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Research Report

Spatiotemporal overlap between brain activation related to saccade preparation and attentional orienting

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ABSTRACT

Recent brain imaging studies provided evidence that the brain areas involved with attentional orienting and the preparation of saccades largely overlap, which may indicate that focusing attention at a specific location can be considered as an unexecuted saccade towards that location (i.e. the premotor theory of attention). Alternatively, it may be proposed that attentional orienting is simply relevant for preparing saccades, but the two processes may also be completely unrelated. In two experiments, we examined temporal activation of brain areas by measuring the electroencephalogram. Central cues indicated the likely side (left or right) at which a to-be-attended target would occur, or to which a saccade had to be prepared. Cue direction-related activity was determined, time-locked to cue onset. In addition, in our second experiment, delayed saccades had to be carried out, which allows to focus on processes strongly related to saccade execution. In nearly all tasks, an early directing attention negativity (EDAN), an anterior directing attention negativity (ADAN), and a late directing attention positivity (LDAP) were observed, time-locked to cue onset. Source analyses supported the view that this activity probably originates from areas within the ventral intraparietal sulcus (vIPS) and the frontal eye fields (FEF). The saccade-locked analysis also indicated that the FEF plays an important role in triggering saccades, but the role of vIPS appears to be minimal. The latter finding disfavors the premotor theory of attention, as it suggests that the relation between attention and action is less direct.

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1. Introduction

Attentional orienting may be defined as the mental ability of selecting positions in space that are relevant for the control of our behavior, without necessarily shifting gaze, whereas saccade preparation may be characterized as the process that presets specific parameters relevant for the execution of saccades towards intended saccade goals. Regarding the functional relationship between these processes, three differ-

ent viewpoints can be distinguished (for reviews, see Corbetta, 1998; Hoffman, 1998). First, Rizzolatti et al. (1987) proposed that attentional orienting might be identical to the planning of saccades: the premotor theory of attention. According to this view, attentional orienting activates the same brain areas as saccade preparation because attentional shifts are considered to be below-threshold activation of saccade motor programs. Secondly, attentional orienting and the planning of saccades may have functional overlap, for example, the locus of

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attention at a critical time point may provide crucial information for the accurate planning of saccades (Deubel and Schneider, 1996; Kowler et al., 1995). As a consequence, the brain areas activated while carrying out these functions may overlap, but additionally, task-specific activations are expected to be found. Finally, there need not be a functional relation at all; although attention is likely to be focused on the saccade goal, simply because this goal is interesting, it may fulfill no special role for the planning of a saccade (for suggestions in this direction, see Henderson et al., 1989). The latter view implies that different brain areas are expected to be activated while carrying out these functions, although some small overlap may be observed.

Results of PET (positron emission tomography) and fMRI (functional magnetic resonance imaging) studies point to large overlap in cortical brain areas between attentional orienting and the preparation and execution of saccades (Astafiev et al., 2003; Corbetta, 1998; Nobre et al., 2000a; Perry and Zeki, 2000). Considering these results together with several studies focusing on the areas involved with attentional orienting and spatial working memory (Corbetta et al., 2002), top-down attentional control (Hopfinger et al., 2000), and crossmodal spatial attention (Macaluso et al., 2003), it may be proposed that activity within two specific brain areas, the ventral intraparietal sulcus (vIPS) and the frontal eye fields (FEF), depends both on the direction at which attention is focused and the direction to which a saccade has to be prepared (e.g. see Astafiev et al., 2003; Corbetta and Shulman, 2002). This activation could reflect the coding of spatial locations in an effector-independent way, but, in line with the premotor theory of attention, it may also reflect activity arising from intended eye movements. Although both the vIPS and FEF have been shown to be involved during tasks requiring attentional shifts or the preparation of eye movements, their temporal interactions may differ between these tasks. Most of the aforementioned evidence with regard to the role of the vIPS and FEF has been derived from slow metabolic responses to neuronal activation, evolving over (tens of) seconds after neuronal activity (fMRI and PET). These techniques, although with rather precise localization accuracy, do not allow for the separation of events around attentional shifts and eye movements, which commonly occur in close succession (in the order of a few hundreds of milliseconds). Thus, the question may be raised whether the deployment of the vIPS and FEF over time is really comparable during attentional orienting and during saccade preparation. Using the EEG (electroencephalogram) enables a high temporal resolution and is therefore perfectly suited to give a more precise answer. Here, we focused on direction-related (or lateralized) EEG potentials in saccade preparation and covert orienting tasks as they provide specific information regarding spatial processing in these tasks and this method cancels out nonspecific differences in activation between tasks (e.g. due to differences in task difficulty).

Harter et al. (1989) examined the influence of attentional orienting on EEG by using arrow cues indicating the visual field in which stimuli to be detected appeared after a fixed interval. In this study and in modifications of this paradigm (Eimer, 1995; Hopf and Mangun, 2000; Nobre et al., 2000b; Van der Lubbe et al., 2005a; Yamaguchi et al., 1994, 1995), several

direction-related ERP (event-related potential) components have been distinguished within this short interval. These components were determined after computing difference waves between ERPs evoked by left-pointing and by right-pointing arrows (e.g. Hopf and Mangun, 2000) or by computing contra-ipsilateral difference waves (in the current study), by extending the computation of the lateralized readiness potential (LRP) to all symmetrical electrode pairs with respect to arrow direction (e.g. Praamstra et al., 1996; Wascher and Wauschkuhn, 1996). The crucial aspect of the latter method is that activity unrelated to the relevant direction (e.g. general hemispherical differences) is additionally subtracted out (De Jong et al., 1988; Gratton et al., 1988), thereby providing a highly specific neuronal index. Three direction-related (or lateralized) ERP components have been distinguished. The earliest component, the early directing attention negativity (EDAN), is a negative (contralateral to arrow direction) deflection over occipital-parietal electrodes from 200–400 ms after cue onset. The EDAN has been replicated in several studies (e.g. Hopf and Mangun, 2000; Van der Lubbe et al., 2005a; Yamaguchi et al., 1994, 1995) and was mostly interpreted as reflecting voluntary arrow-induced shifts of visual attention towards the cued location. Recently, however, Van Velzen and Eimer (2003) found support for the view that the posterior EDAN at least partially reflects attentional selection of the side of the stimulus signaling the to-be-attended side (e.g. selection of the point of the arrow), rather than selection of the to-be-attended side. The second component, the anterior directing attention negativity (ADAN), an anterior negativity evoked at about 400 ms after cue onset (Eimer, 1995; Eimer et al., 2002; Nobre et al., 2000b; Yamaguchi et al., 1994, 1995) was hypothesized to reflect activity from premotor cortex. Finally, the third component, the late direction attention positivity (LDAP), a posterior positivity after about 500–700 ms, may reflect the influence of attention on processing along the ventral stream (Hopf and Mangun, 2000; but see Eimer et al., 2004; Näätänen, 1992).

Interestingly, quite similar components have been observed during both saccade preparation and the preparation of finger movements when the imperative stimuli cued by the arrows were presented foveally rather than peripherally (Jentzsch and Leuthold, 2002; Leuthold and Jentzsch, 2002; Van der Lubbe et al., 2000; Verleger et al., 2000; Wauschkuhn et al., 1997). For example, by employing a principal component analysis, Van der Lubbe et al. (2000) distinguished between several components in the direction-related ERPs while participants were preparing saccades and finger movements: one early negative parietal component, a later negative anterior component, and a third positive parietal component. Despite the methodological differences between both paradigms (e.g. regarding cue validity, the type of cues, the use of markers, etc.), the observed lateralized components in the aforementioned studies seem quite comparable to the earlier described EDAN, ADAN, and the LDAP. Thus, it may be hypothesized that saccade preparation and attentional orienting not only involve the same neural systems, but also show comparable activation patterns over time, which seems perfectly in line with the premotor theory of attention.

In the current study containing two experiments, tasks were used similar to Nobre et al. (2000b) in which participants had to prepare a horizontal eye movement to a saccade goal, and in which they had to attend to a location at which a target would probably appear. In our first experiment, we required both simple responses and choice responses to the targets as there are some indications that the relevance of attentional orienting and the involvement of (pre)motoric processes differs between simple-response and choice-response tasks (e.g. see Mangun and Hillyard, 1991; Tanaka and Shimojo, 1996; Van der Lubbe et al., 2005b). As a consequence, finding different activation patterns between simple-response and saccade preparation tasks could be due to changes in the relevance of attentional orienting and (pre)motoric processes in the simple-response task. Additionally, we performed dipole source analyses on the lateralized activity (see Leuthold and Jentzsch, 2002; Praamstra et al., 1996) to compare source parameters (location, orientation, and strength) and source waveforms between the different tasks. In a first source analysis, we constrained source location parameters to the loci of the vIPS and FEF as reported in the literature, to examine whether the observed lateralized components are indeed likely to originate from these cortical brain areas. In our second source analysis, we left both the location and orientation parameters free, to examine possible differences in source parameters between tasks.¹

2. Experiment 1

2.1. Methods

2.1.1. Participants

Informed consent was obtained from 14 participants, mostly students of the University of Utrecht. Three participants were removed from the analysis because of too many eye movements and/or artifacts (>50%) during critical time intervals, which left 11 participants, mean age 24 years, 9 right- and 2 left-handed. All participants had normal or corrected to normal vision and intact color vision, were in good physical health, and had no history of psychiatric or neurological disorder. Participants were paid €45 for their participation. The study was approved by the local ethics committee of the faculty of social sciences of the University of Utrecht.

2.1.2. Stimuli

All stimuli were presented on a black computer screen. During each trial, a light-gray fixation dot ($0.2^\circ \times 0.2^\circ$) was presented in

the center of the screen, accompanied by two light-gray open circles ($r = 0.34^\circ$) located 8.3° to the left and right of the fixation dot (see Fig. 1). Trials started with a word 0.2° above the fixation dot. In the saccade task and in the choice-response task, the word “START” was displayed, whereas in the simple-response task, the word “LINKS” or “RECHTS” (Dutch equivalents of left and right) was displayed. The display with the word lasted for 400 ms, after which the default-display, consisting of the fixation-dot and the circles to the left and right, was presented again for 600 ms. Next, the cue was presented in the center, replacing the fixation dot for a duration of 400 ms. The cue was a diamond (height: 0.85° , width: 1.71°) constructed of a green and a red triangle, each pointing to one of the circles. After the cue, the default-display was presented again for 600 ms. Thus, the preparatory interval from cue onset to target onset amounted to 1000 ms. Next, the target was displayed within one of the circles for a duration of 200 ms, consisting of either three horizontal or three vertical lines. After target offset, the default-display was presented for another 2000 ms.

2.1.3. Tasks and procedure

Participants performed three tasks, each consisting of 640 trials. Each task, lasting approximately 45 min, was divided into two parts. In the first part, half of the participants were informed that the circle indicated by the green cue was the most probable target location (on 80% of the trials, i.e. the valid trials). On 15% of the trials, the target occurred in the other circle (invalid trials), whereas on 5% of the trials, no target occurred (catch trials). In the second part, they were informed that the red cue indicated the most probable target location. For the other half of the participants, this order was reversed. Each part per task was divided in four blocks of 160 trials, which were preceded by 20 practice trials. The order of the three experimental tasks was counterbalanced. In all tasks, participants had to keep their eyes at fixation during the cue-target interval. In the simple-response task, the required response button was indicated at the start of each trial and varied randomly from trial to trial. Button presses after target onset (the filling of one of the circles with either the horizontal lines or the vertical lines) had to be as fast as possible. In the choice-response task, participants were instructed to press the left button when one of the circles was filled with the horizontal lines, and to press the right button when one of the circles was filled with the vertical lines. Button presses had to be as fast and accurately as possible. In the saccade task, participants were instructed to make an eye movement towards the circle that was filled with the horizontal or vertical lines.

2.1.4. Apparatus

Participants were seated in a comfortable chiroprapist arm-chair in a silenced and darkened chamber. Presentation software (version 0.43 developed by Neurobehavioral Systems) took care of stimulus presentation and the simultaneous transmission of external triggers. The external triggers were received by a Vision Recorder (version 1.0 b BrainProducts GmbH) which measured participants' EEG, EOG and their button presses. The buttons were fixed in two response boxes, which were placed in a comfortable position at the left and

¹ Leaving these parameters free has the consequence that residual variance (RV) will decrease, as there are more variables that can account for the observed data pattern. However, the absolute values of the estimated locations should be considered with caution. Moreover, application of the principle of Occam's razor implies that the number of to be estimated parameters should be kept small. Thus, a model with few free parameters should be preferred above one with a larger number of free parameters unless the reduction of RV is relatively large and there are strong a priori reasons for keeping a specific number of free parameters (e.g. when it is known that activity arises from three rather than from two different regions).

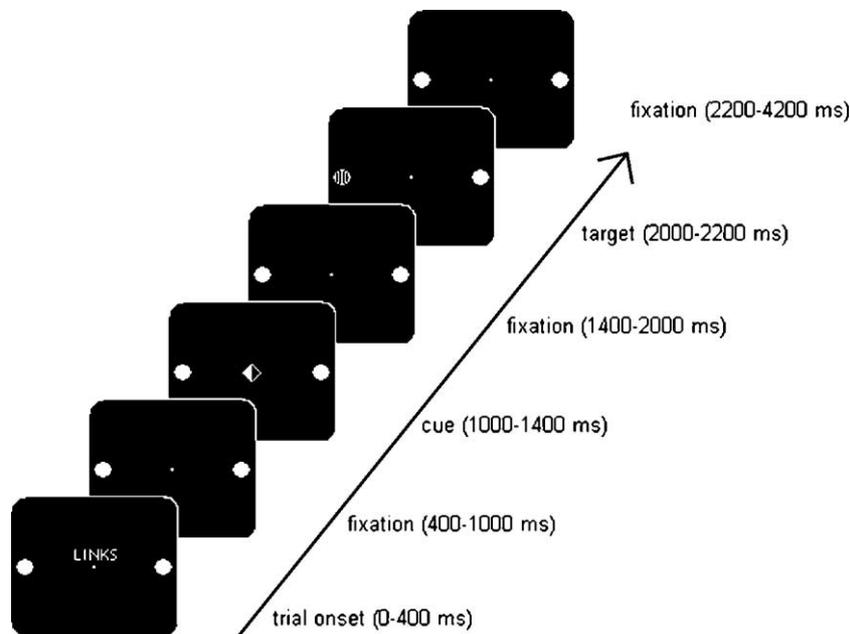


Fig. 1 – An example of the stimuli and their order as employed in the simple-response task. In that task, the required response was indicated at the start of each trial. In the choice-response and the saccade task, the word “START” was displayed. In all other respects, the stimuli in all tasks were identical.

right side on a hand-rest in front of the participant, approximately 25 cm apart. The participants were seated in front of a 17” screen monitor (DELL) at a distance of 100 cm.

2.1.5. Recording

EEG was recorded continuously from Ag/AgCl ring electrodes placed at the following 60 standard scalp sites: Fpz, Fp1, Fp2, AFz, AF3, AF4, AF7, AF8, Fz, F1, F2, F3, F4, F5, F6, F7, F8, FCz, FC1, FC2, FC3, FC4, FC5, FC6, FT7, FT8, Cz, C1, C2, C3, C4, C5, C6, T7, T8, CPz, CP1, CP2, CP3, CP4, CP5, CP6, Pz, P1, P2, P3, P4, P5, P6, P7, P8, POz, PO3, PO4, PO7, PO8, Oz, O1, O2, mounted in an elastic cap (Braincap, Brainproducts GmbH). EOG was measured above and below the left eye and horizontally from the outer canthi of both eyes to determine the vEOG and hEOG. Online, all electrodes were referenced to the Cz electrode. EEG and EOG were amplified by a BrainAmp amplifier (Brainproducts GmbH) and were recorded at 250 Hz and digitally filtered (TC = 5.0 s, low-pass filter of 100 Hz, notch filter of 50 Hz) by Vision Recorder. Electrode resistance was kept below 5 k Ω .

2.1.6. Data analysis

Trials with detectable sideward eye movements (exceeding 60 μ V in the hEOG recording) from cue onset until target onset were removed from all analyses. This procedure left on average 93.8% of the trials in the simple-response task, 93.4% of the trials in the choice-response task, and 91.1% of the trials in the saccade task. For the statistical analyses, Huynh-Feldt epsilon correction was applied to adjust the degrees of freedom whenever appropriate.

2.1.6.1. Behavioral measures. RT was measured relative to target onset. In the saccade task, crossing the criterion of ± 60 μ V was used to define saccadic responses to the left or right. Responses faster than 100 ms (premature responses) or

slower than 1500 ms (misses) and erroneous responses (incorrects) were excluded from the RT analyses. RTs and the proportion of correct responses (PCs) were evaluated statistically by repeated measures analyses of variance (ANOVA) with the factors task (simple-response, choice-response, and saccade), side (left or right), and cue validity (valid vs. invalid). We also examined whether the amount of premature responses and the amount of responses in catch trials differed between tasks.

2.1.6.2. EEG parameters. EEG was offline referenced to the average reference and was analyzed for the interval from -100 to 1000 ms after cue onset. Trials with EEG artifacts (max-min: ± 200 , 150, and 100 μ V for frontal, central, and parietal electrodes, respectively; gradient criterion 120 μ V per sample point, zero lines for 50 ms) and incorrect responses were removed, which left 84.7% of the trials in the simple-response task, 85.9% of the trials in the choice-response task, and 81.8% of the trials in the saccade task. The baseline was determined from -100 to 0 ms before cue onset. Cue-locked contralateral difference potentials, relative to relevant cue direction, were determined by calculating the difference for all symmetrical electrodes above the left and right hemisphere. That is, for cues pointing to the left, the difference was computed as C4-C3 (or P8-P7, etc.), and for arrows pointing to the right, the difference was computed as C3-C4 (or P7-P8, etc.), and averaging these differences yields the general absolute difference contralateral minus ipsilateral relative to cue direction (e.g. P8/7). This was done for each task separately. The location of the electrodes included in the initial EEG analyses, the spline-maps, and the dipole analyses is indicated in Fig. 2. Average amplitudes were computed per participant in 40 ms windows from cue onset until target onset. These amplitudes were first statistically analyzed per

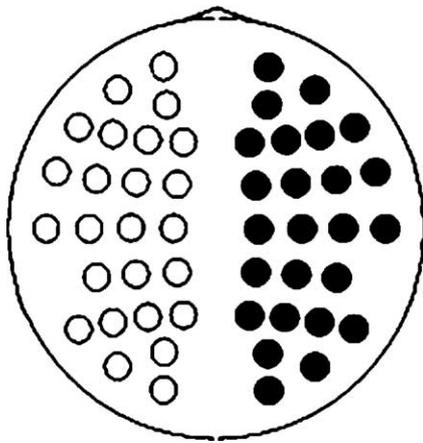


Fig. 2 – Electrodes included in the initial EEG analyses, the determination of the spline-maps, and the dipole source analyses are indicated as black and white (their contralateral counterpart) circles.

time window (25) by using ANOVAs with the factors task (simple-response, choice-response, saccade) and electrode (Fp2/1, AF4/3, AF8/7, F2/1, F4/3, F6/5, F8/7, FC2/1, FC4/3, FC6/5, FT8/7, C2/1, C4/3, C6/5, T8/7, CP2/1, CP4/3, CP6/5, P2/1, P4/3, P5/6, P8/7, PO4/3, O2/1, PO8/7). Intervals were considered to be of interest, either when the signal differed from baseline (intercept), or when activity differed among electrodes ($P < 0.01$). Thereafter, analyses across consecutive significant intervals were performed for a selected set of electrodes with the factors task (3), lateral-medial axis (2), and anterior-posterior axis (7), containing the electrode pairs AF4/3, AF8/7, F4/3, F8/7, FC4/3, FC6/5, C4/3, C6/5, CP4/3, CP6/5, P4/3, P6/5, PO4/3, PO8/7.

2.1.6.3. Source analyses. The parameters of intracranial sources within the cue-target interval were determined by performing source analyses on lateralized potentials using the brain electricity source analysis (BESA) algorithm (version 2.2). This algorithm estimates parameter values of multiple equivalent dipolar sources by calculating the scalp distribution that would be obtained for a given dipole model and comparing it to the original distribution (Scherg, 1990). Iterative changes in the parameter values lead to minimization of the residual variance (RV) between the model and the observed spatiotemporal distribution. In these calculations, BESA assumed an approximated 4-shell head model (brain, skull, cerebrospinal fluid, and scalp). For three participants, exact electrode locations were determined with a 3-D digitizer (Polhemus). The obtained values were used to construct the average spherical coordinates, which were employed for all further analyses. The lateralized potentials were projected on both hemispheres, inverting activity at homologous (here left) electrode pairs (see Leuthold and Jentzsch, 2002; Praamstra et al., 1996). The energy criterion was set at 20% to reduce the interaction among dipoles, and the separation criterion was set at 10% to optimize the separation of the source waveforms over time.

The average coordinates of vIPS and FEF in MNI (Montreal Neurological Institute) space of three studies (Hopfinger et al.,

2000; Macaluso et al., 2003; Neggers et al., 2005; for right vIPS: $x = 29$, $y = -55$, $z = 50$; for right FEF: $x = 30$, $y = 0$, $z = 51$) were transformed into spherical coordinates (see Results), and were used in a first analysis on the grand average lateralized potentials per task to set two symmetrical sources with asymmetrical orientation at appropriate locations. In this analysis, we assumed that the underlying sources are located in vIPS and FEF with a fixed orientation during the time window of interest, whereas source strength varies over time. This location restriction was carried out as these regions were shown (see Introduction) to be sensitive depending on the side that was made relevant for the task at hand. In a second analysis, we determined the source location, source orientation, and source strength for two symmetrical sources with asymmetric orientation per individual lateralized average for each task, thereby allowing the possibility to test for differences between tasks. This testing was done by performing multivariate analyses (MANOVA, Hotelling's trace) with the factors task (3) and source (2; posterior-anterior). The number of to be estimated sources in this second analyses was kept at two as source analyses on the overall grand average showed only a reduction in RV of 0.8% when the number of symmetrical sources was increased from two to three (see also footnote 1).

2.2. Results

2.2.1. Behavioral measures

RTs and PCs as a function of task and cue validity are compiled in Table 1. Responses differed as a function of task, $F(2,20) = 143.9$, $\epsilon = 1.0$, $P < 0.001$. Saccades (in the saccade task) were faster than manual responses in the simple-response task, which in turn were faster than the manual responses in the choice-response task, $F(1,10) > 115$, $P < 0.001$. Responses were always faster for validly than for invalidly cued targets, $F(1,10) = 68.6$, $P < 0.001$, and this effect was not different between the tasks, $F(2,20) = 0.48$. No main effect or interactive effects with side were found. Regarding PCs, no differences were found between tasks, but responses were more accurate for validly than for invalidly cued targets, $F(1,10) = 12.5$, $P = 0.005$. Analyses on the proportion of premature responses

Table 1 – Mean reaction times (RT) and proportion of correct responses (PCs) and standard errors (SE) as a function of task and cue validity (when applicable) for Experiments 1 and 2

Task	Cue	RT (in ms) mean	SE	PC (in %) mean	SE
<i>Experiment 1</i>					
Saccade	Valid	311	17.5	93.6	1.7
	Invalid	393	16.9	89.3	3.5
Simple-response	Valid	450	28.3	95.7	1.4
	Invalid	520	26.4	95.0	1.4
Choice-response	Valid	723	36.6	93.9	1.8
	Invalid	812	35.4	89.1	3.1
<i>Experiment 2</i>					
Saccade	–	1298	49.7	90.2	3.0
Choice-response	Valid	637	40.5	94.3	1.7
	Invalid	702	46.0	90.6	2.0

(RT < 100 ms) revealed a main effect of task, $F(2,20) = 5.5$, $\epsilon = 0.53$, $P = 0.038$. No premature responses were found in the choice-response task, whereas the proportion of premature responses was higher in the saccade task (1.7%) than in the simple-response task (0.3%). The proportion of responses in catch trials differed between tasks, $F(2,20) = 5.1$, $\epsilon = 1.0$, $P = 0.017$, being lowest in the choice-response task (4.0%), somewhat higher in the simple-response task (9.8%), and highest in the saccade task (22.9%).

2.2.2. Lateralized EEG potentials

Cue-direction-related lateralized ERPs for the three tasks for the most relevant electrode pairs are displayed in Fig. 3. In addition, spline maps determined by BESA for the lateralized ERPs (mirrored over the left hemisphere) at positive or negative maxima per task are given in Fig. 4. The first negative component, largest above posterior sites at about 300 ms after cues onset, corresponds with the EDAN. A second negative component, largest above frontal sites at about 450 ms after cue onset, corresponds with the ADAN. A third positive component, largest above posterior sites at 600 ms, fits with the description of the LDAP. Analyses were performed on 40 ms intervals from cue onset until target onset with the factors task (3) and electrode (25) to determine relevant time intervals. Analyses from 0 to 200 ms revealed no significant effects. Activity differed from baseline from 240 to 520 ms, $F(1,10) < 13.7$, $P < 0.001$, and an effect of electrode was found from 200 to 320 ms, from 360 to 520 ms, and from 560 to 640 ms, $F(24,240) > 4.6$, $P < 0.01$. Based on the latter effects, we chose to perform separate analyses for the time windows from 200 to 320 ms, from 360 to 520 ms, and from 560 to 640 ms, corresponding to the EDAN, ADAN, and LDAP, respectively.

2.2.2.1. EDAN. Analyses included the factors time window (200–240, 240–280, 280–320 ms), task (3), lateral–medial axis (2), and anterior–posterior axis (7). A main effect of time, $F(2,20) = 8.8$, $\epsilon = 1.0$, $P = 0.002$, indicated that the EDAN was largest in the 240–280 ms interval, and a main effect of anterior–posterior axis, $F(6,60) = 13.6$, $\epsilon = 0.38$, $P < 0.001$, indicated that the EDAN was largest at the posterior electrode pairs (PO4/5 and PO7/8). The weak interaction between anterior–posterior axis and lateral–medial axis, $F(6,60) = 2.8$, $\epsilon = 0.59$, $P = 0.047$, indicates that negativity was most pronounced at the lateral posterior electrode pair: PO7/8.

The interaction between time window and lateral–medial axis, $F(2,20) = 8.9$, $\epsilon = 0.68$, $P = 0.007$, reflected the fact that the EDAN was larger at lateral than at medial electrodes for the time window from 280–320 ms, which was not the case for the time window from 200–240 ms. The interaction between task and lateral–medial axis, $F(2,20) = 4.8$, $\epsilon = 0.84$, $P = 0.027$, indicated that the EDAN was larger at lateral than at medial electrodes in the saccade task only, tended to show this effect in the simple-response task, and did not differ between lateral and medial electrodes in the choice-response task. Some differences among the tasks are also visible in the spline maps displayed in Fig. 4.

2.2.2.2. ADAN. The factor time window had four levels (360–400, 400–440, 440–480, 480–520 ms). A main effect of anterior–posterior axis was found, $F(6,60) = 10.2$, $\epsilon = 0.40$,

$P < 0.001$, and activity was more negative at the lateral side, $F(1,10) = 6.0$, $P = 0.034$. An interaction was found between time window and anterior–posterior axis, $F(18,180) = 4.1$, $\epsilon = 0.49$, $P < 0.001$. In addition, a second order interaction between time window, anterior–posterior axis, and lateral–medial axis was found, $F(18,180) = 4.6$, $\epsilon = 0.44$, $P < 0.001$. All these effects seem due to the ADAN peaking at the F7/8 electrode pair in the intervals from 400–480 ms after cue onset.

An interaction was found between task and anterior–posterior axis, $F(12,120) = 3.2$, $\epsilon = 0.48$, $P = 0.01$. Post hoc analyses revealed that centroparietal activity as compared to central activity decreased more strongly in the choice-response task than in the simple-response task, $F(1,10) = 9.5$, $P = 0.012$, whereas no difference was found between the choice-response and the saccade task, $F < 0.01$. See also the spline maps at around 400 ms after cue onset displayed in Fig. 4.

2.2.2.3. LDAP. The factor time window had two levels (560–600, 600–640 ms). A main effect of anterior–posterior axis, $F(6,60) = 13.5$, $\epsilon = 0.26$, $P = 0.001$, and an interaction between anterior–posterior axis and lateral–medial axis were found, $F(6,60) = 8.3$, $\epsilon = 0.91$, $P < 0.001$, which seem due to the LDAP peaking at the PO7/8 electrode pair. All results including the factor task were far from significant, $F_s < 1.5$.

2.2.3. Source analyses

Estimated source orientations and source waveforms for the grand averages per task are displayed in Fig. 5. Analyses were based on lateralized activity from 200 to 660 ms after cue onset. For the first analysis, spherical coordinates (theta, phi, ecc) for the right vIPS were determined at 42.7, –46.0, and 81.0, and for the right FEF at 36.0, 26.4, and 75.0. RV with the two fixed dipole pairs with free asymmetrical orientation parameters amounted to 12.5, 13.7, and 11.0% for the grand averages in the simple-response, the choice-response, and the saccade task, respectively. The source waveforms obtained in this first analysis (see Fig. 5) suggest that lateralized activity started within the vIPS, accounting for the EDAN, thereafter the FEF, accounting for the ADAN, and finally vIPS again, which accounts for the LDAP. A comparison between the different conditions suggests that initial activity within vIPS may be prolonged in the simple-response task as compared to the other tasks, which may be related to the task effect found on the ADAN.

In our second analysis, we determined source parameters for each individual average with free location and orientation parameters. Mean RV (with standard deviation in between brackets) in the simple-response, choice-response, and the saccade task amounted to 14.7% (7.9), 14.5% (12.0), and 11.6% (5.6). The result of these analyses on the grand averages for each task is displayed in Fig. 6. RV for the estimated dipole models based upon the grand averages per task was less than 4%. A MANOVA on the estimated source locations (the x, y, and z axes were used as different measures) only revealed a main effect of source, $F(3,8) = 144.7$, $P < 0.001$, but no other effects, $F_s < 0.6$, $P_s > 0.7$. Univariate tests revealed that the source effect was present for the anterior–posterior (y) axis, $F(1,10) = 411.6$, $P < 0.001$, and for the superior–inferior (z) axis, $F(1,10) = 18.1$, $P = 0.002$, which indicated that the anterior source was located

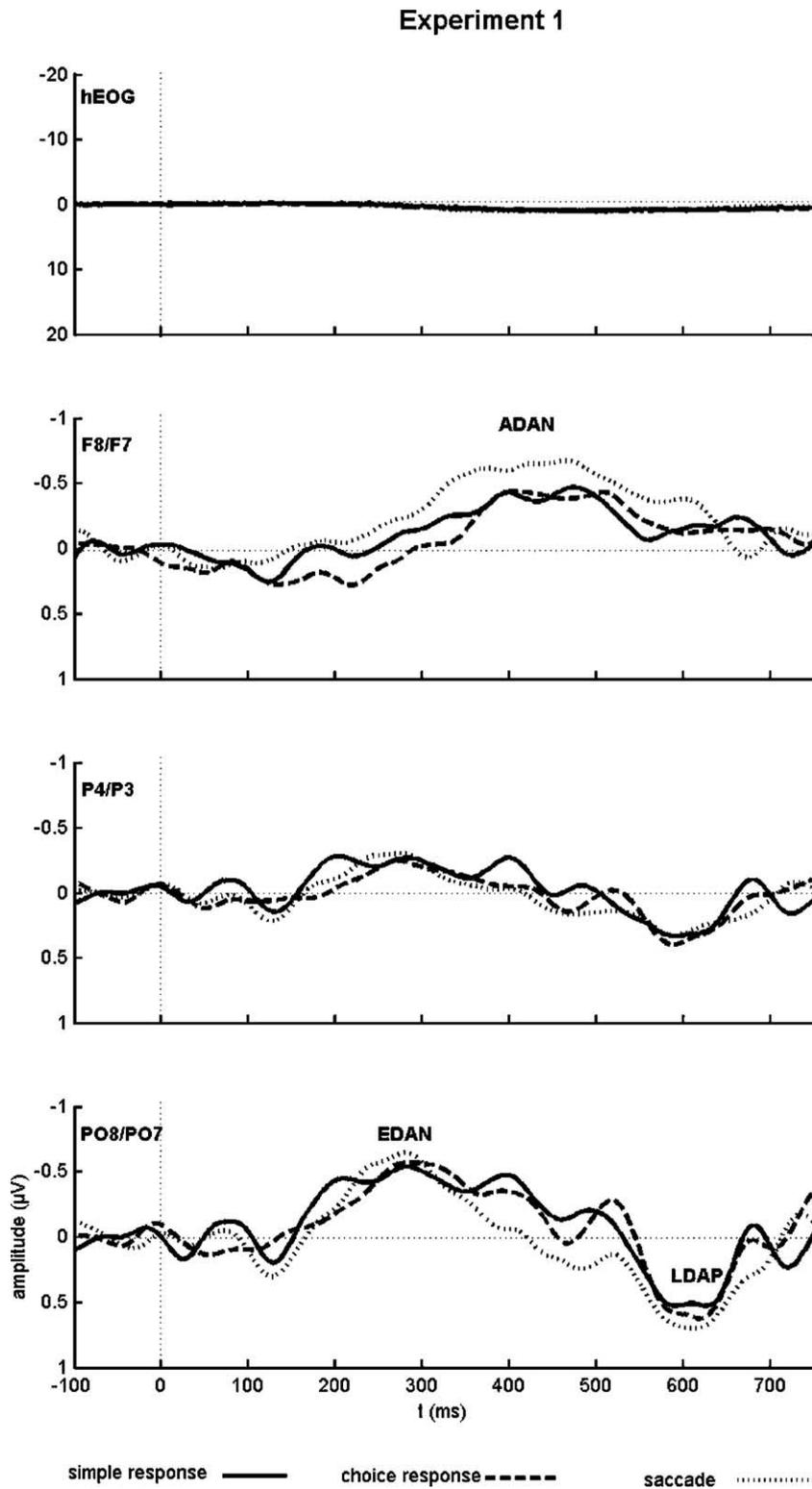


Fig. 3 – Cue-locked direction-related ERPs (ERLs) in the three tasks of Experiment 1 are displayed for the F8/7, the P4/3, and the PO8/7 electrodes. The hEOG (inverted when right was relevant and averaged across left and inverted right) was additionally provided to show that no systematic eye movements were made towards the relevant side. In that case, a clear positive potential would be expected (see Fig. 9). Clearly, in all tasks, the same components can be distinguished, a first negative posterior component (EDAN) is followed by a second negative anterior component (ADAN), and a third positive posterior component (LDAP).

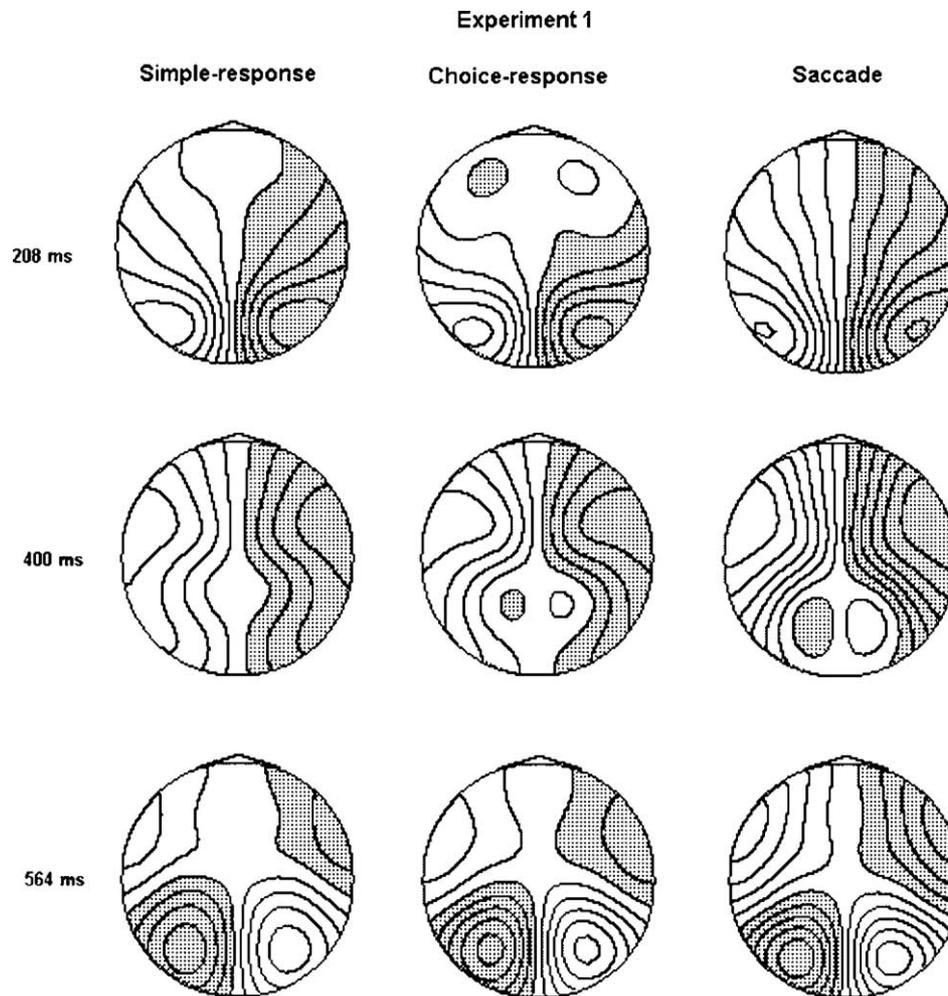


Fig. 4 – Spline maps determined by BESA around the maxima of the EDAN, ADAN, and the LDAP for the simple-response, the choice-response, and the saccade task in Experiment 1. Lateralized activity is projected on the right hemisphere and polarity is inverted at the left hemisphere. The crossing of a line implies a change of $0.1 \mu\text{V}$, where negativity is indicated by hatching. As a consequence, the maximum amplitude of the right posterior positive difference at 564 ms in the choice-response and the saccade task, lower maps, varies between 0.5 and $0.6 \mu\text{V}$, whereas in the simple-response task, it varies between 0.4 and $0.5 \mu\text{V}$.

more superior than the posterior source. A MANOVA on the estimated source orientations revealed a main effect of source, $F(3,8) = 5.5$, $P = 0.025$, which also was due to a difference along the superior–inferior axis, but no other effects, $F_s 1.7$, $P_s > 0.14$. Analyses on source strengths revealed no significant effects, $F_s < 2.8$, $P_s > 0.13$.

2.3. Discussion of Experiment 1

Analyses on the speed of button presses and saccades in the simple-response, choice-response, and saccade task revealed that participants complied with the instructions as responses were faster for validly than for invalidly cued trials (see Table 1). As a consequence, it appears that participants focused their attention at the requested positions in the simple and choice-response task, and that they probably prepared a saccade towards the cued side.

The EDAN (see Figs. 3 and 4) was present in all conditions from 200 to 320 ms after cue onset, which replicates and

extends the findings of several other studies (see Introduction). However, activity was somewhat larger at lateral sites in the saccade task than in the attentional orienting tasks (see Fig. 4). The ADAN was present from 360 to 520 ms after cue onset, which is comparable with the ADAN observed by other studies (Eimer et al., 2002; Nobre et al., 2000b; Verleger et al., 2000). Some task differences were obtained, but now, centro-parietal activity in the simple-response task diverged from activity in the choice-response task and the saccade task. The LDAP was present from 560 to 640 ms after cue onset, which also corresponds with the findings of other studies (Eimer et al., 2002; Hopf and Mangun, 2000; Nobre et al., 2000b). No task differences were found with regard to the LDAP.

The source analyses on the lateralized activity with fixed dipole pairs at left and right vIPS and FEF for the interval from 200 to 660 ms indicate that in all tasks the largest part of lateralized activity can be adequately described by the two dipole pairs, as RV for this rather long time interval was always less than 14%. Secondly, in all tasks, lateralized activity

may arise from subsequent activation of the vIPS, the FEF, and vIPS again. Finally, this source analysis indicates that both the EDAN and the LDAP may be generated by the vIPS, and the FEF can account for the ADAN.² The analyses on the individually estimated parameter values revealed no support that different brain areas are involved with processing relevant locations in these tasks. One could argue that the obviously different locations for the three tasks in Fig. 6 point to the involvement of other sources, but due to large individual differences, these different obtained loci are far from reliable. As a consequence, the current findings are in line with the PET and fMRI findings reported in the Introduction.

At first sight, our results seem to indicate that there is indeed high spatiotemporal overlap in the involvement of cortical brain areas in case of attentional orienting and the preparation of saccades, which would support the premotor theory of attention. However, the question may be raised whether the employed paradigm was really optimal for a possible separation of these two processes. Couldn't one argue³ that in our version of the saccade task attentional orienting was involved as well? As the arrow cue in our saccade task indicates the likely saccade goal, the appearance of this goal may simply need to be checked by attentional orienting, thereby providing an alternative explanation for the observed similarities. Furthermore, the benefit found on the speed of saccadic responses may be due to this attentional effect rather than to actual preparation of the saccade. As a consequence, the results of our first experiment do not allow a decision between two of the three initially mentioned options regarding the relation between attentional orienting and saccade preparation; attentional orienting and saccade preparation need not be the same, instead, there may be functional overlap, as attention may provide relevant information for executing the required saccade.

To provide a better test, a second experiment was carried out with the same choice-response task and a modified saccade task. In the new saccade task, no saccadic goal appeared, but delayed saccades (after approximately one second) had to be carried out towards the cued circle. Hence, attention was no longer relevant to check for the appearance of a subsequent stimulus. An important additional advantage of this procedure is a clear separation between stimulus-related and response-related processes. Namely, apart from a cue-locked ERP analysis for the saccade task, we additionally could perform a saccade-locked ERP analysis⁴ (see also Wauschkuhn et al., 1998), and examine whether comparable lateralized components are present in both analyses. In a

stimulus-locked analysis, those components will be enlarged that are related to processing the relevant stimuli, whereas in a response-locked analysis, those components will be highlighted that are related to execution of the required response. In line with the premotor theory of attention, comparable components should show up in both analyses, though being more pronounced in the response-locked analysis, as activity is thought to be more strongly related with executing actions. Indeed, in case of a stimulus- and response-locked analysis of the LRP (the EEG index for hand-specific motor preparation), it is commonly observed that the amplitude of the LRP is somewhat larger in the response-locked analysis (e.g. see Van der Lubbe et al., 2001; Verleger et al., 2005). If, however, attention mainly provides relevant information for executing the required saccade by coding the relevant location, then no clear components in the response-locked analyses may be found. Thus, apart from the exclusion of a confounding, Experiment 2 allows us to perform an additional, more crucial test for the premotor theory of attention.

3. Experiment 2

3.1. Methods

Several aspects were the same as in Experiment 1. Relevant changes in the methods are given below.

3.1.1. Participants

Informed consent was obtained from 18 participants. Unfortunately, eight participants had to be removed from the analysis, either because of too many eye movements and/or artifacts (>50%) during critical time intervals or because of procedural errors (five), which left 10 participants, mean age 21.4 years, nine right- and one left-handed.

3.1.2. Stimuli, tasks, procedure, apparatus, and recording

Participants performed two tasks, each consisting of 640 trials. In the saccade task, participants were instructed to make a delayed eye movement towards the cued side at approximately 1 s after cue onset, which we checked online by visual inspection of the hEOG, and offline, by analysis of the hEOG. In contrast with Experiment 1, the circle on the side of the required saccade direction remained unfilled. In the choice-response task, left and right buttons were now fixed in one response box, which were placed on a hand-rest in front of the participant. EEG and EOG were recorded at 1000 Hz, and were digitally filtered (TC = 5.0 s, low-pass filter of 100 Hz, notch filter of 50 Hz) by Vision Recorder.

3.1.3. Data analysis

Trials with detectable sideward eye movements from cue onset until target onset in the choice-response task, and from cue onset until 750 ms after cue onset in the saccade task were removed from the analyses. This procedure left on average 82.1% of the trials in the choice-response task, and 83.8% of the trials in the saccade task.

3.1.3.1. Behavioral measures. For the choice-response task, RTs and the proportion of correct responses (PCs) were

² Of course, this interpretation depends on the assumptions made regarding the choice of free and fixed parameters. Nevertheless, the topography of the EDAN and LDAP seems quite comparable, which, apart from earlier mentioned reasons, additionally justifies our choice to model two symmetrical dipole pairs.

³ Thanks are due to two reviewers of this paper who raised this crucial point.

⁴ This analysis was not carried out for the saccade task in Experiment 1 as in that case effects may be partially due to appearance of the saccadic goal, and stimulus- and response-related processes cannot be separated so easily in that task.

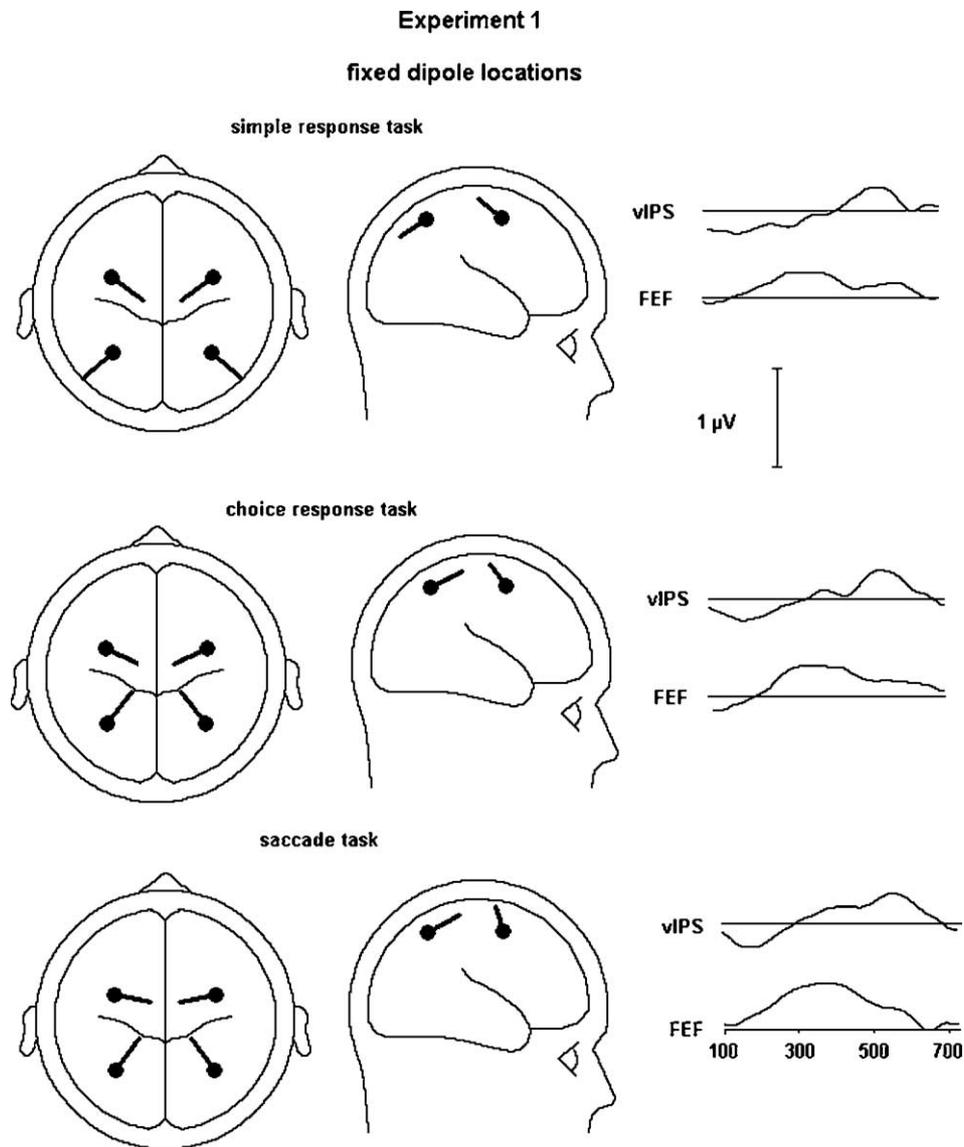


Fig. 5 – Estimated source orientations and source waveforms for left and right sources in the vIPS and FEF determined with BESA, for lateralized activity from 200 until 660 ms after cue onset for the simple-response task ($RV = 12.5\%$), the choice-response task ($RV = 13.7\%$), and the saccade task ($RV = 11.0\%$) in Experiment 1. To facilitate comparisons with the observed direction-related ERPs and the different tasks, activity of vIPS was inverted for the choice-response and the saccade task.

evaluated statistically by repeated measures analyses of variance (ANOVA) with the factors side (left or right) and cue validity (valid vs. invalid). In addition, average saccadic response times and proportion of correctly executed saccades were determined for the saccade task.

3.1.3.2. EEG parameters. Trials with artifacts and incorrect responses were removed, which left 72.9% of the trials in the choice-response task, and 78.5% of the trials in the saccade task. Ocular correction of the EEG was carried out to correct for the contribution of below-threshold eye movements by employing the method of Gratton et al. (1983). Analyses across consecutive intervals containing the EDAN, ADAN, and LDAP (set at the intervals determined in Experiment 1) were performed with the factors task (2), lateral-medial axis (2), and anterior-posterior axis (7). Saccade-locked lateralized

ERPs were additionally determined for the saccade task, with the baseline set from 100 to 0 ms before cue onset, and were examined for the presence of lateralized components related to the actual execution of the saccade. Finally, source analyses were performed on observed lateralized activity (for details see Experiment 1).

3.2. Results

3.2.1. Behavioral measures

RTs and PCs for the choice-response and the saccade task are compiled in Table 1. In the choice-response task, responses were always faster, $F(1,9) = 25.5$, $P = 0.001$, and more accurate, $F(1,9) = 19.0$, $P = 0.002$, for validly than for invalidly cued targets. The proportion of responses in catch trials in the choice-response task amounted to 2.0%.

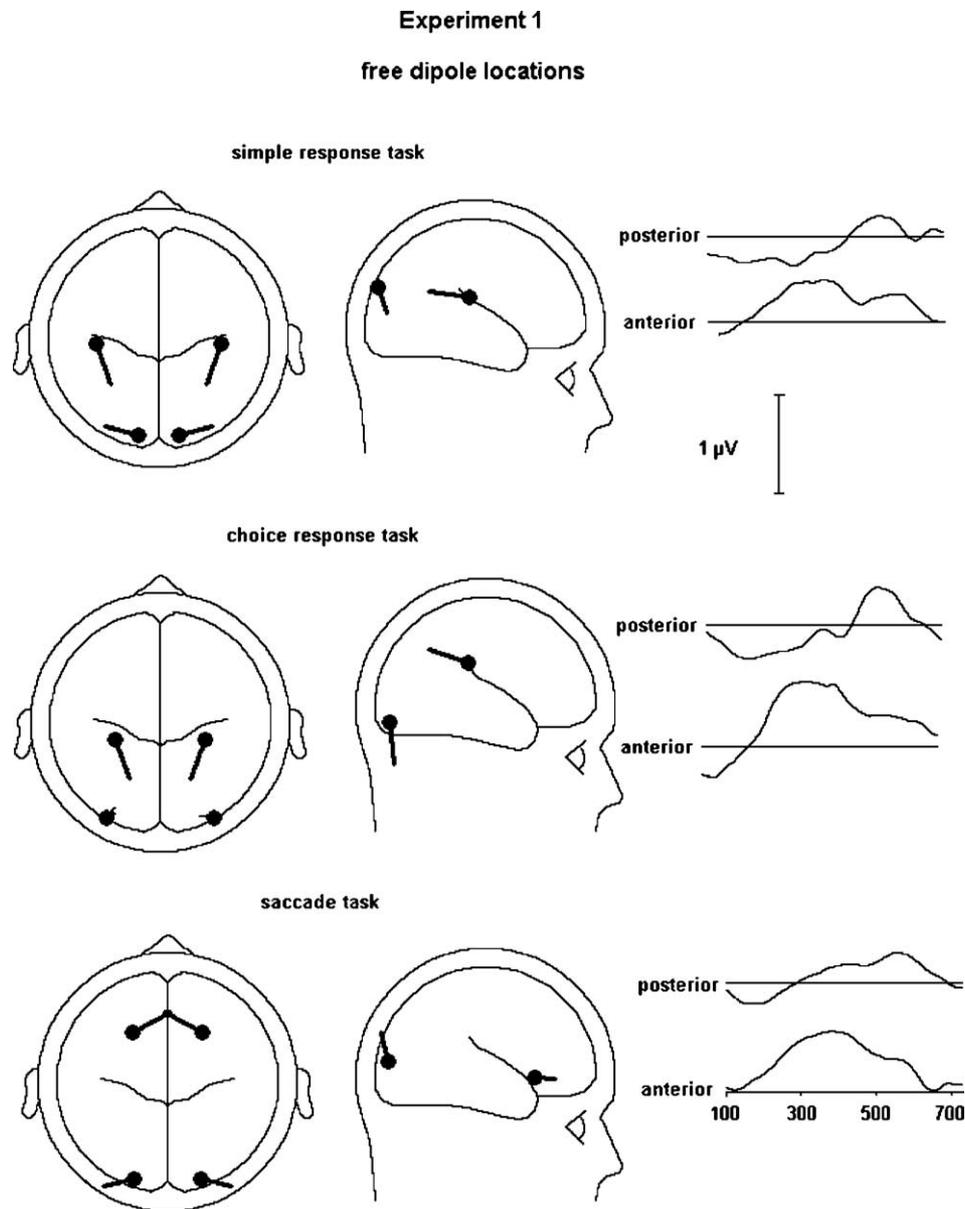


Fig. 6 – Estimated source locations and orientations for two symmetrical dipole pairs with free locations parameters for lateralized activity from 200 until 660 ms after cue onset for the grand averages in the simple-response task ($RV = 3.6\%$), the choice-response task ($RV = 3.9\%$), and the saccade task ($RV = 2.9\%$) in Experiment 1. For reasons given in Fig. 5, posterior activity in the choice-response task and anterior activity in the saccade task are inverted.

3.2.2. Lateralized EEG potentials

Cue-direction-related lateralized ERPs for the two tasks are displayed in Fig. 7 (cue-locked) and Fig. 9 (saccade-locked), and spline maps at relevant time points are given in Figs. 8 and 12.

3.2.2.1. EDAN. Analyses included the factors time window (200–240, 240–280, 280–320 ms), task (2), lateral–medial axis (2), and anterior–posterior axis (7). A main effect of task, $F(1,9) = 11.6$, $P = 0.008$, reflected larger negativity in the saccade task than in the choice-response task. A main effect of anterior–posterior axis, $F(6,54) = 6.5$, $\epsilon = 0.57$, $P = 0.001$, lateral–medial axis, $F(1,9) = 6.1$, $P = 0.036$, and an interaction between anterior–posterior axis and lateral–medial axis were

found, $F(6,54) = 5.3$, $\epsilon = 1.0$, $P < 0.001$, which reflected a larger difference at posterior sites between lateral and medial areas (see Fig. 7). A separate analysis for the most posterior sites (PO4/3 and PO8/7) revealed that the effect along the lateral–medial axis, $F(1,9) = 5.4$, $P = 0.045$, was larger in the saccade task than in the choice-response task (task \times lateral–medial axis: $F(1,9) = 6.0$, $P = 0.037$).

A separate analysis for the choice-response task revealed a main effect of anterior–posterior axis, $F(6,54) = 4.5$, $\epsilon = 0.55$, $P = 0.009$, and a nearly significant interaction between anterior–posterior axis and lateral–medial axis, $F(6,54) = 2.4$, $\epsilon = 0.68$, $P = 0.062$. A separate analysis for the saccade task revealed a main effect of anterior–posterior axis, $F(6,54) = 3.9$, $\epsilon = 0.40$, $P = 0.029$, a main effect of lateral–medial axis, $F(1,9) = 15.0$,

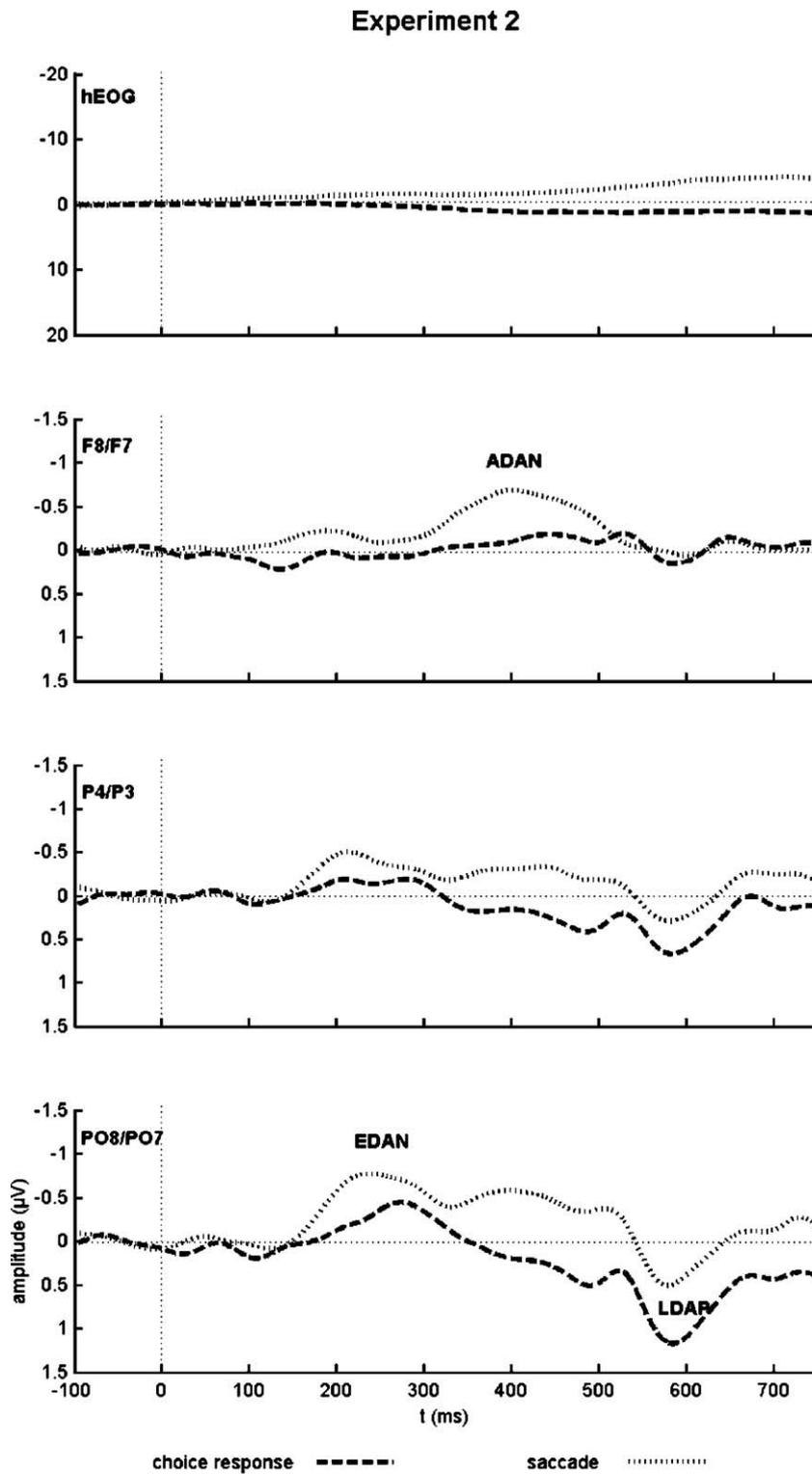


Fig. 7 – Cue-locked direction-related ERPs (ERLs) in the choice-response and the delayed saccade task of Experiment 2 are displayed for the F8/7, the P4/3, and the PO8/7 electrodes. The hEOG waveforms show that no large eye movements were made towards the relevant location.

$P = 0.004$, and a significant interaction between anterior-posterior axis and lateral-medial axis, $F(6,54) = 4.0$, $\epsilon = 0.72$, $P = 0.007$. The latter two analyses show that the EDAN was indeed present in both tasks.

3.2.2.2. ADAN. The factor time window had four levels (360–400, 400–440, 440–480, 480–520 ms). A main effect of time window, $F(3,27) = 9.3$, $\epsilon = 0.71$, $P = 0.001$, anterior-posterior axis, $F(6,54) = 3.1$, $\epsilon = 0.58$, $P = 0.035$, and task was

Experiment 2

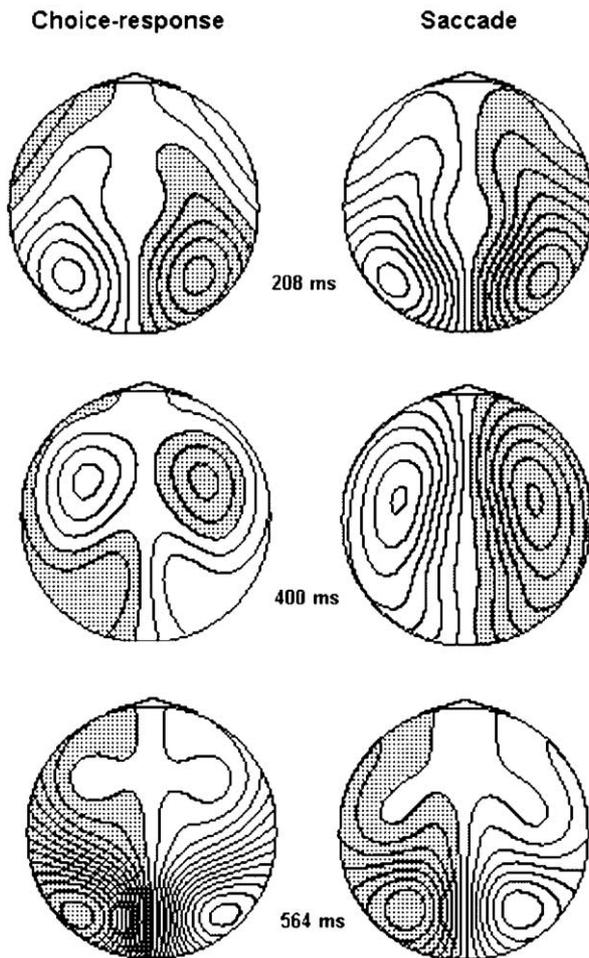


Fig. 8 – Spline maps determined by BESA around the maxima of the EDAN, ADAN, and the LDAP for the choice-response, and the saccade task in Experiment 2. The crossing of a line implies a change of $0.1 \mu\text{V}$, where negativity is indicated by hatching. For the right posterior positivity at 564 ms after cues onset, this implies that the maximum was larger than $1.2 \mu\text{V}$ in the choice-response task, and larger than $0.6 \mu\text{V}$ in the saccade task.

found, $F(1,9) = 18.0$, $P = 0.002$. An interaction between time and lateral–medial axis, $F(3,27) = 4.4$, $\epsilon = 0.72$, $P = 0.024$, and between time, anterior–posterior axis, and lateral–medial axis was found, $F(18,162) = 2.4$, $P = 0.036$, which seems due to the ADAN peaking at 400 ms above lateral frontal sites. The interaction between task and lateral–medial axis, $F(1,9) = 8.4$, $P = 0.018$, suggests that the ADAN was larger in the saccade task than in the choice-response task. Separate analyses for the choice-response task revealed an interaction between time, anterior–posterior axis, and lateral–medial axis, $F(18,162) = 2.8$, $\epsilon = 0.67$, $P = 0.002$, whereas a separate analysis for the saccade task revealed main effects of time, $F(3,27) = 7.4$, $\epsilon = 0.93$, $P = 0.001$, anterior–posterior axis, $F(6,54) = 3.5$, $\epsilon = 0.72$, $P = 0.014$, and lateral–medial axis, $F(1,9) = 12.8$, $P = 0.006$. Inspection of Figs. 7 and 8 indeed shows that a frontal negative component in the saccade

task, being nearly absent in the choice-response task, was responsible for these effects.

3.2.2.3. LDAP. The factor time window had two levels (560–600, 600–640 ms). Main effects of time, $F(1,9) = 5.4$, $P = 0.045$, anterior–posterior axis, $F(6,54) = 12.1$, $\epsilon = 0.68$, $P < 0.001$, and lateral–medial axis, $F(1,9) = 7.5$, $P = 0.023$, were found. In addition, a significant interaction between lateral–medial axis and anterior–posterior axis, $F(6,54) = 2.6$, $\epsilon = 0.77$, $P = 0.045$ was found. These effects seem to reflect the larger LDAP at the lateral posterior sites (PO8/7) in both tasks (see Fig. 8). A separate analysis for the most posterior sites revealed an interaction between task and lateral–medial axis, $F(1,9) = 6.1$, $P = 0.034$, which suggests that the LDAP is slightly larger in the choice-response task.

3.2.2.4. Saccade-locked lateralization. No clear saccade-locked lateralized activity seems present in the saccade task only until shortly before the actual execution of the saccade (Fig. 9). Time intervals (40 ms) from 1000 to 40 ms before saccade onset revealed no difference from baseline, $F(1,9) < 1.5$, $P > 0.24$, and no electrode effect, $F(24,216) < 1.2$, $P > 0.34$. We only found a weak trend effect for a deviation from baseline from 40 to 0 ms before saccade onset, $F(1,9) = 3.2$, $P = 0.11$. Inspection of Fig. 9 suggests that shortly before the rise of the hEOG, increased lateralized positivity was present at the frontal sites, with a maximum from 45 to 25 ms, which could reflect activity from the FEF (see the spline and dipole map in Fig. 12). To examine whether this effect actually preceded the saccade, we performed analyses for 10 ms windows for the F8/F7 electrode pair and the hEOG, and additionally performed a correlational analysis. For the 45–35 ms window, activity at the F8/7 electrode pair differed from baseline, $t(9) = 2.8$, $P = 0.022$, which was not the case for the hEOG, $t(9) = 1.2$. In addition, the correlation between activity at the hEOG and the F8/7 electrode was far from significant ($P = 0.84$). For the 35–25 ms window, activity differed from baseline for the F8/F7 electrode, $t(9) = 4.6$, $P = 0.001$, and for the hEOG, $t(9) = 2.3$, $P = 0.045$. The correlation for that interval approached significance ($P = 0.082$).

3.2.3. Source analyses

Estimated source orientations, source waveforms, and source locations for the cue-locked grand averages in the choice-response and the saccade task, either with fixed or with free location parameters, are displayed in Figs. 10 and 11. In case of fixed dipoles (RV was 20.7% in the choice-response task, and 8.8% in the saccade task) at the vIPS and FEF, comparable activations over time are found for the posterior dipole, and also for the anterior dipole, although activity in the choice-response task seems less strong. With free location parameters (RV was 8.9% in the choice-response task, and 4.9% in the saccade task), comparable solutions were found in both tasks, also somewhat comparable to the solution with fixed locations, although with different orientations. A MANOVA on the individually estimated dipole parameters (Mean RV: 19.8% (9.5) in the choice-response task, and 16.9% (8.5) in the saccade task) revealed a main effect of source location, $F(3,7) = 15.0$, $P = 0.002$, which reflected a main difference along the anterior–posterior axis, $F(1,9) = 36.1$, $P < 0.001$, and the lateral–medial

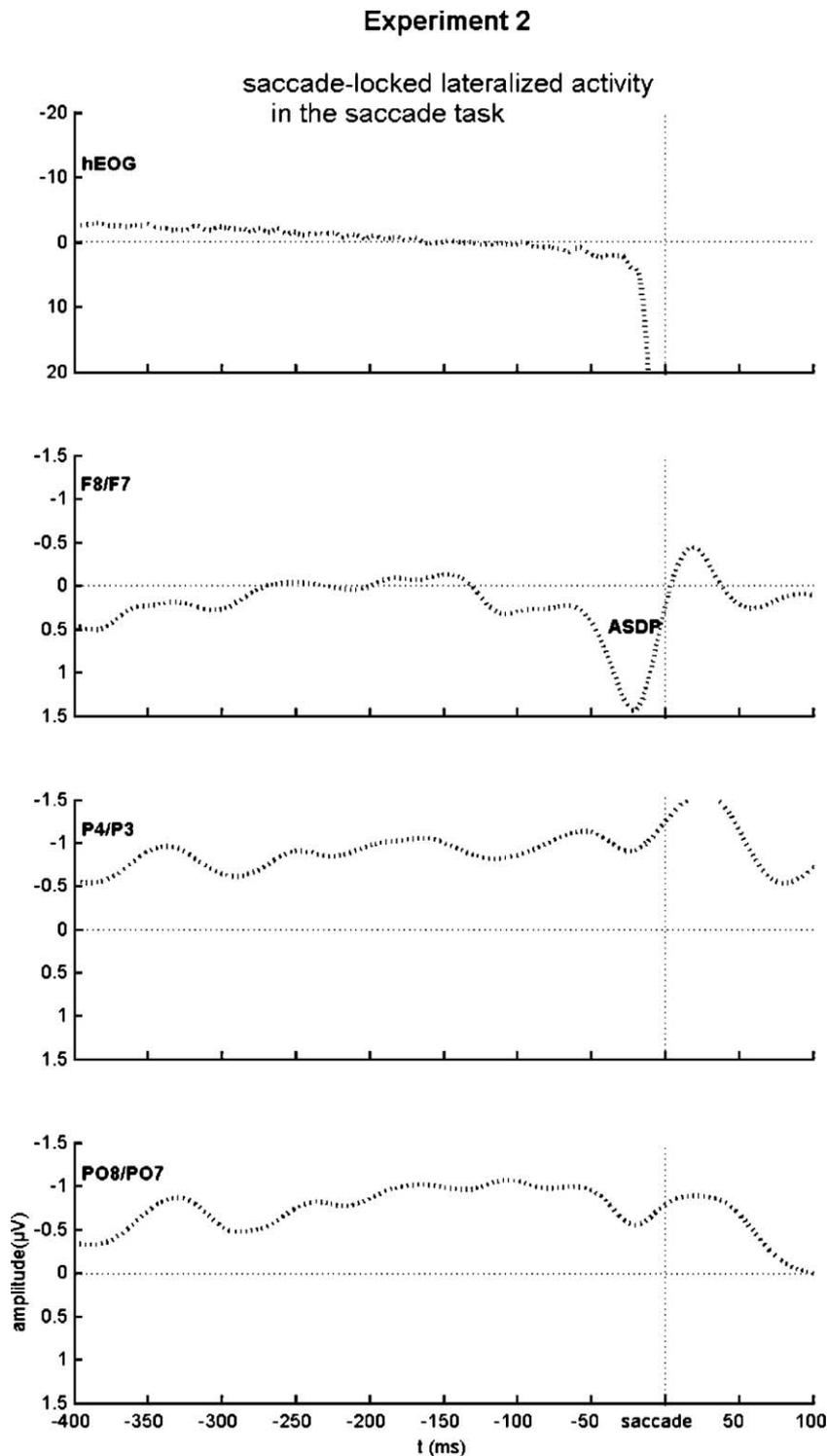


Fig. 9 – Saccade-locked direction-related lateralizations in the delayed saccade task of Experiment 2 for the F8/7, the P4/3, and the PO8/7 electrodes. The hEOG indicates that the saccade started shortly before its onset was detected. The anterior saccade direction-related positivity (ASDP) started shortly before the actual execution of the saccade, which may indicate that this component reflects a cortical trigger for execution of the required saccade (see, Schall, 1991).

axis, $F(1,9) = 5.5$, $P = 0.044$. The latter effects indicated that the anterior source had a more lateral locus than the posterior source. No other effects for estimated location parameters were observed, $F_s < 1.0$, $P_s > 0.47$. The sources seemed to differ in their orientations between tasks, $F(3,7) = 5.4$, $P = 0.031$;

however, separate analyses for the anterior and the posterior sources revealed no effects, $F(3,7) < 1.6$, $P > 0.27$. No other effects were found on estimated source orientations, $F_s < 1.0$, $P_s > 0.56$, and no effects were found on estimated source strengths, $F_s < 2.3$, $P > 0.16$.

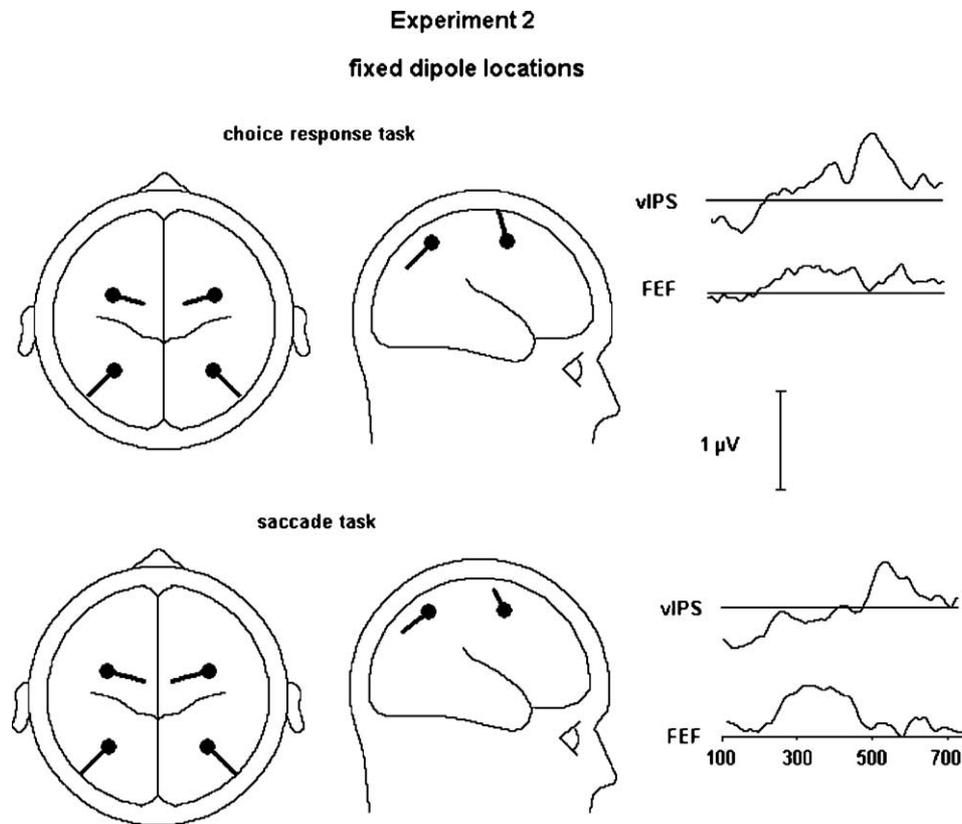


Fig. 10 – Estimated source orientations and source waveforms for left and right sources in the vIPS and FEF determined with BESA, for lateralized activity from 200 until 660 ms after cue onset for the choice-response task (RV = 20.7%), and the delayed saccade task (RV = 8.8%) in Experiment 2.

Finally, a source analysis was performed on activity shortly preceding the execution of the eye movement in the saccade task (see Fig. 12). The analysis with fixed dipole sources in vIPS and the FEF from 55–35 ms before saccade onset revealed a clear peak for the FEF dipole and no clear components for the vIPS dipole (RV: 27.7%). A second analysis with free location parameters and only one dipole pair revealed a comparable solution with only slightly more RV (32.7%). As a consequence, the contribution of a posterior source to actual execution of a saccade seems negligible.

3.3. Discussion of Experiment 2

The behavioral data in the choice-response task replicated the findings of Experiment 1, demonstrating a clear advantage for validly as compared to invalidly cued trials, which can be ascribed to attentional orienting. Saccadic responses occurred slightly earlier, measured relative to cue onset, as compared to Experiment 1, but late enough to distinguish cue-related from saccade execution-related lateralized processing. The EDAN was present in both tasks, though being larger in the saccade task, whereas the ADAN seemed nearly absent in the choice-response task (see Figs. 7 and 8). The LDAP was present in both tasks, though somewhat more pronounced in the choice-response task. The dipole analyses on individual averages revealed no differences in estimated source locations between tasks. Furthermore, the analyses with fixed dipoles again

support the view that the EDAN and LDAP are likely to be generated by the vIPS whereas the ADAN is generated by the FEF. Analyses with free location parameters showed somewhat different solutions, but due to the reduced number of free parameters, the solution with fixed parameters may be preferred. Importantly, saccade-locked lateralized activity revealed one clear positive anterior component shortly before actual execution of the saccade, which is likely to arise from FEF, whereas no saccade execution-related activity seems to arise from vIPS, which indicates that this area plays no important role in the final execution of the saccade.

4. General discussion

Previous neuroimaging studies using PET and fMRI indicated that the brain areas involved in attentional orienting and the preparation and execution of saccades largely overlap. Specifically, results suggest that activity within the vIPS and FEF depends on the direction at which attention is focused, or the direction to which a saccade has to be prepared (see Corbetta and Shulman, 2002). These findings, combined with results from several behavioral studies examining the relation between saccade preparation and orienting towards visual (e.g. Deubel and Schneider, 1996; Kowler et al., 1995) and towards auditory stimuli (Rorden and Driver, 1997), favor the hypothesis that attentional shifts can be considered as

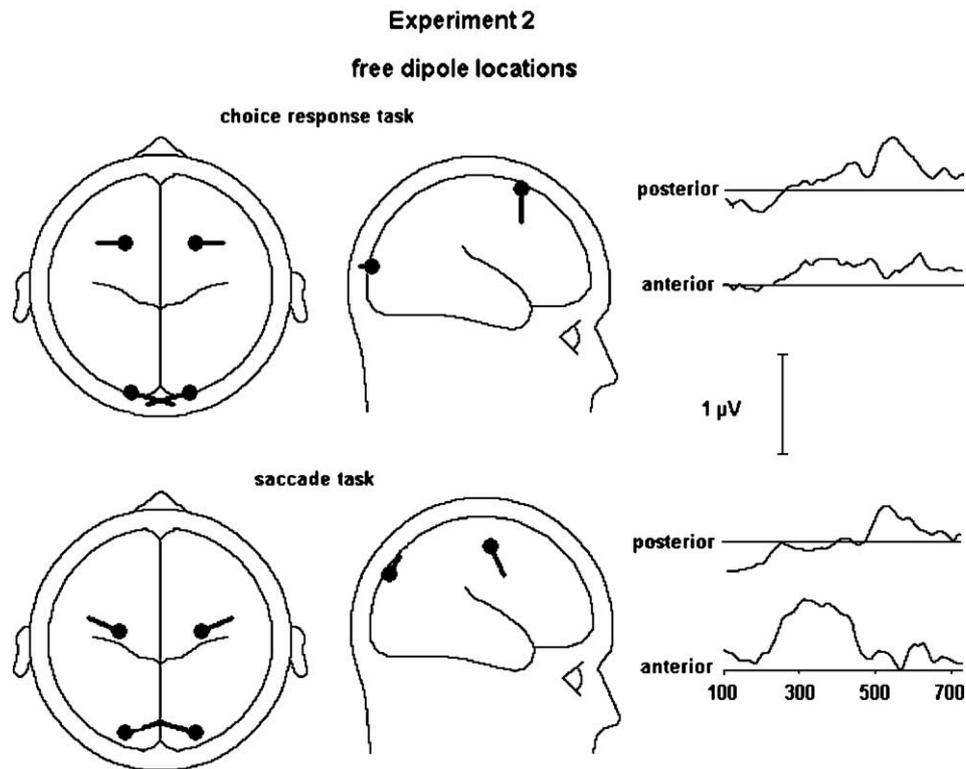


Fig. 11 – Estimated source locations and orientations for two symmetrical dipole pairs with free locations parameters for lateralized activity from 200 until 660 ms after cue onset for the grand averages in the choice-response task ($RV = 8.9\%$), and the delayed saccade task ($RV = 4.9\%$) in Experiment 2. Anterior activity in both the choice-response task and the saccade task is inverted to facilitate comparison with the direction-related ERPs.

unexecuted saccades. It may, however, also be argued that attentional orienting and saccade preparation only partially rely on the same processes (i.e. functional overlap), and these processes may even fulfill different roles for the tasks at hand. For example, whether vIPS and FEF are deployed at comparable moments in time and whether their activations are strongly related to actual execution of saccades or to coding positions relevant for action are not really known. To provide this information, we performed two experiments and focused on direction-related ERP components and also on activation patterns of the likely underlying sources during the interval in which participants either had to attend towards the probable location (left or right) of a target, or in which they had to prepare a saccade to the left or right.

For both experiments, it may be concluded on the basis of the behavioral data that participants indeed focused their attention at the requested positions. Participants, however, had problems suppressing their saccades (see also Van der Lubbe et al., 2005a), which is additionally illustrated by the necessity to remove some participants from the analyses. The latter aspects provide a first and important hint (see later) that saccade preparation and saccade inhibition are always to some extent involved in attentional orienting tasks. Analyses on the cue-locked direction-related ERPs showed the presence of the EDAN, the ADAN, and the LDAP in almost all attentional and saccade tasks in both experiments supporting the view that there is high spatiotemporal overlap between brain activities related to attentional orienting and to the planning

of saccades, although the amplitudes of these components differed between tasks. The EDAN was present in all conditions from 200 to 320 ms after cue onset, which replicates and extends the findings of several other studies. Source analyses with fixed source locations indicated that the EDAN is likely to arise from vIPS. In both experiments, source analyses with free location parameters resulted in a more posterior–inferior source for the EDAN, nevertheless, the solution with fixed location parameters may be preferred as it accords with PET and fMRI studies, which have much better spatial resolution, and it also reduces the number of free parameters to be estimated while keeping RV at an acceptable level (see footnote 1). Given the findings of Van Velzen and Eimer (2003), it seems likely that the EDAN reflects attentional selection of the relevant side of the cue. The ADAN was present from 360 to 520 ms after cue onset, which is comparable with the ADAN observed by Eimer et al. (2002), Nobre et al. (2000b), and Verleger et al. (2000). In our second experiment, the ADAN was clearly more pronounced in the saccade task and nearly absent in the choice-response task, which may indicate that this component is more specific for saccade preparation than for attentional orienting. In fact, one might argue that the presence of this component in attentional tasks is also related to saccade preparation, as there will always be a tendency to make an eye movement towards a to-be-attended location. Importantly, source analyses indicated that this activity may very well originate from the FEF, which provides another hint that saccade preparation and inhibition

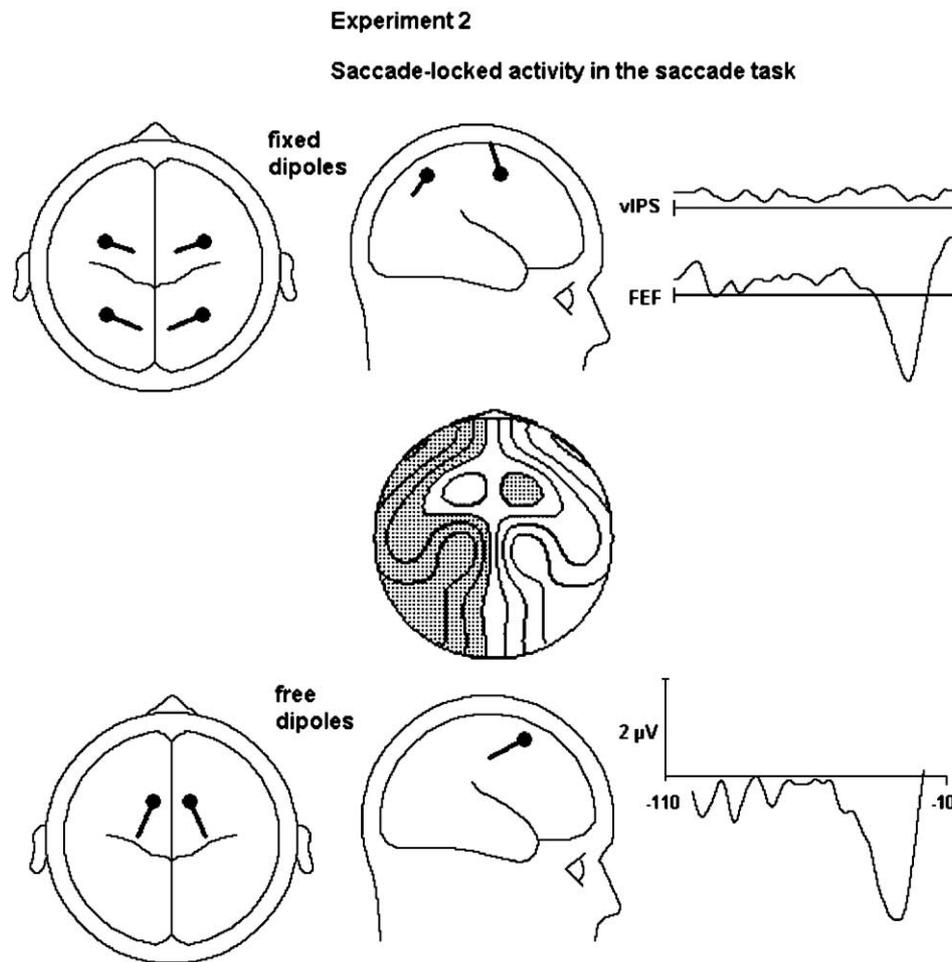


Fig. 12 – Estimated source locations, orientations, and source waveforms for activity shortly preceding the saccade (from 55 to 35 ms). RV in case of fixed dipoles at FEF and vIPS amounted to 27.7%. The spline map at 45 ms before the saccade shows a frontocentral locus. Finally, in case of one dipole pair, again a frontocentral locus was obtained near the FEF, with only slightly increased RV of 32.7%.

take place in attentional orienting tasks (cf. the recent paper by Praamstra et al., 2005, for very similar results of a dipole analysis of the ADAN). The LDAP was present from 560 to 640 ms after cue onset, which corresponds with the findings of Eimer et al. (2002), Nobre et al. (2000b), and Hopf and Mangun (2000). Source analyses also indicated that the LDAP may arise from vIPS. Most importantly, our second experiment clearly revealed that these lateralized components are not restricted to conditions with valid and invalid response cues in the saccade task, indicating that the observed components in this task cannot be ascribed to the requirement to focus attention at the saccadic goal.

The results of both experiments, especially from Experiment 2, point to the conclusion that attentional orienting and saccade preparation largely overlap, as comparable brain areas appear to be activated at comparable moments in time. Nevertheless, the results showed some quantitative differences, which may indicate that some processes are more relevant for attentional orienting, whereas other processes may be more relevant for saccade preparation. Specifically, the process reflected by the LDAP may be more relevant for attentional orienting, whereas the process reflected by the

ADAN may be more relevant for saccade preparation. Furthermore, it seems likely, based upon the hints in the previous section, that saccade-related processes are always to some extent involved in attentional orienting tasks. An implication could be that an appropriate test of the premotor theory of attention is nearly impossible. Fortunately, the result of our saccade-locked analysis, discussed in the following section, enables a way out.

A novel unexpected result from our second experiment seems to provide crucial information. We observed a clear positive anterior lateralized component shortly preceding the execution of the saccade, which may be denoted as an anterior saccade direction-related positivity (ASDP). Source analyses with free location parameters indicate that this ASDP component probably arises from FEF, which nicely accords with single cell studies (e.g. see Schall, 1991). In an experiment by Wauschkuhn et al. (1998), support was found for a negative parietal lateralized component related to actual execution of a horizontal saccade. However, some negative activation of frontocentral areas, possibly related to FEF activity, was found when saccades had to be made away from the cueing stimulus, which delayed saccadic response times. Possibly,

this delay better removed parietal cue-related processing. In another study by [Klostermann et al. \(1994\)](#), however, some support was found for a frontal saccade-related component (see also [Van der Lubbe et al., 2000](#)), but again negativity rather than positivity was observed. Thus, execution of a voluntary saccade to the left or the right is controlled by the FEF, which appears to be visible in the EEG as a short contralateral anterior positive component. Importantly, no saccade-locked parietal component was observed. As a consequence, the parietal cue-locked components (EDAN and LDAP) are not strongly related to actual execution of a saccade, which indicates that these components should not be interpreted as below-threshold activation of saccade motor programs. Obviously, these findings seem not in line with the premotor theory of attention. The anterior component (ADAN) arising from FEF, however, seems to be related to actual execution of the saccade, although the polarity of the saccade-locked SDAP component is reversed. A possible explanation for this reversal is that the observed negativity (ADAN) reflects saccadic inhibition, whereas the positivity reflects saccade activation, which additionally provides an explanation for the findings of [Klostermann et al. \(1994\)](#) and [Wauschkuhn et al. \(1998\)](#).

The reported findings seem to have several implications. First, the strong version of the premotor theory of attention as originally proposed by [Rizzolatti et al. \(1987\)](#) may be rejected, as parietal components indicative for attentional orienting, being clearly present in cue-locked analyses of both experiments, were absent in the saccade-locked analysis of Experiment 2. Source analyses additionally confirmed (see [Fig. 12](#)) that vIPS played no major role in saccade execution. As a consequence, attentional orienting cannot be equated with below-threshold activation of saccade motor programs. Apart from this strong version of the premotor theory, it has also been argued that attentional orienting may be equated with the preparation of actions in general, at a supramodal level (e.g. see [Eimer et al., 2005](#)). This version would also predict more well-defined parietal components in the response-locked analysis, which we did not observe.

The relation between attention and action selection appears to be less direct than the premotor theory proposes. In previous papers, which were focused on the relation between several lateralized components and the planning of lateral hand and eye movements ([Van der Lubbe et al., 2000](#); [Wauschkuhn et al., 1997](#)), a distinction was made between two preparatory processes. First, a general decoding process may be involved that produces a supramodal direction code on the basis of sensory information.⁵ This process may in fact be the same as attentional orienting, although there may also be functional overlap. Secondly, the output of this decoding process may be used by effector-specific processes to activate the required response. This general decoding process may originate from vIPS, whereas saccade-specific processes may

originate from FEF. In numerous studies, this general decoding process (reflected in the EDAN and the LDAP) seems not only relevant for saccade preparation but also for hand preparation, target identification, and target detection, and also when the modality of a forthcoming target is auditory or tactile, which underlines the generality of this process ([Eimer et al., 2002, 2005](#); [Harter et al., 1989](#); [Hopf and Mangun, 2000](#); [Jentzsch and Leuthold, 2002](#); [Nobre et al., 2000b](#); [Van der Lubbe et al., 2000, 2005a](#); [Wauschkuhn et al., 1997](#); [Yamaguchi et al., 1994, 1995](#); for fMRI support see [Astafiev et al., 2003](#)). Moreover, the presence of the ADAN in many attentional tasks is, given its likely underlying source in FEF and its counterpart in response-locked analyses, probably a reflection of saccadic inhibition, which in some tasks may be more relevant, as the tendency to make an eye movement may differ between tasks. As a consequence, this component may have nothing to do with attentional orienting, but may simply arise because participants have the natural tendency to look at relevant locations, which they have to inhibit, in line with the instructions. To paraphrase what may be going on during the time interval in which an endogenous cue indicates the likely position (e.g. here to the right) of a forthcoming target: “Ah, the right side is relevant” (EDAN); “... I shouldn’t look at the right...” (ADAN); “but focus my attention over there” (LDAP).

In conclusion, a comparable activation pattern over time was found for cue-locked direction-related ERPs when a saccade had to be prepared and when attention had to be oriented towards one side. Source analyses confirmed that there is large spatiotemporal overlap and point to the involvement of vIPS and FEF in the examined tasks. However, parietal activation was not strongly related to the actual execution of saccades, which disfavors the premotor theory of attention but points to functional overlap between attentional orienting and saccade preparation because attentional orienting seems to provide crucial input for the preparation and execution of actions, including saccades.

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⁵ This proposal dates back to [Mountcastle et al. \(1975\)](#) and [Mesulam \(1990\)](#), but can also be related with the view on motor preparation as forwarded by [Jentzsch and Leuthold \(2002\)](#), who distinguished between two levels of motor programming, i.e. abstract and effector-specific programming, with an intermediate motor buffer.

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