Research Report

Electrocortical correlates of control of selective attention to spatial frequency

Tineke Grent-'t-Jong[a,b], Koen B.E. Böcker[a], J. Leon Kenemans[a,]*

[a]*Department of Psychonomics and Psychopharmacology, Utrecht University, P.O. Box 80082, 3508 TB Utrecht, The Netherlands*
[b]*Center for Cognitive Neuroscience, Duke University, Durham, NC 27705, USA*

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ABSTRACT

In the present study, we investigated control of selective attention to spatial frequency patterns, using a cueing paradigm. Subjects either used the instruction embedded in a word cue to prepare for the upcoming test stimulus (transient attention condition) or used the instruction they received before a block of trials (sustained reference condition), under completely similar stimulus conditions. The pattern of differential cue responses between these two conditions, reflecting top–down attentional control processes, was different between two groups of subjects, effectively canceling each other out. Despite comparable behavioral performance on both cues and targets, one group ($n = 4$) elicited a fronto-central–parietal positivity, starting 500 ms postcue over frontal and prefrontal areas, later including more central and posterior scalp sites, whereas another group ($n = 8$) started 400 ms postcue over central sites with a negativity, growing in strength over time and stabilizing over fronto-central sites. Only the group of eight subjects showed some evidence of occipital pretarget biasing activity. Independent of group, source modeling of the attentional control activity showed that attentional control was initiated in anterior, not posterior, parts of the brain. Furthermore, different underlying sources were found for both groups, in addition to signs of differential processing of target stimuli. Possible individual differences in attentional control ability and its relation to usage of different brain areas to deal with the task demands are discussed in more detail.

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1. Introduction

Attention serves to select and guide processing of certain stimuli or responses over others. Setting attention selectively to specific events over others is termed 'attentional control'. Attentional control can be invoked by changes in task demands or (bottom–up) by salient changes in the environment and also even before the selectively attended events really occur. Top–down control mechanisms of selective attention have been studied now for more than 20 years, initially only with the use of behavioral or event-related potential (ERP) methods, but nowadays, more predominantly by using brain-imaging techniques such as functional magnetic resonance imaging (fMRI). One straightforward paradigm to study these top–down attentional control mechanisms is the so-called cueing paradigm, in which an attention-directing cue is followed by a target stimulus. This paradigm capitalizes on the possibility that attention may be set selectively by the

attentional control system before the selectively attended event occurs. The brain responses recorded during the cue-target interval are thought to reflect top–down attentional control activity.

The majority of these attentional control studies have focused on the control of visual spatial attention. The global pattern of results found across brain-imaging (fMRI/PET) studies features three characteristics. First, across most studies, there seems to be a core network of cortical areas implementing attentional control, consisting of parietal areas surrounding the intra-parietal sulcus (sometimes also including more superior parietal areas), and medial–dorsal frontal premotor areas, often including the frontal eye fields (Corbetta and Shulman, 2002; Rosen et al., 1999; Shulman et al., 1999; Vandenberghe et al., 2000; Woldorff et al., 2004). Second, numerous studies also report additional involvement of dorsal and ventral lateral prefrontal areas (Giesbrecht et al., 2003; Hopfinger et al., 2001; MacDonald et al., 2000; Weissman et al., 2002; Weissman and Woldorff, 2004). This prefrontal involvement does not seem to depend on whether attention is directed to locations in space or to a non-spatial feature like color. Rather it may relate to demands on working memory (Corbetta et al., 2002) in relation to the anticipated presence of distractors to the target that may even elicit competing response tendencies (Weissman et al., 2002; Yamaguchi et al., 2000). Third, most models on attentional control assume that, in anticipation of the target, a 'higher' controlling area 'biases' the activity in target-specific areas (e.g., visual cortex), making these areas more selectively sensitive to the cued target features (Desimone, 1998; LaBerge, 2001). Indeed, some fMRI studies have revealed retinotopic overlap between areas activated by instruction cues and those activated by targets (Giesbrecht et al., 2003; Hopfinger et al., 2000). In addition, studies that have used ERPs to study visual spatial attention control mechanisms have confirmed the suggestion of a frontal–parietal network controlling baseline activity in visual cortical areas. More specifically, the better temporal resolution available with this technique revealed that activity over occipital–temporal scalp sites, specific to the location of the expected target stimulus, is initiated later in the cue-target interval than activity over frontal and parietal scalp sites (Harter and Anllo-Vento, 1991; Hopf and Mangun, 2000; Nobre et al., 2000; Slagter et al., 2005a; Talsma et al., 2005; Yamaguchi et al., 1994).

Far less effort has been devoted to investigating attentional control (using ERPs) in relation to visual features other than locations in space (Slagter et al., 2005a,b; Yamaguchi et al., 2000). In the Yamaguchi et al. (2000) study, subjects were cued to local or global features of an hierarchically structured letter. Differential effects of attending to global or local features started as early as 240 ms postcue over right temporal–parietal and left posterior temporal areas. In line with these results, an initial posterior phase of directing attention to the color of an expected target stimulus was reported in two studies by Slagter et al. (2005a,b) (with the onset around 340 ms postcue in one study and around 260 ms postcue in the other study). The pattern of results across these three studies suggests a sequence of first posterior cortical and secondly anterior cortical activity. This pattern may be consistent with the medial–dorsal core network outlined above but with a reverse

temporal order of activations as compared to most of the spatial studies discussed above. In addition, it cannot be excluded that the anterior sources are contributed to by lateral, rather than medial prefrontal activation. In one of the two Slagter et al. studies, the posterior–anterior sequence was preceded by an even more posterior (as well as more lateral) activation, which could well originate in the ventral pathway. In addition, the anterior part of the sequence was accompanied by posterior activity suggestive of a biasing effect.

The present study complemented the studies reported by Slagter and colleagues in a number of ways. First, attentional control was investigated in relation to yet another non-spatial visual feature: spatial frequency. Secondly, rigorous measures were taken with respect to the reference condition. Special attempts were made to ensure that it differed from the attentional control condition only in terms of whether the cue could (and should) be used to direct attention selectively. More specifically, cues did not differ in physical aspects between conditions and were very intuitive with respect to the features of the target they were cueing for. This should have ensured quick and easy similar cue discrimination and identification in both conditions, thereby preventing differences in early cue processes that do not reflect top–down attentional control proper. Also, a choice-reaction task with respect to the cue stimuli was added, to ensure that cues would be discriminated equally in attention and reference conditions. Furthermore, test stimuli as well as the task on target test stimuli were similar between the attention and reference condition, preventing differential general strategies in preparation for the anticipated target detection task. The
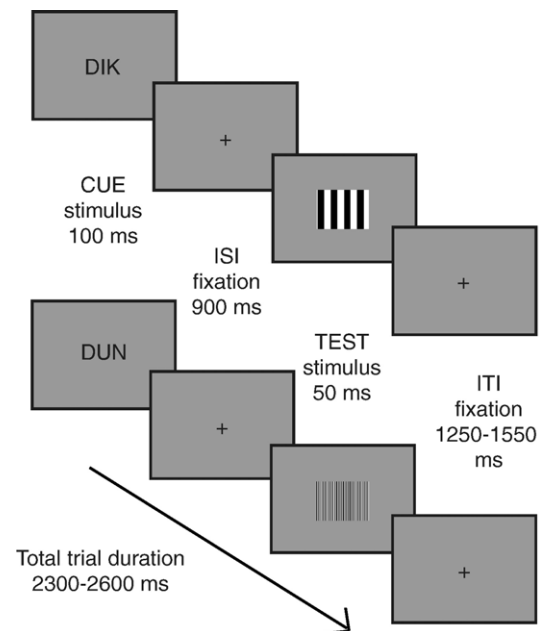

Fig. 1 – Layout of the trial structure and stimuli as used for both Attention and Reference condition. Word cues ("DIK" and "DUN") were presented for 100 ms and were followed 900 ms later by either a low spatial frequency (0.6 c/d) grating (see upper trial; third panel) or high spatial frequency (4.8 c/d) grating (see lower trial; third panel). Intertrial intervals (ITI) were jittered between 1250 and 1550 ms.

attention and reference condition thus only differed in terms of using the task instruction embedded in the cue on a trial-by-trial basis (leading to transient task preparation) or using a task rule instructed before the onset of a block of trials (leading to sustained task preparation). Using such a tightly controlled design, we expected to find ERP indices of attentional control mechanisms in the context of a non-spatial selective attention task. In particular, we were interested in the temporal sequence of posterior and anterior components of attentional control (Fig. 1).

Because transient and sustained selective attention have been shown to affect target processing differently (Eimer, 1997), we also looked at the attentional modulation of the cortical response to the target stimuli, to explore whether these would differ between the two conditions as well.

2. Results

2.1. Behavioral results

2.1.1. Responses to cues
Subjects performed a two-choice reaction time task to the cues, indicating the presence of a Low Spatial Frequency (LSF) cue (word "DIK") by pressing a left button with their left index finger, and the presence of a High Spatial Frequency (HSF) cue (word "DUN") by pressing a right button with their right index finger. In addition, they were instructed to press the same button as used for the cue response to indicate that the presented test stimulus matched the cued spatial frequency (in the Attention condition) or the task-rule as instructed before the start of the run (in the Reference condition). Note that this means that during some Reference condition cue-target trials, the spatial frequency mapping was different (incongruent) for cues and targets. These incongruent trials consisted of the HSF-cue from the Reference Low condition (LSF-pattern is always the target) followed by a LSF-target, and a LSF-cue from the Reference High condition (HSF-pattern is

always the target followed by a HSF-target). As we discuss in more detail in Experimental procedures, incongruent trials were excluded in the main behavioral analyses (as well as in the ERP analyses), and we included behavioral analyses to test the effect of incongruency on behavior for both cue and target responses of the Reference condition.

Table 1 summarizes all grand-average values (n = 12) for mean RTs, percentage of errors or false alarms, percentage of missed trials, and percentage of outliers, separately for the different cue and target conditions. In the main analyses of the 2-choice RT task to cues, concerning the attention and congruent reference conditions, no significant differences between our two conditions were found for mean RTs and percentage of outliers. Subjects responded equally fast in the Attention condition, without differences in percentages of outliers. In contrast, however, significant main effects of CONDITION were found for percentage of errors ($F(1,11)$ = 6.1, $P < 0.03$) and missed trials ($F(1,11)$ = 6.2, $P < 0.03$). Compared to the Attention condition, subjects made more hand errors in the Reference condition and missed also more cue responses in the Reference condition.

Additional ANOVAs, including both congruent and incongruent cue trials from the two Reference conditions, revealed no effect of CONGRUENCY (neither on mean RTs, nor on any of the accuracy measures).

In sum, cue identification processes were more accurate in the Attention than in the Reference condition but showed no differences in speed of processing. Furthermore, incongruency in the Reference condition did not affect the subjects behavioral performance to the cues.

2.1.2. Responses to targets
Repeated measurement ANOVAs on congruent LSF and HSF targets from the Attention and congruent Reference conditions did not reveal any significant differences, neither in processing speed (mean RTs), nor in accuracy (percentage of false alarms, missed targets, or outlier responses). The additional repeated measurement ANOVA

	Condition	Mean RT in ms	%Outliers	%Missed	%Errors
Table 1 – Overview of behavioral performance measurements for 2-choice reaction time (RT) task to cues and Go–NoGo task to test stimuli					
Cues					
LSF-cues	Attention	468	3.8	2.2	2.2
HSF-cues	Attention	460	4.2	1.9	2.0
LSF-cues (cong)	Reference Low	482	5.2	3.0	3.5
HSF-cues (incg)	Reference Low	470	5.2	2.4	3.1
LSF-cues (incg)	Reference High	480	5.1	4.8	2.8
HSF-cues (cong)	Reference High	472	5.7	4.2	3.6
	Condition	**Mean RT in ms**	**%Outliers**	**%Missed**	**%False alarms**
TARGETS					
LSF-targets	Attention	345	3.0	4.0	0.1
HSF-targets	Attention	355	3.1	3.3	0.2
LSF-targets (cong)	Reference Low	347	1.5	4.3	0.3
LSF-targets (incg)	Reference Low	360	1.9	3.2	0.7
HSF-targets (cong)	Reference High	344	2.3	3.0	0.5
HSF-targets (incg)	Reference High	359	2.9	5.1	1.6

LSF—low, HSF—high spatial frequency, incg—incongruent mapping, cong—congruent mapping.

for all target trials in the Reference conditions (including congruently cued and incongruently cued targets) revealed that subjects responded significantly slower to incongruently cued targets than to congruently cued targets (main effect of CONGRUENCY; $F(1,11) = 18.4$, $P = 0.001$).

Because these congruency effects on target responses may actually reflect effects of incongruence on attentional control (see 5.4), they justify the exclusion of incongruent trials from the final ERP analyses (described below).

2.2. ERP and source-modeling results

2.2.1. ERPs to cues
To detect significant ERP differences between the Attention and Reference condition, a Region of Interest (ROI) approach was used. More specifically, data from 10 time windows (collapsed over 100 ms of data from cue until target onset) and six different ROIs (PreFrontal, Frontal, Central, Parietal, Parietal-Occipital, and Occipital; see Experimental procedures for included electrodes) were submitted to repeated measurement ANOVAs. As can be seen in Fig. 2 (upper part; thick solid ERP traces), Grand Average ($n = 12$) ERP difference wave amplitudes (Attention versus Reference cues, averaged over cue type) were surprisingly small in amplitude or even absent (zero amplitude). This observation was confirmed by the statistical results from the ANOVAs applied on all ROIs and for all 100 ms bins of averaged data within the cue-target interval. No main effects of CONDITION were found in any of the windows and/or ROIs. However, interaction effects between CONDITION and CUETYPE were found between 600 and 700 ms (Prefrontal and Frontal ROIs; $F(1,11) = 8.1$, $P < 0.02$, and $F(1,11) = 8.8$, $P < 0.02$, respectively), and between 900 and 1000 ms (Central, Parietal, and Parietal–Occipital ROIs; $F(1,11) = 7.5$, $P < 0.02$, $F(1,11) = 5.4$, $P < 0.05$, and $F(1,11) = 5.6$, $P < 0.04$, respectively). In addition, CONDITION × CUETYPE × ELECTRODES interaction effects were found between 700–800 ms over Occipital sites ($F(1,11) = 3.5$, $P < 0.05$) and Parietal–Occipital sites ($F(1,11) = 5.2$, $P < 0.02$). Post hoc tests, separately per cue type for all of the CUETYPE interaction effects, however, did not reveal any significant CONDITION effects.

The lack of meaningful significant differences in the cue ERPs between the Attention and Reference condition was surprising and somewhat mysterious at first sight. Should we have included more subjects (i.e., is this due to a lack of power?), or did our Reference condition control too tightly (i.e., was this condition too similar to the Attention condition, leaving no detectable differences)? If either of these two possibilities would have been true, we should have found a too low number of subjects (out of the total group) showing a difference or a difference between the two conditions for most of the subjects that was too small to become significant, respectively. Neither of these patterns, however, was present in the data. In contrast, careful observation of the individual ERP responses revealed that all individual subjects showed a clear difference between the Attention and Reference condition, especially in the later part of the cue-target interval (starting at approximately 400–500 ms postcue). However, scalp potential distribution patterns of this differential activity differed between two groups of subjects, effectively canceling each other out when averaged together (see both

ERP traces and scalp potential distribution maps displayed in Fig. 2).

Visual inspection of the ERP difference waves for individual subjects showed that 4 subjects elicited a pattern of broad fronto-central–parietal positivity in the later part of the cue-target interval (GA4 data in Fig. 2), whereas the remaining 8 subjects elicited a pattern of broad negativity mainly over fronto-central scalp sites in the same latency windows (GA8 data in Fig. 2). This classification of the subjects into two different groups of respectively 4 and 8 subjects (based on their individual ERP profiles) was confirmed by a K-means cluster analyses (2 clusters) on individual ERP difference wave amplitude values over time (using five consecutive 100 ms bins of averaged data between 500–1000 ms postcue from four frontal ERP channels; Fz, Cz, F3, and F4). Specifically, based on the amplitude values of the five windows, all 8 GA8 subjects were categorized in one cluster for each of the 4 electrodes; and all 4 GA4 subjects were categorized in a second cluster for each of the 4 electrodes, except for two electrodes for one subject. Thus, based on the observation and classification of two different groups showing clear differences between the two conditions – indicative of attentional control activity – in the absence of an overall difference, we decided to investigate attentional control activity per group separately. For reasons of clarity, a direct comparison between the groups is postponed until subparagraph 2.2.4.

2.2.2. ERPs to cues: analyses, separately per group
As could be expected on the basis of the opposite ERP patterns, statistical analysis of both these groups of subjects (GA8 and GA4) separately revealed many significant differences between the two main conditions, in contrast to the lack of any significant effect when all subjects were taken into account (GA12). To start with the group of eight subjects (GA8), an early CONDITION × ELECTRODES interaction effect was present over central scalp sites (central ROI: C3, Cz, C4) between 100 and 200 ms ($F(1,7) = 5.8$, $P < 0.05$). Attention cues evoked a greater central positivity (maximum amplitude at Cz) in this time window than Reference cues did. Thereafter, a negative difference between the two conditions started to emerge at 400–500 ms over central sites, lasting until target onset, in the meantime spreading over frontal (700–1000 ms), prefrontal (600–1000 ms), parietal (600–700 ms), and occipital sites (900–1000 ms). At central sites, CONDITION × ELECTRODE interaction effects were found between 400–900 ms (smallest $F(1,7) = 5.2$, $P < 0.03$), as well as a main effect of CONDITION between 900 and 1000 ms ($F(1,7) = 7.7$, $P < 0.03$). Prefrontal sites started to become significant between 600 and 700 ms ($F(1,7) = 6.0$, $P < 0.02$) and stayed significant throughout the rest of the cue-target interval (smallest $F(1,7) = 6.8$, $P < 0.03$). Frontal sites started later than the prefrontal sites (700–800 ms; $F(1,7) = 8.3$, $P < 0.03$), but also remained significant until target onset (smallest $F(1,7) = 8.5$, $P < 0.03$). Furthermore, parietal sites showed significant differences between conditions (main effect of CONDITION) between 600 and 700 ms only ($F(1,7) = 5.9$, $P < 0.05$). Finally, in the last window before target onset (900–1000 ms), a CONDITION × ELECTRODE interaction effect was present over occipital sites ($F(1,7) = 5.5$, $P < 0.03$). This reflects the
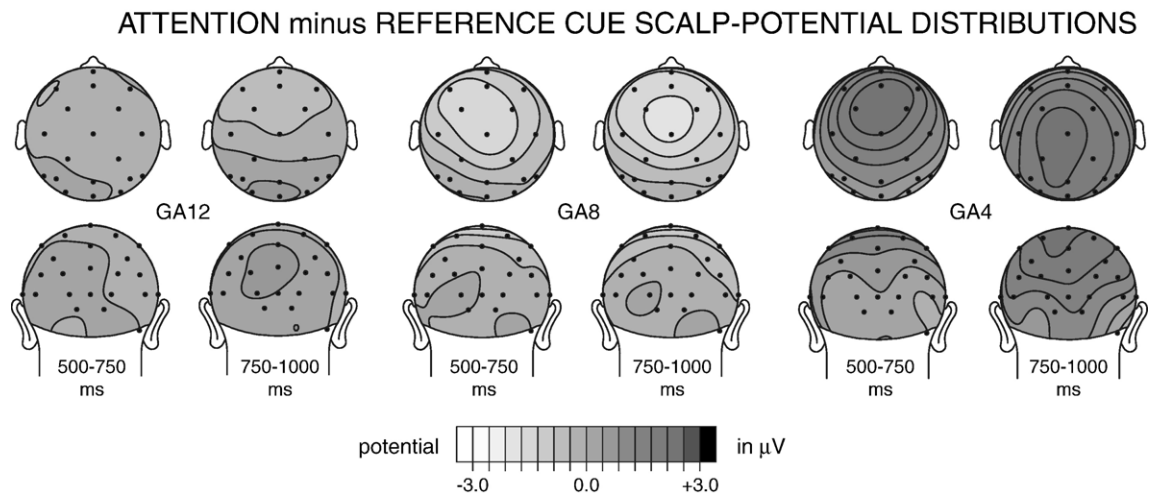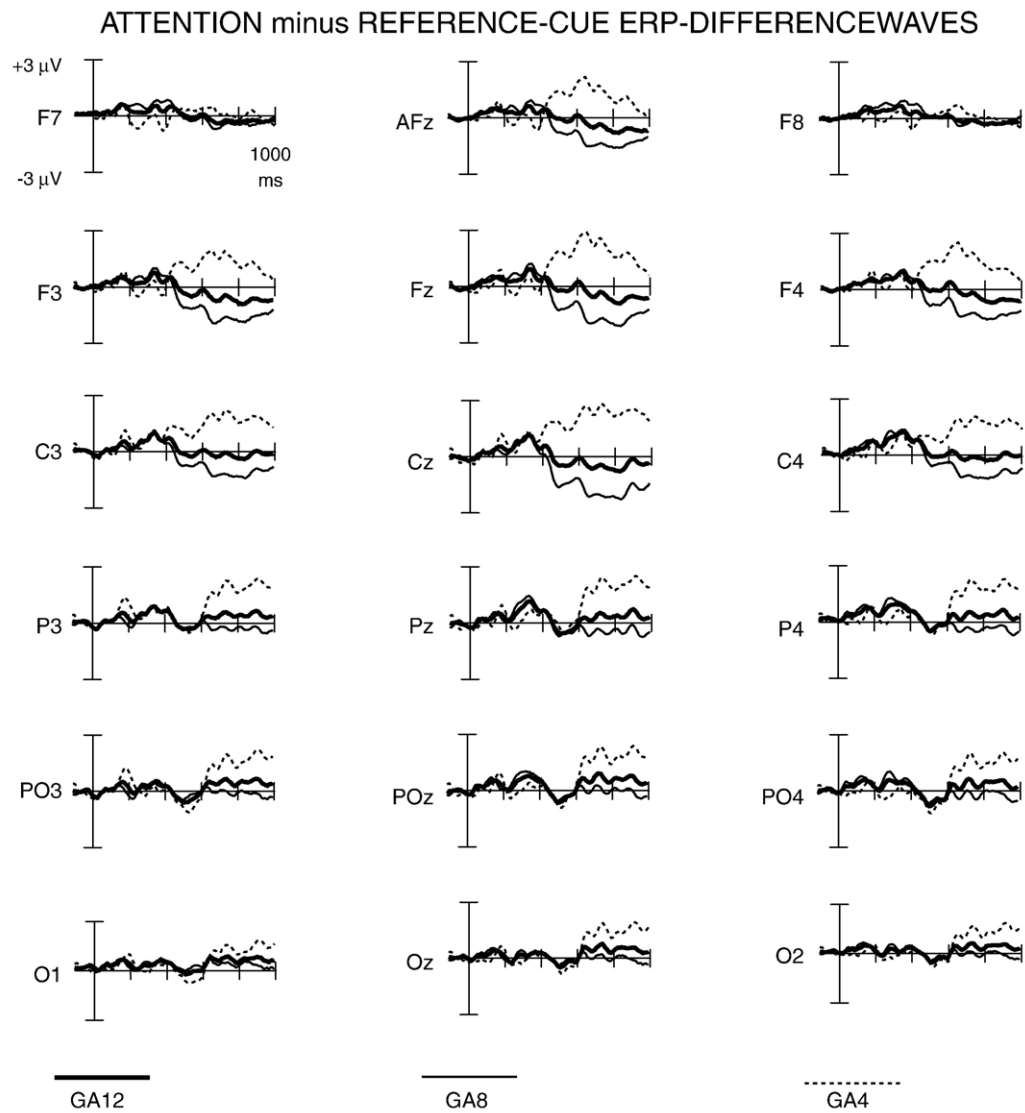
Fig. 2 – Upper panel with ERP traces shows overlays of cue-ERP difference waves between Attention cues and Reference cues for all subjects (GA12: n = 12), and two subgroups of subjects (GA8: n = 8 and GA4: n = 4), separately, on 18 channels covering almost the whole scalp. Positive polarity is plotted upwards and ERP-traces lasted until target onset. The lower panel displays scalp potential distribution maps (top-view and back-view) for two windows of averaged data (500–750 ms and 750–1000 ms postcue), for all three groups, separately as described above for the ERPs.

very small negativity visible in the GA8 difference wave (Fig. 2) at Oz and O2 at the uttermost end of the cue-locked epochs. No interaction effects including the factor CUETYPE were found in any of the windows, suggesting that attentional control processes did not differ depending on the spatial frequency (and respond hand) information embedded in the cue.
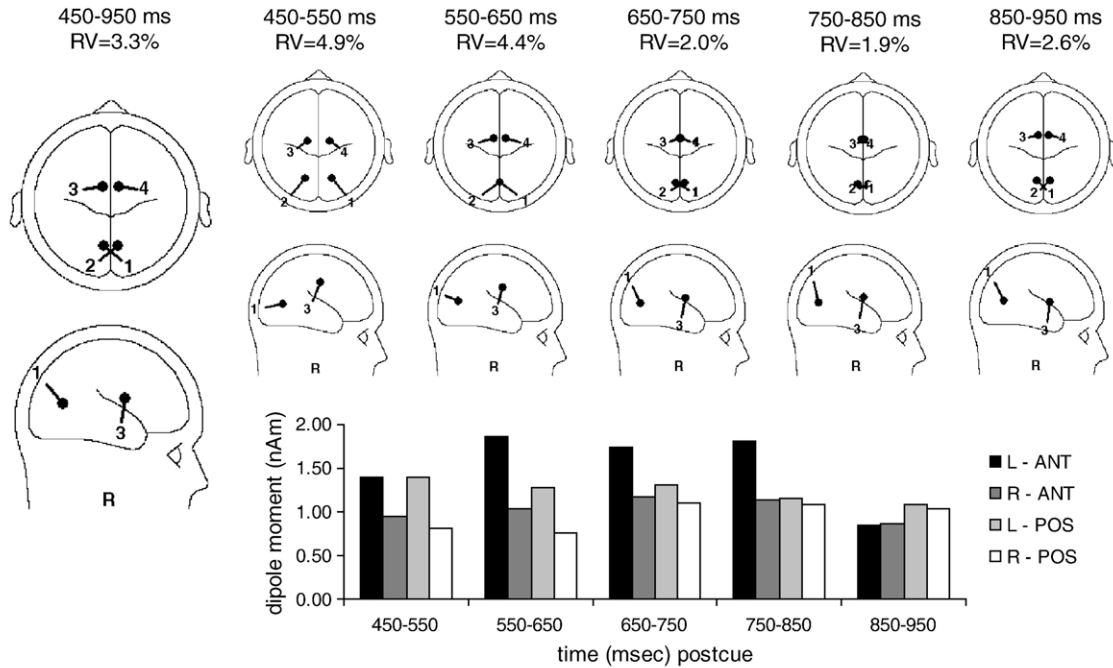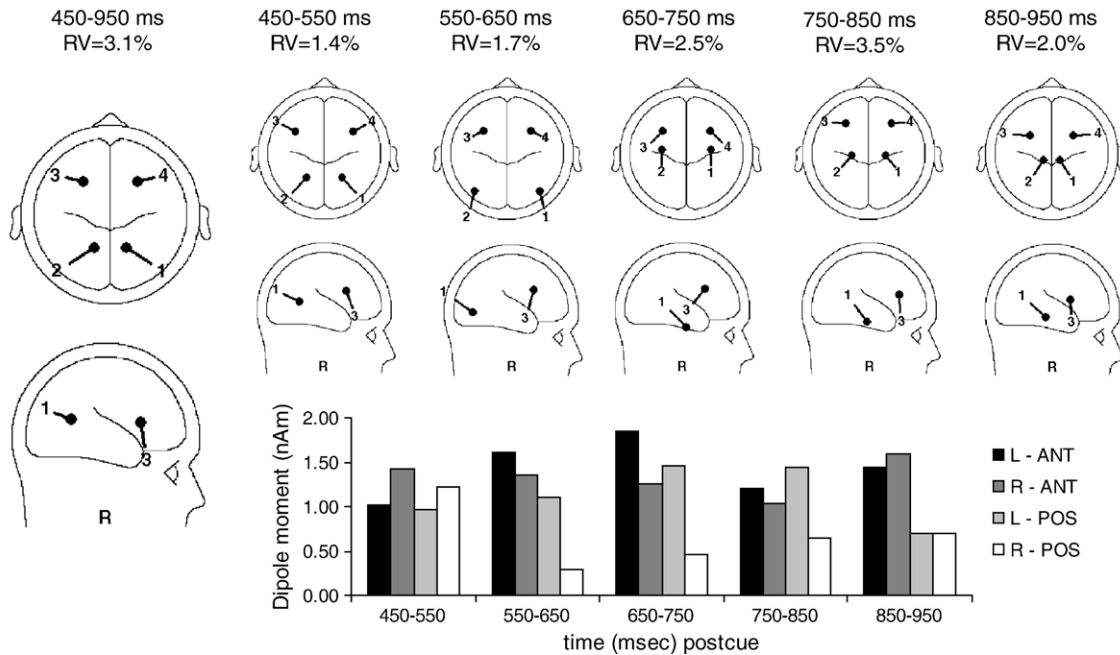

Fig. 3 – Both upper and lower panel display grand average source solutions for late cue-induced attentional control activity, separately for both subgroups of subjects (upper panel displays solutions for group of 8 subjects; lower panel for group of 4 subjects). Larger heads on the left show the solutions found for the total window of interest between 450 and 950 ms postcue, using a 2 × 2 symmetrical dipole-pair fitting procedure. The upper two rows on the right site display the solutions in 5 different time windows within the larger window displayed on the left, again for a 2 × 2 dipole-pair procedure. Bar diagrams show dipole moments for anterior and posterior dipoles as a function of time.

The group of four subjects (GA4) showed a different pattern, although most of the effects were again found over anterior parts of the scalp. The earliest effect for this group was found over prefrontal, frontal, and central sites between 500 and 600 ms. Prefrontal sites showed a CONDITION × CUETYPE interaction effect ($F(1,3) = 10.8$, $P < 0.05$), resulting from a larger amplitude difference between the two conditions for the HSF-cue (mean amplitude 1.0 μV) than the LSF-cue (mean amplitude 0.2 μV), and revealed a CONDITION × ELECTRODE interaction effect ($F(1,3) = 33.9$, $P < 0.02$). In the same window, the frontal sites showed a CONDITION effect ($F(1,3) = 28.2$, $P < 0.02$) and the central sites a CONDITION × ELECTRODE interaction effect ($F(1,3) = 11.5$, $P < 0.03$). The same three ROIs also revealed CONDITION × ELECTRODE interaction effects in the next window between 600 and 700 ms postcue (prefrontal ROI: $F(1,3) = 35.3$, $P < 0.001$; frontal ROI: $F(1,3) = 34.9$, $P < 0.001$; central ROI: ($F(1,3) = 10.1$, $P < 0.03$). Thereafter, only the prefrontal ROI showed significant CONDITION × ELECTRODE interaction effects (700–800: $F(1,3) = 21.8$, $P < 0.02$; 800–900 ms: $F(1,3) = 11.5$, $P < 0.05$). All CONDITION × ELECTRODE interaction effects resulted from higher amplitude differences at the medial electrodes, compared to the lateral electrodes.

In sum, the two groups were comparable in that they had most of their effects over medial anterior scalp sites. The groups differed, however, in the polarity of the attention effects (GA8 negative, GA4 positive), in onset latency (GA8 earlier than GA4), location of onset (GA8 over central sites, GA4 most prominent over frontal and prefrontal sites, less prominent over central sites), and extent of their activity (GA8 including also some posterior channels (parietal and occipital) in some latency windows).

2.2.3. Source modeling of cue-induced attentional control activity

Assuming a frontal–parietal network of brain areas as the most likely generators, to model the grand average difference topographies for the two groups, we started with two equivalent current dipole pairs with symmetrical orientation and location. The default four shell (head, shell, bone, csf) spherical head model was used, as well as an Energy Criterion of 20% (Berg and Scherg, 1994). Fig. 3 (left enlarged figures) displays the results of the best fits for the total window between 450 and 950 ms postcue (a window best overlapping with the effects for both groups), as well as for 5 subwindows of 100 ms within this window, for both groups separately. These grand-average solutions found for both datasets turned out to be very good, with all of the fits resulting in less than 5% Residual Variance (RV) in any of the windows.

As in Kenemans et al. (2002), models for the individual-subject difference topographies were also estimated. The mean RV and standard error (stderr) across individuals for the 450- to 950-ms window amounted to 9.0% and 1.4% for GA4, and 15.1% and 3.6% for GA8), respectively. Individual location coordinates were expressed as positions in a normalized head with a radius of 1 (Kenemans et al., 2002). Across individuals, the mean locations of the anterior sources seemed to be more lateral and anterior for the GA4 group (X location (medial to lateral) = ±0.345, stderr 0.131; Y location (posterior to anterior) = 0.439, stderr 0.161; Z location (inferior

to superior) = 0.261, stderr 0.082), than the sources found for the GA8 group (mean X = ±0.216, stderr 0.071; mean Y = 0.172, stderr 0.046 mm; mean Z = 0.239, stderr 0.070). The location of the posterior sources showed the same trend to being more lateral for the GA4 group (mean X = ±0.086, stderr 0.171; mean Y = –0.390, stderr 0.015 mm; mean Z = 0.167, stderr 0.050) than for the GA8 group (mean X = ±0.003, stderr 0.144; mean Y = –0.342, stderr 0.057; mean Z = 0.145, stderr 0.041), but this effect was less consistent throughout time (they moved to more medial and frontal locations over time).

This pattern is consistent with the grand-average results depicted in Fig. 3 but was not confirmed by an ANOVA for the group effect on the individual x-locations of the anterior and posterior sources. Only an expected main effect of location in the y-direction (anterior–posterior axes) became significant, independent of group ($F(1,10) = 138.3$, $P = 0.000$); mean y-location (averaged over all 12 subjects) was 0.306, and –0.366 for anterior and posterior sources respectively). This effect simply reflects the fact that the two dipole pairs were located in different parts of the brain, one pair located significantly more anterior than the other. The more interesting group effects were restricted to a trend for a TIME × GROUP interaction effect for y-location ($P = 0.060$), consistent with the observed movement of the posterior sources over time for the GA4 group.

The relative timing of activations of anterior versus posterior sources is shown in the bar diagrams in Fig. 3. Apparent differences were tested using the dipole moments for the 4-source solutions in each window (subsequent windows of 100 ms between 450 and 950 ms postcue) in a repeated measurement design including the within subject factors ANTPOS (Anterior, Posterior) and HEMISPHERE (Left, Right) and a between GROUP factor (GA8, GA4). This analysis revealed a main effect of ANTPOS between 550 and 650 ms ($F(1,10) = 10.0$, $P = 0.010$) and a main effect of HEMISPHERE ($F(1,10) = 4.0$, $P = 0.028$) in the same window, with mean dipole-moments pointing to stronger anterior activity (1.5 nAm and 0.9 nAm for anterior and posterior sources respectively, averaged over hemisphere) and stronger left hemispheric activity (1.5 nAm and 0.8 nAm for left and right hemisphere sources respectively, averaged over antpos). In addition, in the last window between 850 and 950 ms postcue, an ANTPOS × GROUP interaction effect was found ($F(1,10) = 5.0$, $P = 0.050$), with mean dipole moments showing a cross-over effect on the ANTPOS factor (0.9 nAm and 1.1 nAm for anterior and posterior sources for the GA8 group, and 1.5 nAm and 0.7 nAm for anterior and posterior sources for the GA4 group respectively, averaged over hemisphere). In conclusion, anterior activations preceded posterior ones in time for both groups. For the GA4 group, the anterior activation was relatively more persistent in the late time segment, and the posterior sources gradually shifted to anterior locations across time since the cue.

2.2.4. Direct comparisons between groups

Clearly different patterns were observed between groups in terms of differential ERPs as presumably related to attentional control. This prompts two question. First, were there any behavioral differences between groups suggestive of differences in the efficacy of attentional control, or in strategy? Second, did the difference between groups for the (Attention

minus Reference) contrast reflect differences between groups for the Attention or for the Reference condition?

As to the first question, post hoc analyses including the factors CONDITION, CUETYPE (OR TARGETTYPE), and GROUP did not reveal any significant (interactions with) GROUP effects on any of the behavioral parameters assessed in the initial analyses (as described in Section 2.1). As to the second question, Fig. 4 shows ERPs to Attention and Reference cues separately, with GA8 and GA4 waveforms superposed. Significant GROUP × CONDITION effects were observed from 500- to 1000-ms latency (Central and Frontal ROIs, $5.1 < F(1,10) < 25.5$), from 600- to 1000-ms latency (Parietal, $5.7 < F(1,10) < 13.7$), from 700- to 1000-ms latency (Parietal–Occipital, $6.6 < F(1,10) < 9.6$), and from 900- to 1000-ms latency (Occipital, $F(1,10) = 8.7$). To meet possible concerns about Type I errors in relation to unequal sample sizes (8 versus 4), the GA8 group was split into 4 subjects with the largest late (Attention minus Reference) difference wave and 4 with the smallest one. Both subgroups were tested against the GA4 group separately, and for both the pattern outlined above was replicated, except for three individual time windows, each in a specific ROI.

As can be seen in Fig. 4, some differences between groups are present both for the attention and the reference condition and therefore do not contribute to the group difference in difference waves (Attention minus Reference). Other differences have different polarities across conditions, e.g., more late anterior negativity for the GA8 group in the Attention condition, but for the GA4 group in the Reference condition. This might be taken to suggest that the negative difference wave for GA8 versus the positive one for GA4 reflect differences in attentional control processes in both the Attention and the Reference condition. However, it is equally possible that the differences between groups in the two conditions reflect to a substantial extent simple main effects of GROUP. For example, suppose that the 'true' attentional control values are 0 in the Reference condition for both groups, and in the Attention condition –2 and 2 for GA8 and GA4, respectively. Then an additional simple main effect of Group (e.g., 2 for GA8 versus 0 for GA4, in both conditions) would result in observed values of 0 (GA8) and 2 (GA4) in the Attention condition and of 2 (GA8) and 0 (GA4) in the Reference condition, very much like the pattern of late anterior differences depicted in Fig. 4.

In sum, we conclude that that there were clear interactions between the groups factor and CONDITION, which may reflect genuine differences in attentional control mechanisms, which were however not paralleled by differences in performance.

2.2.5. ERPs to test stimuli

Fig. 5 shows an overview of ERP difference waves (target minus non-target selection-potentials, averaged over spatial frequency) on channels best representing the four attention effects of interest (FSP, OSN, N2b, and P3b). Selection potentials are shown separately per condition (Attention and Reference Condition), as well as for the same three Grand Averages ($n = 12$, $n = 8$, and $n = 4$) as used for the analyses of the cue ERPs. As can be seen in the figure (middle and most right ERPs), the two groups did not only show different patterns in their cue-responses, but also in their responses to test stimuli. As stated, behaviorally the two groups could not be distin-

guished from each other, despite these different patterns of selection potentials.

In the ERP analyses, the FSP was tested statistically on both the prefrontal ROI [F7, AFz, F8] and the frontal ROI [F3, Fz, F4] with repeated measurement ANOVAs in a factorial design (factors ATTENTION (target, non-target), CONDITION (attention, reference) and ELECTRODES), using time windows of 20 ms of averaged data between 140- and 260-ms latency. For the GA8 group, an ATTENTION × CONDITION × ELECTRODE interaction effect was found between 180–220 ms for the prefrontal ROI ($F(1,7) = 6.4$, $P < 0.04$) and frontal ROI ($F(1,7) = 7.2$, $P < 0.01$). Post hoc tests separately per condition revealed that the FSP reached significance only in the Attention condition (ATTENTION × ELECTRODE effect for prefrontal ROI, $F(1,7) = 22.9$, $P < 0.01$; ATTENTION effect for frontal ROI, $F(1,7) = 31.0$, $P < 0.01$). No significant FSP was elicited in this group for the Reference condition. Mean FSP amplitudes for this group at the prefrontal and frontal ROIs were 0.88 and 1.66 µV for the Attention condition, and 0.72 and 0.67 µV for the Reference condition.

The FSP for the GA4 group was much larger in amplitude (mean amplitudes at the prefrontal and frontal ROIs 2.03 and 2.70 µV for the Attention condition and 1.18 and 1.59 µV for the Reference condition) but had also an earlier onset and a longer duration (ATTENTION × ELECTRODE interaction effect between 160–260 ms for prefrontal ROI, $F(1,3) = 13.4$, $P < 0.04$; main effect of ATTENTION between 160 and 240 ms for frontal ROI, $F(1,3) = 12.3$, $P < 0.04$). Although no interaction was found between ATTENTION and CONDITION effects for this group, ATTENTION effects were still tested separately per condition, to allow comparison with the pattern found for the GA8 group. These tests revealed that no significant FSP was elicited in the Reference condition, as was found for the GA8 group, but a significant FSP was present in the Attention condition on both prefrontal and frontal ROIs (ATTENTION × ELECTRODE effect for prefrontal ROI, $F(1,3) = 10.2$, $P < 0.05$; ATTENTION effect for frontal ROI, $F(1,3) = 19.3$, $P < 0.03$). Thus, in both conditions, an FSP was only found in the Attention condition and was significantly earlier and longer lasting for the GA4 group than the GA8 group.

Both groups showed little to no evidence of an OSN over occipital scalp sites. Only the GA8 group analyses exhibited a significant ATTENTION × ELECTRODE interaction effect between 180 and 220 ms (Occipital ROI; $F(1,7) = 7.4$, $P < 0.03$), but this certainly did not reflect a robust selection negativity across these electrode sites. The N2b was not significant for the GA4 group, not even in the Reference condition. The GA8 group, in contrast, exhibited an N2b in both conditions, becoming significant between 360 and 400 ms posttarget over both frontal ROI (ATTENTION effect; $F(1,7) = 5.6$, $P < 0.05$) and central ROIs (CONDITION × ATTENTION effect; $F(1,7) = 14.9$, $P < 0.01$). The P3b was clearly significant for both the GA8 and the GA4 groups but, as with the FSP difference, differed in duration and amplitude between the groups. For the GA8 group, the P3b was significant from about 200–500 ms, with an ATTENTION effect (averaged over conditions) between 200 and 300 ms ($F(1,7) = 11.0$, $P < 0.02$) and a CONDITION × ATTENTION interaction effect between 300 and 500 ms ($F(1,7) = 15.0$, $P < 0.01$). The later interaction effect was caused by a prolonged P3b for the

GrandAverage ERPs to ATTENTION CUES; differences between GROUPS

GrandAverage ERPs to REFERENCE CUES; differences between GROUPS

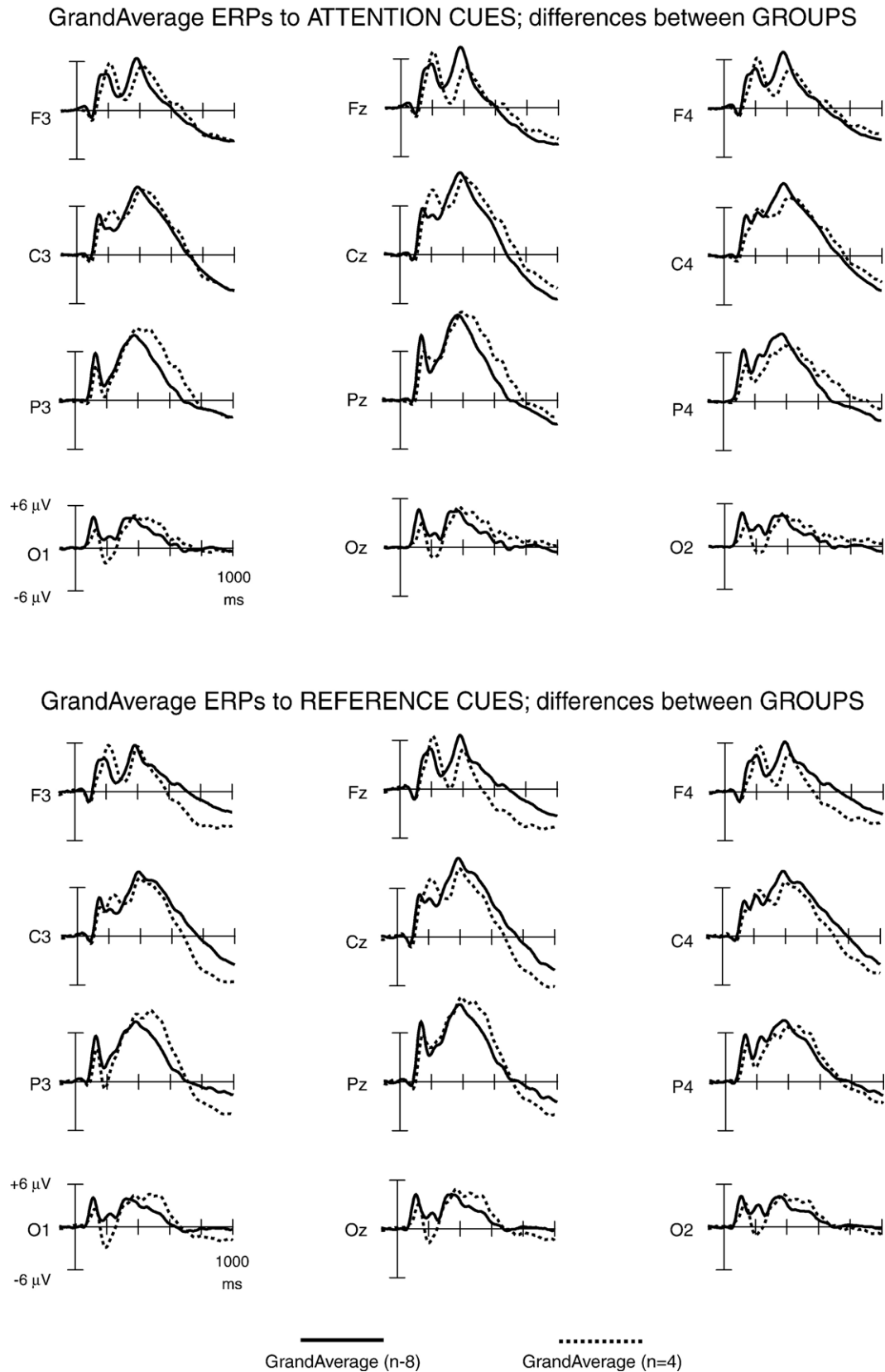GrandAverage (n-8)   GrandAverage (n=4)

Fig. 4 – Overview of group effects per condition. Upper panel: Cue-locked ERP overlays for the two groups (GA4 and GA8) for the Attention condition. Lower panel: Same for Reference condition. Positivity plotted upwards. Epochs last until S2 onset.

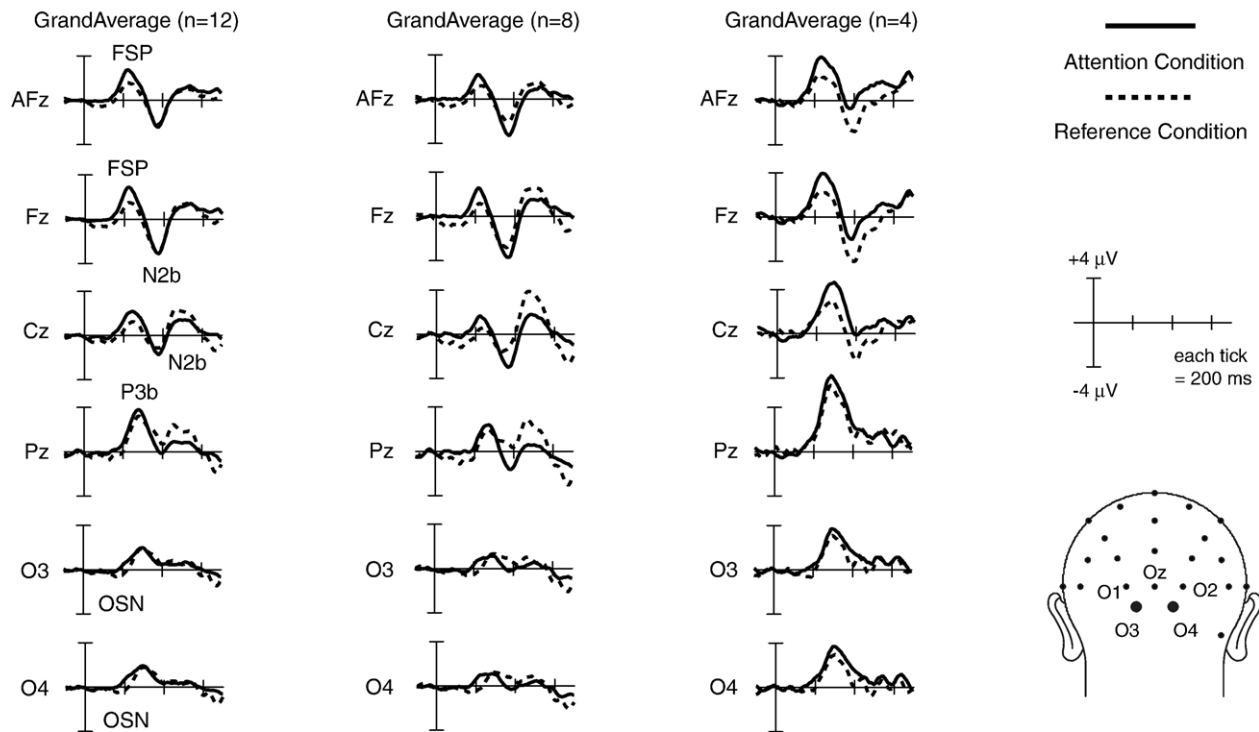## Selection-potentials (SP): target minus non-target ERPs (avg over SF)

Fig. 5 – Selection potentials (SPs) to test stimuli (target minus non-target ERPs; averaged over spatial frequency), displayed for all subjects (left: *n* = 12 traces), a subgroup of eight subjects (middle: *n* = 8 traces), and the remaining four subjects (right: *n* = 4 traces). SPs are shown on those channels best representing the SPs of interest (FSP, OSN, N2b, and P3b).

Reference condition, compared to the Attention condition (see Fig. 5, middle panel, P3 and P4 ERPs). The GA4 group showed highly significant P3bs between 200–600 ms over parietal cortex ($F(1,3) = 312.1$, $P < 0.001$), irrespective of condition.

3.   Discussion

In the present study, directing attention selectively on a trial-by-trial basis to one of two grating patterns (low or high spatial frequency), was compared to using selective attention in a sustained way throughout a block of trials. We expected to find the same pattern of effects as found in two earlier ERP studies (Slagter et al., 2005a,b) on attentional control to color (i.e., earliest effects over posterior scalp sites, followed somewhat later in time by a more anterior effect). The results from the present study, however, were not consistent with these earlier findings. Specifically, in relatively early phases of the cue-target interval, activation was significantly greater for the anterior, relative to the posterior sources.

This anterior precedence was present in two groups of subjects that were distinguished based on waveforms and scalp topographies. Both groups showed a pattern of initially mainly anterior activity, but with opposite polarity (thus canceling each other out). More specifically, the activity for the largest group of 8 subjects started as a negative difference over central sites between 400 and 500 ms, growing in strength over time, thereby stabilizing over a broader fronto-central region. In addition, this group elicited a small occipital negativity in the last 100 ms before target onset, independent of cue type. The pattern found for the remaining 4 subjects consisted of a positive difference, starting between 500 and 600 ms over frontal and prefrontal sites, growing rapidly in strength over time, thereby expanding to a broad fronto-central–parietal positivity until target onset. In contrast to the other group, this group did not show significant late posterior occipital activity.

These results are unexpected and surprising in a number of ways. First of all, comparing ERP responses to the cues in the Attention and Reference condition over all subjects surprisingly yielded no meaningful significant differences between these conditions during the entire cue-target interval. Careful inspection of the differences between conditions on the level of individual subjects, including cluster analysis, revealed that the lack of overall results was caused by opposite patterns of differential activity generated by two distinctive groups of subjects, effectively canceling each other out when taken together. Such differential effects across subsets of subjects have not been reported before for top–down control of attention. However, a growing number of studies, focusing on relations between working-memory capacity and attentional control, have described patterns of individual differences suggestive of brain networks involved in those processes (Gevins and Smith, 2000; Kane et al., 2001; Osaka et al., 2003). Both the groups of Gevins and Smith and Kane and colleagues,

for example, have suggested that high-span working memory capacity subjects are better able to focus and sustain attention to task performance, than subjects with low working memory capacity. In addition, Osaka et al. (2003) showed that this better attentional control ability in high-span subjects is supported strongly by the medial frontal areas, as part of the attentional control network. Although we do not have any evidence that the present two groups of subjects can be dissociated on the basis of their working memory capacity profiles, the suggestion of better use of attentional control as based on medial frontal areas in high-span subjects, pointed out by Osaka et al., fits the strong medial frontal sustained negativity during attentional orienting as revealed in the GA8 group.

Secondly, despite their clearly different ERP-profiles on both cues and targets, the two groups could not be distinguished on the basis of their behavioral performance. This can be explained as resulting from a floor effect because obviously the task on both cues and targets was not difficult, leaving simply not enough room for improvement. On the other hand, despite the fact that no differences between the two groups were obtained for task performance on the targets, the groups did show differential selection potential profiles. The GA4 group exhibited earlier and greater FSP and P3 components under these similar performance levels. A comparable pattern was described recently by Roche et al. (2005) as exhibited by more absent-minded subjects. The authors suggested that the greater activity arises from neural substrates of response inhibition in order to accomplish the same task performance as less absent-minded participants. Thus, in other words, more absent-minded subjects have to compensate more during processing of task-relevant stimuli. In the present study, this could explain the profile found for the GA4 group target ERPs because this group did not elicit an N2b, a component known to be linked to attentional orienting (Lange et al., 1998; Wijers et al., 1989), whereas the GA8 group showed clear N2b components. Taking into account the clear medial frontal location of the N2b component, this suggests that the GA8 group used a more efficient variant of attentional control, while the GA4 group had to rely on other, compensatory, strategies to achieve the same performance level.

Thirdly, the present results do not support an early posterior start of attentional control activity, as was reported before. In contrast, source-modeling results clearly favored an anterior start over a posterior one, and this was true for all subjects, despite all the other differences elicited by the two subgroups. Slagter et al. (2005b) suggested that the early posterior cue activity most likely reflects generic processes involved in generating the attentional set, because the observed differences in early posterior activity could be explained in terms of differences across tasks in demands placed on processes involved in updating of the attentional set. Note that this reasoning is in fact not contradicted by the present results because in the present study demands did NOT differ between conditions, as reflected in similar behavior to the cues, and posterior activity preceding anterior activity was NOT found. Thus, the present study underscores the idea of early posterior activity as resulting from differential cue translation processes.

A fourth unexpected finding is the lack of clear biasing activity in the present study. Does this mean that we cannot prepare for spatial frequency? Some evidence of at least occipital activity that could represent biasing activity was found in the last 100 ms before target onset in the GA8 group, although this was not target feature specific. If our suggestion is correct that this group exhibited better attentional control ability, then biasing obviously has to be initiated by frontal brain areas, an idea suggested before by a number of authors (LaBerge, 2002; Miller and Cohen, 2001). The fact that we did not find evidence for target-feature-dependent biasing effects might simply be a result of the design features; that is, it is very likely that there was not enough time for proper biasing activity to become full blown. As was proposed by LaBerge (2001), posterior preparatory activity needs time to build up, at least a second, and in the present study the cue-target interval was exactly 1 s, and subjects also had to perform an additional choice RT task during that second. Alternatively, the task on target was too simple to require strong prebiasing occipital activity to facilitate target-selective processes later on.

Finally, behavioral results collected for both the cue discrimination task as well as for the detection task on targets, revealed no significant differences in speed of responding between conditions. The only difference that was found concerned accuracy of the cue responses and consisted of better task performance (less errors and omissions) to the cues in the transient Attention condition than in the more sustained attention Reference condition. This pattern of result cannot easily be explained by a speed–accuracy trade-off on the basis of subjects strategy differences between the transient and sustained condition. That is, if subject would have chosen a more liberal strategy in one of the two conditions, they would have responded both faster and less accurate, with the opposite pattern if their strategy would have been more conservative (Strayer and Kramer, 1994). This was clearly not the case. We suggest that a possible alternative explanation for the present findings could be that subjects allocated more attentional resources in the transient Attention condition because of the second task embedded in the Attention cues (translation in terms of target spatial frequency) that was absent in the Reference condition, as has been described for dual-task performance on integral objects before (Kramer et al., 1985).

A final further point to consider concerns the contribution of motor preparation. The right hemisphere may be more specialized for low-SF processing and the left hemisphere more for high-SF processing (e.g., Yamaguchi et al., 2000). Directing attention to low versus high SFs then could involve differential processing in the right and left hemisphere, respectively. In the present study, behavioral responses to low-SF cues were always left-sided (right-hemisphere controlled) and those to high-SF cues always right-sided. This could have interacted with attentional control so as to produce right-hemisphere dominance for low-SF cues, and left-hemisphere dominance for high-SF cues, and perhaps stronger so for the Attention than for the congruent Reference condition, in which the motor requirements were identical but attention presumably did not have to be directed that much. However, the only sign of lateralized attentional control was not specific for low- versus high-SF

cues but concerned stronger left-hemisphere involvement for both.

4.   Conclusion

The present results indicate that top–down control visual attention to features other than location originates in anterior cortical areas. This anterior activity may guide more posterior areas to prepare for the upcoming stimulus event. These attentional control mechanisms, however, are not used by all subjects in the same way. The present findings suggest individual differences that not only affect the way subjects deal with the task demands, but probably also which brain areas they use for task preparation. The interaction between individual differences and attentional control abilities clearly needs further investigation.

Furthermore, the present results again bring to the fore the problem of a valid operationalization of attentional control. The fact that the earliest effects of directing of attention in both visual spatial and visual non-spatial cueing paradigms have been found in posterior areas in some studies and in anterior areas in other studies might be due to the differences in the exact processing components (and their on- and offset timing) isolated by the contrast between experimental conditions that was intended to reveal just 'attentional control'. For example, relatively non-specific differences in task demands between the attentional control and the reference condition may result in relatively rapid differences in posterior cortical areas. That is, differences between conditions in the amount of time needed to identify the cue and translate its meaning into an attentional set (processing steps that all seem to be more likely to activate posterior than anterior areas) could lead to earliest effects over posterior brain areas. One way to estimate and eliminate this interpretation problem is to include a behavioral discrimination tasks on the cues, as shown in the present study. Any posterior difference between the attentional control and the reference condition that remains without behavioral evidence for speed and/or accuracy differences between conditions can be considered pure attentional control activity. Anything else should perhaps be viewed more as attentional modulation due to differences in general task demands of extracting the target-specific task-relevant information from the cues, rather than as correlates of subsequently initiated top–down attentional control processes (see also van Velzen and Eimer, 2003).

5.   Experimental procedure

5.1.   Subjects

Twelve healthy volunteers (11 females/1 male, mean age 22.4, range 19–30 years) with normal or corrected-to-normal vision agreed to participate in this study. Two subjects reported a history of concussion of the brain but claimed to be fully recovered. One subject reported epileptical seizures of closely related family members but did not suffer from epileptical seizures herself. No history of psychiatric disease was reported by any of the subjects. All of the subjects reported right-handedness. Subjects were paid € 4.50/h for their participation.

5.2.   Stimuli and procedure

Subjects were presented with a series of event trials, each beginning with a word cue (S1) at fixation, followed by a test stimulus (S2), also at fixation (non-spatial design; see also overall trial-structure in Fig. 1). Word cues consisted of either the word DIK (Dutch for "thick"; 50% of all cues) or the word DUN (Dutch for "thin"; 50% of all cues), presented with a duration of 100 ms. Both DIK and DUN cues were presented in the letter type Lucida Console (28 pt, bold; width 1.66°, height 0.75°). Test stimuli consisted of square, black–white, square-wave gratings with a vertical orientation, presented with a duration of 50 ms. For each of the cue types, half of the target events consisted of high spatial frequency gratings (HSF; 4.8 c/d, width 6.30°, height 6.64°), and the other half of the target events were of low spatial frequency (LSF; 0.6 c/d, width 6.30°, height 6.64°). Constant Stimulus Onset Asynchronies (SOAs) of 1000 ms were used between S1 and S2 stimuli (cue-target interval). Inter-Trial Intervals (ITIs; S2—next S1) varied randomly between 1250 and 1550 ms.

All stimuli were presented against a grey background in the center of a computer screen (non-spatial design), positioned at a distance of 138 cm from the subject's eyes. Series of event trials were presented block-wise in pseudo-random order, meaning that the order of trials within each block was corrected after randomization to ensure a maximum of two equal, subsequently presented S1–S2 pairs of stimuli. The total experiment included 8 blocks (4 Attention and 2 × 2 Reference blocks) of each 240 trials (120 S1–S2 pairs). In all blocks, subjects performed a 2-choice reaction time (RT) task to the S1 cue stimuli and a Go–Nogo task to the S2 target test stimuli. In the Attention condition, subjects were instructed to press a left button with the left index finger at the presentation of the LSF-cue (DIK) and a right button with the right index finger in case of a HSF-cue (DUN). A subsequent target in this condition was defined as a SF pattern indicated by the cue (DIK-cue meant LSF pattern is target; DUN-cue meant HSF pattern is target). In the case of receiving the cued subsequently presented target pattern, subjects were to press the same button as used for the response to the preceding cue (same response hand for R1 and R2). Subjects were instructed to respond as rapidly and accurately as possible in all cases.

The Reference condition consisted of two separate sub-conditions; a low spatial frequency (Reference Low) and a high spatial frequency control (Reference High) condition (2 blocks each). Cues, as well as subsequently presented gratings, were identical to those used in the Attention condition, but cues were no longer indicative of the target-specific spatial frequency (i.e., non-instructive cues). In the Reference Low condition, the targets were defined (instructed before a block of trials) as the LSF-patterns (thick stripes), irrespective of whether they were preceded by the LSF-cue or the HSF-cue. Similarly, instruction for the Reference High condition defined targets as HSF-patterns (thin stripes), irrespective of which cue was presented before. Response characteristics were the same as in the Attention condition; press left after the LSF-cue and right after the HSF-cue, and use the same response hand for S1

and S2 trials. This setup ensured that, although Reference cues were non-instructive with respect to indicating the task specific spatial frequency for the immediately following test stimulus, Reference cues were still instructive (i.e., controlling) for response hand and response button. Thus, the difference between the Attention and Reference condition(s) should only concern the extraction of target-feature-specific information from the cue, and the use of this information in guiding attentional task preparation for the next test stimulus.

Finally, in all (sub)conditions, subjects received a block of 96 trials for training purposes. The order of blocks and conditions was carefully controlled, according to the rule that each block and each (sub)condition should be presented equally on each possible position in the sequence of 11 blocks (including 3 training blocks) over the total amount of 12 subjects.

5.3. ERP recordings

Electroencephalographic (EEG) data were recorded from 30 tin electrodes (AFz, Fz, F3, F4, F7, F8, FC1, FC2, Cz, C3, C4, CP1, CP2, Pz, P3, P4, P5, P6, PO3, PO4, POz, Oz, O1, O2, O3, O4, T7, T8, P7, and P8, arranged according to the International 10–10 system), mounted in an elastic cap. Horizontal eye movements (HEOG) were monitored by two bipolar tin electrodes placed at the left and right outer canthi of each eye. Vertical eye movements and eye blinks (VEOG) were recorded bipolarly by two tin electrodes, one placed above and the other below the right eye. The forehead was grounded. All scalp electrodes were referred to the right mastoid during recording. Impedances of all electrodes were kept below 5 kΩ. Data acquisition was continuous, with a sampling rate of 200 Hz (each 5 ms), and band pass filtered online between 0.05 and 40 Hz. Recordings took place in an electrically shielded, sound attenuated, dimly lit, experimental chamber.

5.4. Behavioral analyses

Performance data were analyzed separately for the 2-choice RT task to the cue stimuli (S1-word cues) and the Go–Nogo task to the test stimuli (S2-spatial frequency target patterns). For both tasks, trials were included in the mean RT only if they were found between 200 and 700 ms poststimulus. Trials that did not match this criterion were excluded, as were error responses (wrong hand-responses to the cues), false alarms (incorrect responses to non-target spatial frequency test stimuli), missed responses, or outlier responses (trials with RTs slower than 700 ms or faster than 200 ms). Repeated measurement ANOVAs with the within-subject factors CONDITION (Attention, Reference), CUETYPE (LSF-cue, HSF-cue), or TARGETTYPE (LSF, HSF), were used to test for significant differences (α-level 0.05). For the Reference conditions, only trials were included in which the instructed target type was congruent with the cue type.

A second analyses was performed on trials from the Reference condition to address exactly the effect of (in)congruence between instructed target type and cue type. More specifically, the Reference subconditions included both congruent trials, in which the cue type (varying from trial to trial) and the instructed target type matched, as well as

incongruent trials in which they did not. These incongruent trials consisted of the HSF-cue from the Reference Low condition followed by an LSF-target and the LSF-cue from the Reference High condition followed by a HSF-target. Such incongruence has several possible undesirable consequences: the cue could induce directing attention to the cued spatial frequency, followed by redirecting to the instructed one; or a right-hand response to an LSF target, because it followed a right-hand response to an HSF cue, involves a switch in stimulus–response mapping, relative to the standard mapping maintained for the cue choice RT throughout all blocks of trials (LSF-left, HSF-right hand). Especially the former consequence may affect attentional control during the Reference condition, which might be expected to in turn affect the selective processing of S2 targets and non-targets. Repeated measurement ANOVAs were applied to cue and (non-)target stimuli from the Reference conditions separately, using the factors CONGRUENCY (congruent, incongruent) and CUETYPE (LSF-cue, HSF-cue), or TARGETTYPE (LSF-target, HSF-target).

5.5. ERP analyses

5.5.1. Cue-ERPs (S1-trials)

5.5.1.1. *Trial selection and generation of ERPs.* ERPs time-locked to cues (S1 stimuli) were computed separately for LSF-cues and HSF-cues, and separately for each condition, with an epoch length of 1100 ms, including a prestimulus baseline of 100 ms. Incongruent Reference trials (see 5.4) were excluded from the analyses. Only cue trials with correct behavioral responses were included in the averages, and only when the reaction times were between 200 and 700 ms postcue, to ensure that the last 300 ms of the cue-target interval was not contaminated by any late response related activity, but in contrast, only reflected preparatory activity.

Trials contaminated by excessive muscle-related activity, slow drift or amplifier blocking were discarded from the analyses. Artifacts caused by eye movements or eye blinks were corrected before general artifact removal and final averaging, using the regression method developed by Gratton et al. (1983). Furthermore, average ERPs were digitally low-pass filtered with a non-causal, zero-phase shift, running average filter of 9 points, which strongly reduces frequencies at and above 22 Hz at our sampling frequency of 200 Hz. Finally, difference waves were computed between Attention cues (averaged over both cue types) and Reference cues (averaged over both cue types).

5.5.1.2. *Statistical approach and source localization of significant effects.* To detect significant differences between the Attention and Reference condition, an ROI approach was used, including 6 Regions-Of-Interest (ROIs): (1) Prefrontal ROI (F7, AFz, F8), (2) Frontal ROI (F3, Fz, F4), (3) Central ROI (C3, Cz, C4), (4) Parietal ROI (P3, Pz, P4), (5) Parietal–Occipital ROI (PO3, POz, PO4), and (6) Occipital ROI (O1, Oz, O2). For these 6 ROIs, mean ERP amplitudes were computed over 20 data points (100 ms), starting 100 ms postcue and ending at target onset (at 1000 ms postcue). Each of the 100 ms bins and ROIs was then submitted to repeated measurement ANOVAs using the within-subjects factors CONDITION

(Attention versus Reference condition), CUETYPE (LSF versus HSF cue), and ELECTRODES (left, midline, right electrode). Significance was assumed for P values <0.05 (if necessary, Greenhouse–Geisser corrected).

Furthermore, to investigate possible locations of neural generators underlying the significant differences found between the Attention and Reference condition, Grand Average difference waves were submitted to source analyses (using the software-package BESA Version 2.2). Dipole fitting included one or two bilateral equivalent current dipoles with symmetrical (mirrored) location and orientation. The default four shell (head, shell, bone, csf) spherical head model was used as well as an energy constraint of 20% (as opposed to 80% for the residual variance; see Berg and Scherg handbook, 1994). Finally, to evaluate onset locations (anterior or posterior) of attentional orienting activity, as well as changes of dipole locations and strength of individual dipoles over time, individual source parameters (dipole location and dipole moments) were estimated and submitted to repeated measurement ANOVA, separately for each contrast of interest.

5.5.2. ERPs to test stimuli (S2-trials)

5.5.2.1. *Trial selection and generation of ERPs.*
ERPs time-locked to test stimuli (S2 stimuli) were computed, separately per condition and separately for targets and non-targets (collapsed over LSF and HSF), using an epoch length of 700 ms, including a prestimulus window of 100 ms. Trials were included in these ERP averages only if they matched the following inclusion criteria: (1) congruence between instructed target-SF and cue type (see 5.4), (2) preceded by correctly identified cues (correct response hand and RT between 200–700 ms postcue), (3) in the case of a target, correctly identified as such with the proper response hand and within the response window of 200–700 ms poststimulus, and (4) not contaminated by excessive muscle-related activity, slow drift or amplifier blocking. In addition, artifacts caused by eye movements or eye blinks were corrected before averaging, using the regression method developed by Gratton et al. (1983). Furthermore, selection potentials (difference waves between target and non-target ERPs) were computed within each condition separately. Finally, all computed average ERPs were digitally low-pass filtered with a non-causal, zero-phase shift, running average filter of 9 points, which strongly reduces frequencies at and above 22 Hz at our sampling frequency of 200 Hz.

5.5.2.2. *Statistical analyses of selection potentials.*
Selective attention to spatial frequency (SF) patterns has been shown (Baas et al., 2002; Kenemans et al., 1993, 2002; Martinez et al., 2001) to involve a sequence of selection potentials (FSP—frontal selection positivity; OSN—occipital selection negativity; fronto-central N2b, and parietal P3b), reflecting selective attention to the task-specific spatial frequency stimuli. In the present study, these selection potentials (reflected in ERP difference waves between targets and non-targets) were investigated both between and within the two main conditions (Attention and Reference condition). Attention effects were identified and tested for significance using windows of averaged data around the peaks of the different attention

effects, and a comparable ROI approach as used in the cue-analyses: (1) FSP: frontal [F3, Fz, F4] and prefrontal [F7, AFz, F8] ROIs, (2) OSN; occipital ROI [O3, Oz, O4]; (3) N2b: frontal [F3, Fz, F4] and central [C3, Cz, C4] ROIs, and (4) P3b: parietal [P3, Pz, P4] ROI. The repeated measurement ANOVAs on these ROIs included the within-subject factors CONDITION (Attention, Reference), ATTENTION (targets, non-targets), and ELECTRODES (left, midline, right electrode).

REFERENCES

Baas, J.M., Kenemans, J.L., Mangun, G.R., 2002. Selective attention to spatial frequency: an ERP and source localization analysis. Clin. Neurophysiol. 113, 1840–1854.

Berg, P., Scherg, M., 1994. Besa Version 2.0 Handbook. Megis, Munich.

Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat. Rev., Neurosci. 3, 201–215.

Corbetta, M., Kincade, J.M., Shulman, G.L., 2002. Neural systems for visual orienting and their relationships to spatial working memory. J. Cogn. Neurosci. 14, 508–523.

Desimone, R., 1998. Visual attention mediated by biased competition in extrastriate visual cortex. Philos. Trans. R. Soc. Lond., B Biol. Sci. 353, 1245–1255.

Eimer, M., 1997. An event-related potential (ERP) study of transient and sustained visual attention to color and form. Biol. Psychol. 44, 143–160.

Gevins, A., Smith, M.E., 2000. Neurophysiological measures of working memory and individual differences in cognitive ability and cognitive style. Cereb. Cortex 10, 829–839.

Giesbrecht, B., Woldorff, M.G., Song, A.W., Mangun, G.R., 2003. Neural mechanisms of top–down control during spatial and feature attention. NeuroImage 19, 496–512.

Gratton, G., Coles, M.G., Donchin, E., 1983. A new method for off-line removal of ocular artifact. Electroencephalogr. Clin. Neurophysiol. 55, 468–484.

Harter, M.R., Anllo-Vento, L., 1991. Visual-spatial attention: preparation and selection in children and adults. Electroencephalogr. Clin. Neurophysiol., Suppl. 42, 183–194.

Hopf, J.M., Mangun, G.R., 2000. Shifting visual attention in space: an electrophysiological analysis using high spatial resolution mapping. Clin. Neurophysiol. 111, 1241–1257.

Hopfinger, J.B., Buonocore, M.H., Mangun, G.R., 2000. The neural mechanisms of top–down attentional control. Nat. Neurosci. 3, 284–291.

Hopfinger, J.B., Woldorff, M.G., Fletcher, E.M., Mangun, G.R., 2001. Dissociating top–down attentional control from selective perception and action. Neuropsychologia 39, 1277–1291.

Kane, M.J., Bleckley, M.K., Conway, A.R., Engle, R.W., 2001. A controlled-attention view of working-memory capacity. J. Exp. Psychol. Gen. 130, 169–183.

Kenemans, J.L., Kok, A., Smulders, F.T., 1993. Event-related potentials to conjunctions of spatial frequency and orientation as a function of stimulus parameters and response requirements. Electroencephalogr. Clin. Neurophysiol. 88, 51–63.

Kenemans, J.L., Lijffijt, M., Camfferman, G., Verbaten, M.N., 2002. Split-second sequential selective activation in human secondary visual cortex. J. Cogn. Neurosci. 14, 48–61.

Kramer, A.F., Wickens, C.D., Donchin, E., 1985. Processing of stimulus properties: evidence for dual-task integrality. J. Exp. Psychol. Hum. Percept. Perform. 11, 393–408.

LaBerge, D., 2001. Attention, consciousness, and electrical wave

activity within the cortical column. Int. J. Psychophysiol. 43, 5–24.

LaBerge, D., 2002. Attentional control: brief and prolonged. Psychol. Res. Psychol. Forsch. 66, 220–233.

Lange, J.J., Wijers, A.A., Mulder, L.J., Mulder, G., 1998. Color selection and location selection in ERPs: differences, similarities and 'neural specificity'. Biol. Psychol. 48, 153–182.

MacDonald III, A.W., Cohen, J.D., Stenger, V.A., Carter, C.S., 2000. Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. Science 288, 1835–1838.

Martinez, A., Di Russo, F., Anllo-Vento, L., Hillyard, S.A., 2001. Electrophysiological analysis of cortical mechanisms of selective attention to high and low spatial frequencies. Clin. Neurophysiol. 112, 1980–1998.

Miller, E.K., Cohen, J.D., 2001. An integrative theory of prefrontal cortex function. Annu. Rev. Neurosci. 24, 167–202.

Nobre, A.C., Sebestyen, G.N., Miniussi, C., 2000. The dynamics of shifting visuospatial attention revealed by event- related potentials. Neuropsychologia 38, 964–974.

Osaka, M., Osaka, N., Kondo, H., Morishita, M., Fukuyama, H., Aso, T., Shibasaki, H., 2003. The neural basis of individual differences in working memory capacity: an fMRI study. NeuroImage 18, 789–797.

Roche, R.A., Garavan, H., Foxe, J.J., O'Mara, S.M., 2005. Individual differences discriminate event-related potentials but not performance during response inhibition. Exp. Brain Res. 160, 60–70.

Rosen, A.C., Rao, S.M., Caffarra, P., Scaglioni, A., Bobholz, J.A., Woodley, S.J., Hammeke, T.A., Cunningham, J.M., Prieto, T.E., Binder, J.R., 1999. Neural basis of endogenous and exogenous spatial orienting. A functional MRI study. J. Cogn. Neurosci. 11, 135–152.

Shulman, G.L., Ollinger, J.M., Akbudak, E., Conturo, T.E., Snyder, A.Z., Petersen, S.E., Corbetta, M., 1999. Areas involved in encoding and applying directional expectations to moving objects. J. Neurosci. 19, 9480–9496.

Slagter, H.A., Kok, A., Mol, N., Kenemans, J.L., 2005a. Spatio-temporal dynamics of top–down control: directing attention to location and/or color as revealed by ERPs

and source modeling. Brain Res. Cogn. Brain Res. 22, 333–348.

Slagter, H.A., Kok, A., Mol, N., Talsma, D., Kenemans, J.L., 2005b. Generating spatial and nonspatial attentional control: an ERP study. Psychophysiology 42, 428–439.

Strayer, D.L., Kramer, A.F., 1994. Strategies and automaticity: II. Dynamic aspects of strategy adjustment. J. Exper. Psychol., Learn., Mem., Cogn. 20, 342–365.

Talsma, D., Slagter, H.A., Nieuwenhuis, S., Hage, J., Kok, A., 2005. The orienting of visuospatial attention: an event-related brain potential study. Brain Res. Cogn. Brain Res. 25, 117–129.

Vandenberghe, R., Duncan, J., Arnell, K.M., Bishop, S.J., Herrod, N.J., Owen, A.M., Minhas, P.S., Dupont, P., Pickard, J.D., Orban, G.A., 2000. Maintaining and shifting attention within left or right hemifield. Cereb. Cortex 10, 706–713.

van Velzen, J., Eimer, M., 2003. Early posterior ERP components do not reflect the control of attentional shifts toward expected peripheral events. Psychophysiology 40, 827–831.

Weissman, D.H., Woldorff, M.G., 2004. Hemispheric asymmetries for different components of global/local attention occur in distinct temporo-parietal loci. Cereb. Cortex 15, 870–876.

Weissman, D.H., Mangun, G.R., Woldorff, M.G., 2002. A role for top–down attentional orienting during interference between global and local aspects of hierarchical stimuli. NeuroImage 17, 1266–1276.

Wijers, A.A., Mulder, G., Okita, T., Mulder, L.J., 1989. Event-related potentials during memory search and selective attention to letter size and conjunctions of letter size and color. Psychophysiology 26, 529–547.

Woldorff, M.G., Hazlett, C.J., Fichtenholtz, H.M., Weissman, D.H., Dale, A.M., Song, A.W., 2004. Functional parcellation of attentional control regions of the brain. J. Cogn. Neurosci. 16, 149–165.

Yamaguchi, S., Tsuchiya, H., Kobayashi, S., 1994. Electroencephalographic activity associated with shifts of visuospatial attention. Brain 117 (Pt 3), 553–562.

Yamaguchi, S., Yamagata, S., Kobayashi, S., 2000. Cerebral asymmetry of the "top–down" allocation of attention to global and local features. J. Neurosci. 20, RC72.