similar to the 2-arrow condition of Experiment 1, alternative pointing directions were always to adjacent targets on the left or right side. In the latter condition they were to non-adjacent targets, always both to the left or both to the right. In addition, the experiment had a 3-arrow condition, like Experiment 1.

The permanently displayed configuration of six possible pointing targets measured 3.7° by 2.7° of visual angle, with the targets lying on a circle of 1.7° of visual angle radius. The individual targets were indicated by circles of 0.3° of visual angle radius. The angular distance between targets (on each side of fixation) was 45° . Cue and response arrow stimuli were very small (0.6° of visual angle) and were centered on the middle of the screen (instead of having their origin at the centre), in order to minimize the asymmetry of the stimulus. The response arrow stimulus was accompanied by a white dot placed in the relevant target circle, along with a similar dot in the homologous target on the opposite side to maintain a symmetrical display. The stimuli were presented in white against a gray background. The stimulus display with six possible targets was represented in an enlarged size on a horizontal response surface aligned to the participants’ body midline. Subjects responded by sliding their left or right index finger from home position to target.

The experiments were run in a normally illuminated room and consisted of 12 blocks of ~4 min duration each, preceded by a practice block. Each block had 72 trials with equal numbers of trials for the three cue conditions and an equal number of trials for left and right hand. Trial order was randomized across conditions and response hand. The interval between trials (onset to onset) was 3400 ms and the cue-response signal delay was 1200 ms. Cue and response stimuli were presented for 200 ms each.

4.3. Data acquisition

EEG was recorded continuously with Ag/AgCl electrodes from 130 scalp electrodes relative to CMS and DRL electrodes adjacent to the vertex electrode location Cz. The electrodes were placed according to the 10–5 extension of the

International 10–20 electrode system using an elastic cap, carefully positioned relative to landmarks nasion, inion and preauricular points. Vertical and horizontal eye movements were monitored using EOG electrodes positioned under the left and right eye and lateral to the left and right eye. EEG and EOG signals were amplified with a band-pass of 0–128 Hz by BioSemi ActiveTwo Amplifiers and sampled at 512 Hz.

4.4. Data processing

The continuous EEG data were re-referenced to an averaged mastoids reference and segmented in epochs from 500 ms before to 2000 ms after the cue stimulus. Individual trials containing eye-movements and other artifacts were removed before averaging. The baseline was defined as the time period from 200 ms before until the onset of the cue stimulus. Averaged data were created for each participant and condition separately.

Analyses focused on the cue-induced preparatory activity developing during the 1200 ms delay period, expressed in the lateralized ADAN, LRP, LDAP, and EDAN components. These components were isolated by means of the LRP derivation (Coles, 1989). The amplitude of the lateralized ERPs was quantified as the mean activity from pooled electrodes over selected time intervals, identified on the basis of scalp waveforms and their respective topographies. Analyses relevant to this report used repeated measures MANOVA and *t*-tests. The Greenhouse–Geisser procedure was applied to all repeated measures with more than one degree of freedom. The adjusted degrees of freedom and *p*-values are reported.

EEG dipole source analysis (BESA 5.1.8; MEGIS software GmbH) was applied to the EDAN, ADAN and LDAP, to evaluate whether the inferred origin of the EDAN in the parietal cortex, based on interpretation of its scalp topography, was physically and neurophysiologically plausible. The analysis used a standard ellipsoid 4-shell head model. Results of source analyses are depicted in a schematic head model with dipole locations represented in terms of Talairach–Tournoux coordinates.

4.5. Review of N2pc scalp distribution

To review the N2pc scalp distribution in previous publications, we performed a PubMed search with search term “N2pc”. This produced 92 publications published between 1994 and 2009. This list was supplemented with four publications known to us but not identified by the search. Subsequently, we identified 87 of these 96 papers as containing information on the scalp distribution of the N2pc, measured with EEG. This information was processed as follows. Non-standard EEG electrode labels were converted to corresponding locations within the 10–5 system (Oostenveld and Praamstra, 2001). A single-electrode scalp maximum was recorded, for a particular study, if (i) this electrode was explicitly identified in the study as representing the scalp maximum, or (ii) this electrode was consistently used to represent the N2pc. Multiple electrode locations were recorded if (i) the N2pc was reported as being of equal amplitude at these locations, (ii) no further information was available, or (iii) electrodes were pooled for analyses and representation.

Conversion of EGI geodesic net electrode locations was based on information from EGI (ftp://ftp.egi.com/pub/documentation/technotes/200_ElectrodePositions.pdf). Other non-standard locations, such as OL, OR, TO1, TO2 were already defined relative to 10–20 locations. Of note, we found TO1/TO2 defined in different ways. Accordingly, they were converted to PO7/8 or to PO5/6, dependent on the definition.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.brainres.2009.12.090](https://doi.org/10.1016/j.brainres.2009.12.090).

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