DOI: 10.1111/j.1469-8986.2005.00304.x

# Generating spatial and nonspatial attentional control: An ERP study

# HELEEN A. SLAGTER,<sup>a</sup> ALBERT KOK,<sup>a</sup> NISAN MOL,<sup>b</sup> DURK TALSMA,<sup>c</sup> and J. LEON KENEMANS<sup>b</sup>

<sup>a</sup>Department of Psychonomics, University of Amsterdam, Amsterdam, The Netherlands

#### Abstract

The present study used event-related potentials and dipole source modeling to investigate dimension specificity in attentional control. Subjects performed cued attention tasks in which the task-relevant information (a) was always the same, (b) varied between features within the same dimension, or (c) varied between features of two different dimensions. Thus, both demands on control processes involved in generating an attentional set and the dimension (color or location) of the task-relevant feature were varied. Attentional control was associated with a dorsal posterior positivity starting at 260 ms postcue, which was stronger over left posterior scalp regions from 580 ms onward, especially when color was task relevant. This positivity likely reflects generic processes involved in the generation of an attentional set that were followed in time by dimension-specific processes related to the persistence of the task-relevant information in working memory.

Descriptors: Spatial, Nonspatial, Attentional control, Attentional selection, Event-related potentials, Dipole modeling

Attention can be dynamically allocated to aspects of the outside world that are relevant to our immediate goals. In this way, taskrelevant information can be processed selectively and we can respond faster and more accurately to behaviorally important events (e.g., Posner, 1980). In the past, event-related potential (ERP) studies investigating how the brain mediates selective processing of task-relevant information have shown that that spatial attention yields earlier and qualitatively different ERP effects than nonspatial attention. Whereas visuospatial attention results in enhanced amplitudes of the exogenous P1 and N1 components as early as 80-90 ms post stimulus (e.g., Eason, 1981; Mangun, Hansen, & Hillyard, 1986), selection based on nonspatial visual stimulus features, such as color or shape, is reflected by effects starting at around 150 ms after stimulus onset, which are superimposed on the evoked components and have a very different morphology (e.g., Harter & Previc, 1978). These electrophysiological findings indicate that the mechanisms underlying the selective processing of task-relevant information differ between spatial and nonspatial attention. They are also in line with models of attention that, based upon results from

We thank Giuseppe Cipriani for assistance in collecting the data of the behavioral experiment. This research was supported by Dutch NWO grant 42520206 to A.K and J.L.K.

Heleen Slagter is now at the University of Wisconsin.

Address reprint requests to: Heleen A. Slagter, Waisman Center, University of Wisconsin, Laboratory for Brain Imaging & Behavior, T139, 1500 Highland Avenue, Madison, WI 53705-2280, USA. E-mail: slagter@wisc.edu.

behavioral studies, have assigned a special role for spatial attention in visual processing (Treisman, 1993; van der Heijden, 1993).

More recent work has begun to address the question of how spatial and nonspatial attention afford selective processing of task-relevant information by studying the top-down control mechanisms that specify what information should be attended (Driver & Frith, 2000; Nobre, 2001; Yantis & Serences, 2003). This line of research may provide insight into the mechanisms that actually produce the observed differences in modulatory effects between spatial and nonspatial attention. A task that is typically employed to study top-down attentional control is the cued attention task. Here, subjects are first presented with a cue that instructs them to direct attention to a certain stimulus attribute, which is then followed by a test stimulus that may or may not possess the cued attribute. By evaluating what is happening in the brain in the period between the attention-directing cue and the test stimulus, processes involved in controlling attention can be examined. Because ERPs provide precise information on the timing of neural events, they are ideally suited to identify the different processes involved in attentional control, such as the generation of an attentional set and the biasing of feature-specific visual areas (Posner, Inhoff, Friedrich, & Cohen, 1987). Yet, attention-directing cues not only elicit activity in brain systems that control the focus of attention, but also in brain systems involved in other stages of information processing, such as cue identification and motor preparation. To isolate attentional control processes, the attention-directing condition should there-

<sup>&</sup>lt;sup>b</sup>Departments of Psychonomics and Psychopharmacology, Utrecht University, Utrecht, The Netherlands

<sup>&</sup>lt;sup>c</sup>Department of Clinical Neuropsychology, Vrije Universiteit, Amsterdam, The Netherlands

fore be compared with a reference condition that controls for these nonspecific processes.

Several ERP studies have previously investigated the processes involved in directing attention to spatial position (Eimer, 1993; Eimer, Van Velzen, & Driver, 2002; Harter & Anllo-Vento, 1991; Harter, Miller, Price, LaLonde, & Keyes, 1989; Hopf & Mangun, 2000; Mangun, 1994; Nobre, Sebestian, & Miniussi, 2000; Yamaguchi, Tsuchiya, & Kobayashi, 1994, 1995) or nonspatial visual stimulus attributes (Kenemans, Grent-'t-Jong, et al., 2002; Yamaguchi, Yamagata, & Kobayashi, 2000) using cued attention tasks. Most of the studies of spatial attentional control compared ERP responses elicited by cues directing attention to the left and right hemifields (Eimer, 1993; Eimer et al., 2002; Harter et al., 1989; Hopf & Mangun, 2000; Nobre et al., 2000; Yamaguchi et al., 1994, 1995; but see Harter & Anllo-Vento, 1991; Mangun, 1994; Wright, Geffen, & Geffen, 1995). This contrast reveals all processes that are specific to the task-relevant hemifield and eliminates all processes not related to attention, such as the sensory processing of the cue. However, this approach is not ideal for isolating the full temporal pattern of attentional control, as it may cancel out nonlateralized attentional control processes that may be mandatory for the establishment of an attentional bias. In addition, results from studies using this approach cannot easily be compared to results from studies of nonspatial attentional control (Kenemans, Grent-'t-Jong, et al., 2002; Yamaguchi et al., 2000) in which such an attend-left versus attend-right comparison is obviously not possible. On the basis of these studies, it is therefore unclear to what extent spatial and nonspatial attentional control rely on common mental operations.

To gain more insight into the extent to which the processes involved in attentional control are specific to the dimension (i.e., spatial or nonspatial) of the behaviorally relevant information, we recently conducted an ERP study employing a cued attention task in which both the number and type of task-relevant feature(s) were varied (Slagter, Kok, Mol, & Kenemans, 2005). Cues instructing subjects to direct attention to a color, a location, a conjunction of a color and location, or informing subjects that no specific color or location was task relevant on that trial (i.e., so-called no-feature cue) were presented randomly mixed in a trial block. Comparison of ERPs elicited by color and location attention-directing cues and by no-feature cues revealed three principal attentional control-related effects: (1) a parieto-occipital positivity around 340 ms post cue, which was related to linking the cued symbol to its associated stimulus feature. This effect was localized to the ventral posterior compartment of cortex. (2) A negativity over fronto-central scalp regions that was maximal around 540 ms post cue. This effect was related to generic processes involved in directing attention. (3) Late in the cue-target interval, differences in ERP were observed between directing attention to color and location. The latter effects originated from anterior and ventral posterior areas and may represent differences in, respectively, maintenance and perceptual biasing processes. Thus, in general, similar ERP patterns were observed for directing attention to color and location, suggesting that spatial and nonspatial attention rely to a great extent on similar control mechanisms.

It has been argued, however, that when tasks occur in a mixed design, subjects may adopt a more generalized task strategy because they have to be prepared for all the different possibilities (e.g., Strayer & Kramer, 1994). The previously observed overlap in color and location cue-related ERPs may hence reflect activity related to the use of generalized task-preparation strategies rath-

er than mechanisms that are common to spatial and nonspatial top-down control. In addition, the no-feature reference cue condition used in our previous study differed from the attention-directing cue condition in demands on preparatory processes related to both the specification of the task-relevant information and the maintenance of this information, making it difficult to distinguish between these two operations.

The present study sought to address these issues and complement the findings from our previous study using ERPs and dipole source modeling. In particular, we employed additional controls for maintenance processes, while varying demands on processes involved in the specification of the behaviorally relevant information. In addition, color and location cues were presented both randomly mixed in a block and in separate blocks. Three types of task blocks were used: blocks in which the cued attribute (a specific color [blue or yellow] or a specific location [left or right]) (1) was always the same ("repeated" task), (2) varied between features within the same dimension (either color or location; "transient" task), or (3) varied between features of both dimensions (color and location) within a block of trials ("mixed" task). Sensory and motor demands were equal across tasks and there was always only one relevant feature. Yet, demands on processes involved in specifying the task-relevant information increased progressively from the repeated to the transient to the mixed task. Therefore, by contrasting cue-related activity in the transient and mixed tasks with cue-related activity in the repeated task, for the location and color attention-directing conditions separately, we could more specifically examine the nature and dynamics of top-down attentional control.

We predicted that if spatial and nonspatial attention rely on common control operations, the two types of attention should show no differences in brain activity when comparing ERPs elicited by transient and mixed cues with ERPs elicited by repeated cues. This would be reflected by a main effect of task (repeated, transient, mixed). On the other hand, if attentional control operations are to some extent dimension specific, this would be revealed by an interaction between dimension (location, color), task, and recording site. To be better able to compare results from this study with our previous study (Slagter et al., 2005) in terms of global location, the neural generators of the most pronounced effects of task and dimension were estimated using dipole source modeling. We furthermore expected that if the intermixed presentation of location and color cues led subjects to adopt more generalized task-preparation strategies, the effects of dimension on attentional control processes should be less prominent in the mixed than the transient task, as expressed by a task by dimension interaction. Also, to ensure that subjects had indeed directed their attention, we examined the presence of the commonly reported modulatory effects of spatial attention (i.e., P1 and N1) and nonspatial attention (i.e., frontal selection positivity [FSP] and occipital selection negativity [OSN]) on test stimulus processing (Hillyard & Munte, 1984; Lange, Wijers, Mulder, & Mulder, 1998). In addition, we investigated whether the size of these modulatory effects was affected by our attentional control manipulation.

To establish that demands on control processes were indeed higher in the mixed versus the transient versus the repeated task, we conducted a separate behavioral study in which the duration of the interval between cue onset and test stimulus was varied between 200 and 600 ms. Increased processing demands would be reflected by an increase in interval time needed for the reaction time function to reach asymptote in the mixed relative to the

transient relative to the repeated task. In the ERP experiment, the cue—test stimulus interval was always minimally 800 ms to ensure that we could investigate the full temporal pattern of attentional control.

#### Methods

#### **Participants**

Eighteen volunteers participated in Experiment 1, the behavioral study (5 men; aged 18–30 years; mean age of 21.9 years), and 16 volunteers participated in Experiment 2, the ERP study. The data of 2 subjects were discarded from the ERP analysis due to ocular artifacts. Thus, 14 subjects (7 men; aged 19–25 years, mean age of 20.7 years) remained in the ERP sample. All participants were students at the University of Amsterdam and were right-handed. They reported having no history of mental or sustained physical illness and normal or corrected-to-normal vision. Participants received credits as part of an introductory course requirement at the University of Amsterdam.

#### Stimuli

Experiment 1. Behavioral study. Each trial began with a 100-ms presentation of a cue (0.92° in width and 2.8° in height) that was located at fixation. Then, with SOAs of 200, 300, 400, 500, or 600 ms, this cue was followed by a test stimulus (3° in height, 3° in width). This test stimulus was a blue or yellow square and appeared 7.13° to center from fixation in either the left or the right visual field and 1.73° to center above the horizontal meridian. The next trial started randomly after 1400 to 2100 ms. During the entire trial, a fixation cross (0.31° in width and 0.20° in height) was shown at the center of the screen. All stimuli were presented on a black background.

Each cue consisted of four white uppercase letters (all equal in width [0.36°] and height [0.51°]) presented around the fixation cross in a vertical array: "B," "G," "L," and "R." Each letter corresponded to a stimulus feature: "B" to blue, "G" to yellow ("geel" in Dutch), "L" to left, and "R" to right. Letter order was counterbalanced across subjects with the restriction that the location coding letters (L and R) and color coding letters (B and G) were always grouped together, resulting in eight possible combinations of letters. There were five different cues, four attentiondirecting cues (i.e., blue, yellow, left, and right cues) and one so-called "catch cue." These were defined by the position of two small horizontal bars  $(0.20^{\circ})$  in width,  $0.08^{\circ}$  in height) that either flanked one of the four letters (attention-directing cue) or the fixation cross (catch cue). In case of an attention-directing cue, the letter flanked by the two bars indicated the feature to which attention was to be directed (e.g., when presented next to L, attention had to be directed to the left).

When presented with an attention-directing cue, subjects were instructed to respond as fast and accurately as possible to test stimuli presented at the cued location or of the cued color. On 50% of all trials, the test stimulus possessed the cued attribute. Upon presentation of a catch cue, subjects were required to press a button as fast as possible. On these catch cue trials, subject did not have to direct attention and could ignore the subsequent test stimulus. Catch cue trials were randomized into the stimulus sequence to ensure that subjects identified and interpreted the cue to a similar extent in all types of tasks. Subjects used their right index finger to respond both to target test stimuli and catch cues.

Subjects performed three types of cueing tasks: (1) a repeated task: Subjects were repeatedly cued to direct attention to the same stimulus feature (a color [blue or yellow] or a location [left or right]) during an entire run, (2) a transient task: Subjects were cued on a trial-by-trial basis to direct attention to one of two features of the same dimension (either color [blue and yellow] or location [left and right]), and (3) a mixed task: Subjects were cued on a trial-by-trial basis to direct attention to either a color (blue, yellow) or a location (left, right). On a given trial, subjects were thus cued to attend to a particular stimulus feature of a given dimension. In all tasks, catch cues were presented on 13.5% of all trials and all possible attention-directing cues were presented with equal probability in the remainder of trials.

Each task run started with a 10-s presentation of a warning screen, which indicated to subjects which task would be presented next. A task run consisted of 74 trials and lasted approximately 3 min. In the repeated task, trial categories were varied randomly per run. In the transient and mixed tasks, the cue-test stimulus sequence was randomized similarly per run with the restriction that the same cue could not be presented for more than five successive trials in a row. Subjects practiced one run of each task first. Then, subjects performed one run of each repeated task, two runs of each transient task, and four runs of the mixed task. The order of tasks was counterbalanced across subjects with the restriction that the repeated and transient color tasks, the repeated and transient location tasks, and the mixed tasks were each always presented together. Subjects sat at 80 cm in front of the computer screen.

Experiment 2: ERP study. The same stimuli and tasks were used as in Experiment 1 with the exception that the cue—test stimulus interval was now randomly varied between 800 and 1500 ms (rectangular distribution), so that we could examine the full temporal pattern of attentional control and to mitigate the possibility of overlapping ERP waves. As noted by one of the reviewers, one should keep in mind that a possible disadvantage of using long cue—test stimulus intervals is that the neural operations of attentional orienting may become invoked in a less tight manner, possibly smearing the ERP signature. A second difference between the ERP and the behavioral experiment was that test stimuli were divided into targets (150 ms) and standards (50 ms). Targets were presented on 25% of trials, and subjects were instructed to respond only to target test stimuli with the cued feature.

The ERP study consisted of three sessions: a practice session and two EEG sessions. During the practice session, subjects practiced each task twice, to become familiar with the specific task requirements. In addition, it was made sure that subjects did not show excessive eyeblink activity while performing the task. In total, subjects performed 4 runs of each condition of the repeated task (i.e., left, right, blue, yellow), 8 runs of each condition of the transient task (i.e., color, location), and 16 runs of the mixed task during the EEG sessions. During one EEG session, subjects performed all runs of the repeated and transient tasks of one dimension (e.g., location) and half the runs of the mixed task. During the other EEG session, they performed all runs of the repeated and transient tasks of the other dimension (e.g., color) plus the other half of the runs of the mixed task. The order of these two sessions was counterbalanced. Repeated and transient task runs were presented intermixed and their order was randomized across subjects. Subjects were allowed to pause between the runs if they wished to do so. Subjects practiced each task used

in a given EEG session once more after placement of the electrode cap, right before the EEG recordings started.

#### **ERP Recordings**

Recordings were made with 60 Ag/AgCl electrodes mounted in an elastic cap (Quick Cap) according to the International 10–20 system. All scalp channels were referenced to the right mastoid. Horizontal eye movements were monitored with two bipolar electrodes placed on the left and right of the external canthi. Vertical eye movements and blinks were measured bipolarly with two electrodes placed above and below the left eye. EEG was recorded in DC mode with a low-pass filter of 60 Hz and digitized at 250 Hz. Impedances were kept below 5 k $\Omega$ .

The raw data were filtered off-line with a noncausal 40-Hz low-pass filter (24 dB/oct). Epochs were created starting 100 ms before and ending 500 and 800 ms after, respectively, each test stimulus and cue of interest, re-referenced to the mean of both mastoids, and averaged according to category type. Trials containing artifacts (VEOG  $> \pm 60 \mu V$ , HEOG  $> \pm 30 \mu V$ , and EEG  $> \pm 60 \mu V$ ), and behavioral errors were excluded from further analysis. About 15% of trials (standard deviation: 2.2%) were rejected from the cue analyses based upon our artifact rejection criterion. This number did not differ appreciably between conditions and tasks. For each task (i.e., repeated, transient, mixed), four test stimulus-locked ERPs were created: (1) location attended, (2) location unattended, (3) color attended, and (4) color unattended. In addition, six types of ERPs were constructed for the cue stimuli, according to the two types of cues (color [blue and yellow] and location [left and right]) and the three types of tasks (repeated, transient, and mixed). If residual horizontal  $(>2 \mu V)$  or vertical eye movement-related activity (greater voltage at VEOG than FP1 or FP2) was present in the individual average ERP waveforms, the individual trials were visually inspected and manually excluded from the average process when contaminated with EOG activity.

## Analysis

Experiment 1: Behavioral Study

To investigate the time course of attentional orienting, repeated-measures analyses of variance (ANOVAs) with the within-subject factors dimension (color, location), task (repeated, transient, mixed), and interval (200, 300, 400, 500, 600 ms [with respect to cue onset]) were performed on (1) response latencies of correct responses to attended test stimuli, (2) arc sin-transformed omitted response rates, and (3) arc sin-transformed false alarm rates to attended test stimuli. In case of a significant interaction of dimension or task with the factor interval, separate repeated-measures ANOVAs were run for each interval with the factors dimension and task.

# Experiment 2: ERP Study

Behavioral analysis. Repeated-measures ANOVAs with the within-subject factors dimension (color, location) and task (repeated, transient, mixed) were performed on (1) response latencies of correct responses to target test stimuli, (2) arc sintransformed omitted response rates, and (3) arc sin-transformed false alarm rates to (a) attended test stimuli, which were presented briefly, (b) unattended test stimuli, which were presented slightly longer, and (c) unattended test stimuli, which were presented briefly. These analyses were performed to test for differences in behavioral performance between task conditions. In addition, to investigate whether or not subjects kept identifying

the cue symbol in the repeated task, response times to and arc-sin transformed omitted response rates for catch cues were entered into repeated-measurements ANOVAs with the within-subject factor task (repeated, transient, mixed).

Test stimulus-locked ERP analyses. P1 and N1 attention effects were investigated at electrodes P7 and P8, between 80 and 140 ms and 140 and 200 ms poststimulus, respectively, for the location condition. P1 and N1 attention effects are generally most pronounced over lateral occipito-temporal areas (Hillyard, Vogel, & Luck, 1998), as also confirmed by inspection of the current data. Voltage values, sampled every 4 ms within these intervals, were submitted to repeated-measures ANOVAs, which tested for the effects of task (repeated, transient, mixed; task), attention (attended, unattended; location-attention), hemisphere (left, right; hemisphere), and stimulus feature (left, right; location).

The presence of FSP and OSN effects was examined, respectively, at electrodes F3 and F4 between 100 and 248 ms poststimulus, and at electrode Oz between 148 and 300 ms for the color condition. Selection of the F3 and F4 electrodes was motivated by the current data and findings from prior studies (e.g., Anllo-Vento, Luck, & Hillyard, 1998), while selection of the Oz electrode was motivated based on findings from prior studies alone, as we did not observe an OSN (see below). Voltage values, sampled every 4 ms within these intervals, were submitted to repeated-measures ANOVAs, which tested for the effects of task (repeated, transient, mixed; task), attention (attended, unattended; color-attention), and stimulus feature (blue, yellow; color). In the FSP analyses, the additional factor hemisphere (left, right; hemisphere) was tested. Because of multiple interrelated comparisons, and hence the likelihood of false-positive spurious significant effects, for all analyses performed, effects were only considered reliable if they persisted for at least six successive time bins (4 ms each, p value < .05).

Cue-locked ERP analyses. The 800-ms cue-test stimulus interval was divided into 40 time bins of 20 ms (five sample points), and for each time bin, the average voltage was computed for each electrode and task condition of interest. To detect ERP differences between the different task conditions, these mean voltage values were subjected as dependent variables to separate regional repeated-measures ANOVAs (anterior analysis [F7/F8, F3/F4, FC5/FC6], central analysis [T7/T8, C3/C4, CP5/CP6], and posterior analysis [P7/P8, P3/P4, PO5/PO6]) for each time bin separately. In these analyses, the following four factors were tested within subjects: task (repeated, transient, mixed), dimension (color, location), electrode position within hemisphere (e.g., P7/ 8, P3/4, PO5/6; site), and hemisphere (left, right). In case of statistical effects including the factor task, post hoc contrasts were used to determine which tasks specifically differed from one another. The following two orthogonal contrasts were specified for the factor task: repeated versus the average of the transient and mixed tasks and transient versus mixed task. For topographical analysis, the data were normalized according to the scaling procedure described by McCarthy and Wood (1985). These normalized data were analyzed with the same ANOVAs described above. If interaction effects between the factors task and/or dimension with the factor site identified using the nonnormalized data were still present after normalization, this was taken as evidence for a difference in scalp topography between conditions. Given our relatively small sample size, only results from "mixed-model" tests were examined for all the

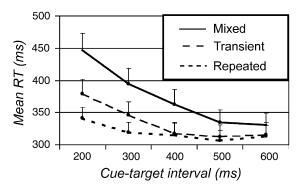
repeated-measurements analyses performed. The Huynh–Feldt or Greenhouse–Geisser epsilon correction factor (whenever the Huynh–Feldt epsilon was smaller than .75) was applied where appropriate, to compensate for possible effects of nonsphericity in the measurements compared. Only the corrected F and probability values and the uncorrected degrees of freedom are reported. Because of multiple interrelated comparisons, and hence the likelihood of false-positive spurious significant effects, effects were only considered reliable if they persisted for at least three successive time bins (20 ms each, (corrected) p value < .05).

Source localization. To investigate the neural generators of the most pronounced effects of task and dimension, a subtraction logic and source modeling were applied (cf. Kenemans, Lijffijt, Camfferman, & Verbaten, 2002). For each electrode, four cuelocked grand average average-reference difference waves were calculated: (1) location transient – repeated, (2) color transient – repeated, (3) location mixed - transient, and (4) color mixed transient. Then, for each sample point, the global field power was calculated as the square root of the sum of squares of the averagereferenced activity over all channels. Peaks in the time-varying global field power function thus indicate latencies where the underlying brain activity is maximal, taking into account all electrode channels (Lehman & Skrandies, 1984). Next, dipole fitting was conducted, using one or two bilateral dipole pairs with mirror-symmetric locations, at a 20-ms window around global field power peak latencies of interest. Source models were determined using the BESA program (version 4.2), using the default fourshell model. An energy constraint (weighted 20% in the compound cost function, as opposed to 80% for the residual variance criterion; see Berg & Scherg, 1994) was used to reduce the probability of interacting dipoles and to favor solutions with relatively low dipole moments. To evaluate apparent similarities/differences in equivalent dipole locations and orientations across the different conditions, individual source parameters (dipole location and orientation) were estimated for global field power latencies of most interest. Then, the resulting x-, y-, and z-coordinates were entered into one multivariate test with the within-subjects factors dimension (color, location) and contrast (transient-repeated, mixed-transient), separately for each type of parameter and global field power latency of interest.

#### Results

#### Experiment 1: Behavioral Study

In line with the hypothesis that task demands were greater in the mixed versus the transient versus the repeated tasks, it took significantly longer for the reaction time function to reach asymptote in the mixed versus the transient versus the repeated tasks, as expressed by a significant interaction between task and interval, F(8,136) = 17.5; p < .001 (see Figure 1). Only when subjects were allowed 600 ms to direct attention (i.e., during the longest cuetest stimulus interval) were subjects equally fast in responding to target stimuli in all tasks. In addition, not shown in Figure 1, with longer cue-test stimulus intervals, subjects were faster in responding to test stimuli presented at the cued location than to test stimuli of the attended color (interaction between dimension and interval, F[4,68] = 3.2, p = .019). When investigating differences in response time between the location and color conditions for each cue-test stimulus interval separately, however, no significant differences were observed. In addition, with shorter cue-test stimulus intervals, subjects made more false alarms to unattend-



**Figure 1.** Mean reaction time (+ standard error) obtained in Experiment 1 displayed as a function of cue—target interval duration for the mixed, transient, and repeated tasks.

ed test stimuli in the mixed and transient tasks compared to the repeated task, as reflected by a significant interaction between task and interval, F(8,136) = 3.7, p = .001. No differences in the number of missed attended test stimuli were observed between any of the tasks or between the color and location condition across intervals.

## Experiment 2: ERP Study

Behavior

Table 1 lists the average response times, percentage of false alarms, and percentage of omitted responses in the color and location attention-directing conditions for the repeated, transient, and mixed tasks. There were no significant differences between the different task conditions in response latency, any of the false alarm rates, or omitted response rates to target test stimuli. Subjects responded faster to catch cues in the repeated (560 ms) compared to the transient (571 ms) and mixed (579 ms) tasks as expressed by a main effect of task, F(2,26) = 6.57, p = .001. This indicates that subjects identified the cue symbol more quickly in the repeated tasks. Moreover, although relatively few catch cues were missed, a greater number of omitted responses to catch cues was found for the mixed (1.47%) compared to the repeated (0.67%) and transient (0.80%) tasks (main effect of task, F[2,26] = 8.40, p = .002).

## Test Stimulus-Locked ERP Effects

Both P1 and N1 amplitudes were modulated by spatial attention, confirming that subjects had indeed directed their attention to the cued location (see Figure 2A). P1 amplitudes were larger for stimuli presented at attended compared to unattended locations between 112 and 148 ms post test stimulus, F(1,13) = 5.4-14.7, p < .05. This attention-related effect did not depend on the type of task performed, and was greater in size over contralateral scalp regions as indicated by an interaction between the factors location-attention, hemisphere, and location between 104 and 124 ms poststimulus at electrodes P7 and P8, F(1,13) = 4.7-17.1, p < .05. Interestingly, this P1 effect appeared to be preceded by an effect that was dependent on the type of task performed (see Figure 2A). Close inspection of the test stimuluslocked ERPs revealed that this unexpected effect represented an early attentional modulation of the P1 in the mixed task, which was not lateralized with respect to the cued location. This was confirmed by additional analyses at electrodes P7 and P8, showing that stimuli presented at attended locations elicited greater positivity over lateral posterior scalp regions than stimuli presented at unattended locations in the mixed task compared to the

	Color			Location		
	Reaction times	% False alarms	% Omitted responses	Reaction times	% False alarm	% Omitted responses
Repeated task	566	0.5	9.9	549	0.6	8.5
Transient task	568	0.7	9.7	561	0.7	8.8
Mixed task	559	0.6	9.8	563	0.6	7.6

**Table 1.** Average Response Times, Percentage of False Alarms, and Percentage of Omitted Responses to Test Stimuli in the Color and Location Attention-Directing Conditions

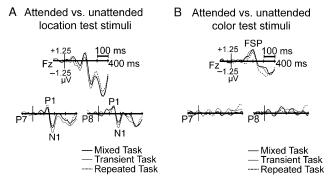
repeated and transient tasks between 68 and 92 ms poststimulus (interaction between task and location-attention: F[2,26] = 4.0-4.4, p < .05).

Just like P1 amplitudes, N1 amplitudes were larger for attended versus unattended location test stimuli between 160 and 212 ms, F(1,13) = 5.2-27.1, p < .05. In addition, the size of this N1 spatial attention effect was dependent on the type of task performed (interaction between task and location-attention between 156 and 200 ms, F[2,26] = 3.8-5.6,  $\varepsilon = .66-.92$ , p < .05), being greater in the transient compared to the repeated or mixed task. This indicates that spatial attention may have been most effectively directed in the transient task.

Compared to test stimuli of the unattended color, test stimuli of the attended color elicited a larger positive response at electrodes F3 and F4 between 144 and 228 ms in the color condition, F(1,13) = 5.3-34.2, p < .05 (see Figure 2B). The size of the effect did not differ as a function of the attentional control manipulation, indicating that subjects had indeed directed their attention to the cued color and did so in a similar way in each task. In addition, a significant main effect of attention was observed at Oz between 156 and 184 ms reflecting a larger positive response to stimuli of the attended versus the unattended color, F(1,13) = 6.0-15.5, p < .05. It should be noted that this latter effect does not reflect the conventional color occipital selection negativity (Harter & Aine, 1984).

## Cue-Locked ERPs Effects

Effects of attentional control and dimension on cue-related ERPs. In all conditions and tasks, cues elicited positivity with a dorsal posterior maximum between 260 and 800 ms. However, the amplitude of this positivity was affected by demands on attentional control processes, being largest in the mixed task, intermediate in the transient task, and smallest in the repeated task (Posterior analysis: main effect of task, F[2,26] = 5.4-83.3,

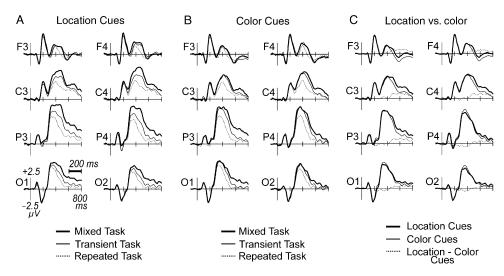


**Figure 2.** Effects of spatial (A) and nonspatial (B) attention on test stimulus processing displayed for the repeated, transient, and mixed tasks at electrodes P7 and P8 and Fz.

 $\varepsilon$  = .61–.94, p < .05, and interaction effect between task and site, F[4,52] = 3.0–41.6,  $\varepsilon$  = .40–.55, p < .05, between 260 and 800 ms; Central analysis: main effect of task between 260 and 800 ms, F[2,26] = 5.8–2.6,  $\varepsilon$  = .61–.90, p < .05; interaction effect between task and site between 260 and 760 ms post cue, F[4,52] = 2.8–30.3,  $\varepsilon$  = .43–.64, p < .05; Anterior analysis: main effect of task between 300 and 380 ms, F[2,26] = 3.6–17.0,  $\varepsilon$  = .77–.96, p < .05, and 420 and 520 ms, F[2,26] = 3.9–11.8,  $\varepsilon$  = .60–.76, p < .05). Tests on the normalized data showed that this posterior effect did not simply represent a difference in the strength of the effect between tasks, as the interaction effect between task and site remained significant after normalization. This indicates that the scalp topographies of the cue-evoked posterior positivity differed between the mixed, transient, and repeated tasks.

Two phases of ERP modulation could be distinguished. In the first phase of ERP modulation (i.e., between 260 and 520 ms post cue), the difference in posterior positivity between tasks was not affected by the dimension of the cued stimulus feature and had a midline posterior maximum (see Figures 3 and 4). This suggests that this difference may represent generic attentional control processes. In the second phase of ERP modulation, the difference in posterior positivity between tasks was more pronounced over left dorsal posterior scalp regions from 580 ms onward (interaction effect between task and hemisphere between 580 and 660 ms post cue, F[2,26] = 4.4-7.0,  $\varepsilon = .60-.79$ , p < .05, and 680 and 800 ms post cue, F[2,26] = 5.6-11.7,  $\varepsilon = .68-.96$ , p < .05), in particular when color was task relevant. Whereas the positivity elicited by location cues in the mixed and transient tasks versus the repeated task had a slightly left from center posterior maximum, the greater positivity evoked by color cues in the mixed and transient tasks versus the repeated task was clearly focused over left posterior electrode sites. This was confirmed in additional analyses restricted to electrodes P3 and P4, which revealed an interaction between the factors task, dimension, and hemisphere between 520 and 800 ms post cue, F(2,26) = 3.2-10.2,  $\varepsilon = .82-$ .99, p < .05. Thus, the dimension of the task-relevant information did not affect early attentional control operations, but did affect late attentional control operations as indicated by differences in late (i.e., from 580 ms onward), but not early (i.e., 260-520 ms), attentional control-related posterior positivity between color and location cues.

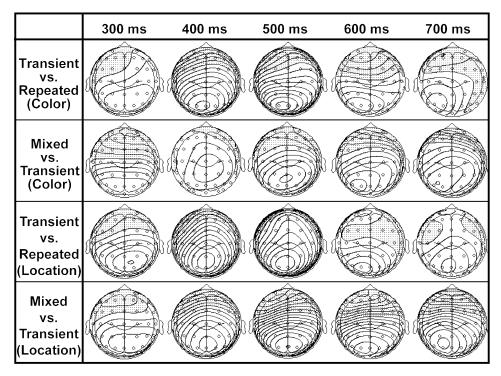
To investigate whether this difference in cue-related posterior positivity between tasks was related to greater demands on processes involved in switching attentional sets in the mixed and transient tasks compared to the repeated task, cue trials within the transient and mixed tasks were categorized as to whether they involved the same feature and dimension as on the preceding trial (repeat trial; e.g., blue—blue), the same dimension but a different feature as on the preceding trial (switch-within trial; e.g., blue—yellow), or a different feature and dimension as on the preceding trial (switch-across trial; e.g., blue—left). Repeated-measures



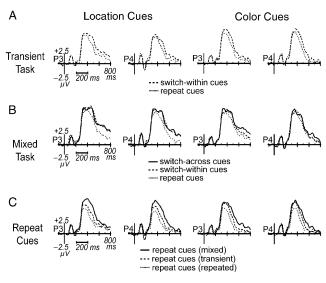
**Figure 3.** A,B: Grand average ERP waveforms to location (A) and color (B) cues in the repeated, transient, and mixed tasks at selected electrodes. C: Grand average ERP waveforms to location and color cues and their ERP difference waveform (location – color) at selected electrodes.

ANOVAs revealed that switch cues (i.e, switch-within and/or switch-across cues) elicited greater positivity over dorsal posterior scalp regions than repeat cues from 300 ms onward in both the transient, F(1,13) = 4.8-62.5, p < .05 (see Figure 5A) and mixed task, F(2,26) = 4.4-53.4,  $\varepsilon = .75-1.0$ , p < .05 (see Figure 5B). This within-tasks effect strongly resembled the posterior positivity observed when comparing cue-related responses across tasks (i.e., mixed vs. transient vs. repeated) both in terms of scalp topography and latency. Notably, these within-task differences in posterior positivity between switch and repeat cues were smaller than the across-task differences in posterior positivity.

These additional findings thus indicate that the posterior positivity reflects processes common to switch and repeat trials, which are called upon more strongly when a new stimulus feature is cued and are affected by the number of possible cues in a block. Importantly, the cue-related posterior positivity was larger on repeat trials in the mixed and transient tasks than in the repeated task between 260 and 680 ms, F(2,26) = 3.5-61.7,  $\varepsilon = .65-.82$ , p < .05, arguing against the possibility that the differences in posterior positivity observed across tasks were driven by a difference in the proportion of switch and repeat trials (see Figure 5C).



**Figure 4.** Grand average average-reference spline-interpolated isopotential maps for the different contrasts between cue conditions at several latencies post cue. The spacing between isopotentials is  $0.2 \mu V$ . White: areas of positive amplitude. Shaded: areas of negative amplitude.



**Figure 5.** A, B: Grand average cue-related ERP waveforms on repeat trials, switch-within trials, and switch-across trials in the transient task (A) and in the mixed task (B), separately for location (left column) and color (right column) cues. C: Grand average cue-related ERP waveforms on repeat trials elicited in the repeated, transient, and mixed tasks, separately for location (left column) and color (right column) cues.

The amplitude of the cue-related positivity was, in addition, affected by the dimension of the cued stimulus feature (i.e., color or location), independently of demands on attentional control processes. This indicates that the dimension of the task-relevant information not only affected processes related to attentional control, but also affected processes not involved in attentional control. As can be seen in Figure 3C, from 480 ms onward, location cues elicited greater positivity than color cues over fronto-central electrodes, bilaterally, and posterior electrodes, particularly those located over the left posterior scalp regions (Frontal analysis: main effect dimension between 480 and 540 ms, F[1,13] = 5.7-10.8, p < .05, and between 560 and 720 ms, F[1,13] = 4.8-7.5, p < .05; Central analysis: main effect of dimension between 680 and 720 ms, F[1,13] = 4.7-5.6, p < .05, and interaction effect between dimension and site between 480 and 800 ms, F(2,26) = 6.0-12.1,  $\varepsilon = .57-.81$ , p < .05; Posterior analysis: interaction between dimension and site between 580 and 660 ms, F[2,26] = 3.8-5.3,  $\varepsilon = .76-.90$ , p < .05, and interaction between dimension, hemisphere, and site between 700 and 760 ms, F[2,26] = 3.4-3.7,  $\varepsilon = .74-.85$ , p < .05).

Strategy effects. Next to examining the nature and temporal dynamics of attentional control, the present study investigated the effects of presenting spatial and nonspatial attention-directing conditions intermixed in a block versus in separate blocks. We predicted that if the intermixed presentation of color and location cues in the same block led subjects to a generalized task preparation strategy, differences in cue-related ERP between the color and location attention-directing conditions should be smaller in the mixed task compared to the transient task. Contrary to this prediction, we observed that location cues elicited greater positivity over dorsal posterior scalp locations than color cues in the mixed task between 460 and 520 ms, whereas both types of cues elicited similar amounts of positivity over these scalp locations in the transient task (see Table 2). Thus, the difference in posterior positivity between the color and location attention-directing

**Table 2.** Mean (Averaged across 460–520 ms) Voltage Differences (Plus Standard Error) for Transient versus Repeated Cues and Mixed versus Transient Cues Coding for Location or Color at Electrodes P3 en P4

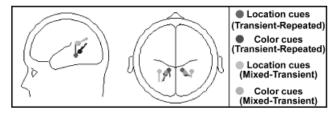
	Transient	Transient-repeated		Mixed-transient	
	P3	P4	P3	P4	
Location cues Color cues	2.7 (0.4) 2.7 (0.5)	2.4 (0.5) 2.6 (0.5)	2.5 (0.5) 1.6 (0.5)	2.6 (0.6) 1.0 (0.5)	

The difference in voltage elicited by mixed compared to transient cues was larger when location compared to color was task relevant.

conditions was actually more pronounced in the mixed rather than the transient task in this time interval. This effect was related to a greater increase in posterior positivity in the mixed relative to the transient task when location compared to color was task relevant, as expressed by a significant interaction between task and dimension between 480 and 520 ms post cue, F(2,26) = 3.5–3.5,  $\varepsilon = .95$ –.99, p < .05. Results from additional analyses confined to electrodes P3 and P4 showed that this effect began at 460 ms post cue and disappeared after 520 ms post cue, F(2,26) = 3.4–3.7,  $\varepsilon = .78$ –.97, p < .05. This finding suggests that the type of task performed (i.e., mixed or transient) may affect the way the brain controls attention to spatial position or color.

Source localization results. In the time window in which the main effect of task was most significant at posterior electrodes sites, the most pronounced peaks in global field power were observed for the contrasts transient versus repeated location cues (440 ms), transient versus repeated color cues (428 ms), mixed versus transient location cues (468 ms), and mixed versus transient color cues (464 ms). The neural generators underlying these effects were therefore estimated, first for the grand average difference waveform, and then for the individual subject difference waveforms, where the grand average solution parameters were used as a starting point (cf. Kenemans, Lijffijt, et al., 2002). Modeling these effects with one symmetric dipole pair localized all effects to the posterior compartment of the cortex with low residual variance (RV; see Figure 6; RV = 2.4% [transient vs. repeated location cues], 1.7% [transient vs. repeated color cues], 2.9% [mixed vs. transient location cues], and 4.9% [mixed vs. transient color cues]). The different dipole solutions were stable across different starting positions. Adding a second dipole pair to the model did not substantially change the location of the first dipole pair for any of the contrasts. Therefore, all effects were modeled with one symmetric dipole pair.

Statistical analysis revealed no differences in dipole locations between any of the modeled contrasts. However, when dipole orientations were compared, significant main effects of contrast



**Figure 6.** Grand average dipole source solutions for the four contrasts modeled at around 450 ms post cue.

(left dipole, F[3,11] = 5.6, p < .05; right dipole, F[3,11] = 4.9, p < .05) and interaction effects between contrast and dimension (left dipole, F[3,11] = 4.7, p < .05; right dipole, F[3,11] = 6.3, p < .01) were found. Univariate tests and visual inspection of the dipole solutions revealed that the dipoles obtained for the mixed versus transient contrasts were oriented to slightly more ventral posterior areas than those obtained for the transient versus repeated contrasts, especially when location was task relevant. This indicates that slightly different brain areas or more extended patches of cortex may have been activated depending on the type of task performed.

#### Discussion

The goals of the present study were (1) to examine dimension specificity in attentional control, and (2) to determine the effects of the intermixed versus blocked presentation of color and location cues on dimension-specific attentional control-related activity, using high-density ERP recordings, dipole source modeling, and cued attention tasks in which both demands on attentional control processes and the dimension of the behaviorally relevant information were varied. The results from the behavioral study confirmed our hypothesis that the mixed and transient tasks imposed a higher load on attentional control operations than the repeated task: The interval time between cue and test stimulus was longer before the reaction time function reached asymptote in the mixed relative to the transient relative to the repeated task (see Figure 1). Also, false alarm rates were higher for short cue-test stimulus intervals in the mixed and transient tasks compared to the repeated task.

# Attentional Control-Related Posterior Positivity: Early Phase

The most pronounced attentional control-related effect observed for both the location and color attention-directing conditions was a dorsal posterior positivity starting at 260 ms post cue (see Figures 3 and 4). Between 260 and 520 ms, this effect was maximal over midline dorsal posterior scalp regions and not sensitive to the dimension of the cued feature (i.e., color vs. location). This suggests the attentional control operations represented by this early difference in posterior positivity are generic, that is, they can code for both spatial and nonspatial tasks. One clear candidate process is the updating of the attentional set. On each trial, it was necessary to specify which feature and, thus, dimension should be selectively attended. Yet, in the mixed task, this taskrelevant information had to be updated on a trial-by-trial basis at both the feature and dimension levels; in the transient task, this only had to be done at the feature level, and in the repeated task, the task-relevant information could be tonically maintained at both levels. Thus, demands placed on processes involved in generating an attentional set increased from the repeated to the transient to the mixed task. This may in turn have affected the amplitude of the posterior positivity.

The posterior positivity elicited by attention-directing cues displayed characteristics of the widely studied P3, being maximal over midline parietal electrodes and displaying latency in the appropriate time range (Pritchard, 1981). Although the P3 has been argued to reflect a number of related processes (Kok, 2001), the weight of evidence supports an interpretation in terms of updating a cognitive model of the environment in working memory stores (Donchin & Coles, 1988). This advocates an interpretation of the observed differences in posterior positivity in the P3 latency win-

dow in terms of differences across tasks in the demands placed on processes involved in updating an attentional set.

This conclusion if further supported by results from additional analyses that showed that in the transient and mixed tasks, cues directing attention to a different stimulus feature as on the preceding trial (i.e., switch trial) and cues directing attention to the same stimulus feature as on the preceding trial (i.e., repeat trial) both elicited dorsal posterior positivity. However, this posterior positivity was larger when the cue indicated a new task (see Figure 5). This indicates, first of all, that the differences in cuerelated posterior postivity observed between tasks (i.e., collapsed across switch and repeat trials) were not simply due to the number of possible cues that were presented in a block. In that case, one would have expected no difference in cue-related posterior positivity between switch and repeat trials in the transient and mixed tasks. Second, these findings indicate that the cognitive processes reflected by the dorsal posterior positivity occurred on both repeat trials and switch trials, but worked harder when the cued feature changed, rather than remained the same with respect to the preceding trial. Critically, this implies that having to switch attention called more strongly on basic preparatory processes that occur whenever the current attentional set needs to be activated, not only when a switch is indicated. It is also important to note that the dorsal posterior positivity was larger on repeat trials in the mixed and transient tasks than on repeat trials in the repeated task, arguing against the possibility that the differences in posterior positivity observed across tasks were driven by a difference in the proportion of switch and repeat trials. It is likely that demands on processes involved in updating the attentional set were higher when the cued feature changed with respect to the preceding trial, and also when having multiple possibilities in mind, as in the mixed (four) versus the transient (two) versus the repeated (one) tasks. These results are consistent with current models of set switching, in which basic processes related to updating of rules for upcoming task demands are considered a crucial aspect of task preparation (Altmann, 2004; Mayr & Kliegl, 2003).

The fact that similar dipole source solutions were obtained at around 450 ms post cue, when differences in posterior positivity were largest between tasks, for effects of shifting attention within a dimension and of shifting attention between dimensions (see Figure 6), is in line with the idea that the same control processes were activated by all tasks, albeit more strongly in the more demanding tasks. The relative posterior location of these sources suggests a relatively strong contribution from posterior brain areas to these effects. This would be in line with findings from recent event-related fMRI studies that support a crucial role for the parietal cortex, rather than the frontal cortex, in top-down attentional control (Corbetta & Shulman, 2002).

The story may, however, be somewhat more complex, as although the location of the dipoles did not differ between the different contrasts, their orientations did. This indicated that the scalp distribution of the posterior positivity differed between tasks, as was also confirmed by analysis of the normalized cuerelated ERPs. These data therefore suggest that switching attentional sets may not just have increased activity in brain areas involved in repeated attentional control, but may also have activated additional brain areas. These brain areas may have been involved in similar control processes as those called upon in the repeated task, but may have been recruited extra, because of increased demands on these processes under shifting conditions. Alternatively, however, these areas may have been involved in

additional control processes, specific to the transient and/or mixed task, such as processes related to inhibition of the previously relevant stimulus feature.

Previous ERP studies also observed increased activation over posterior scalp regions in the P3 time window in conditions where attention was directed to location (Harter & Anllo-Vento, 1991; Mangun, 1994; Wright et al., 1995) compared to a reference condition in which attention did not have to be directed to a specific peripheral location. In our previous study (Slagter et al., 2005), differences in posterior positivity were found for both location and color cues relative to the no-feature cues, but these effects peaked slightly earlier (around 340 ms after cue presentation), were maximal over lateral parieto-occipital recording sites, and were localized to more lateral ventral posterior areas than in the present study. These effects were related to processes involved in linking the cue symbol to its associated stimulus feature. Differences between this and the current study in the specific comparison used to isolate attentional control processes might explain these differences in posterior positivity. In our previous study, no specific color or location was task relevant on reference cue trials, whereas in the reference task (i.e., the repeated task) used in the present study, subjects always had to direct attention to a specific color or location, albeit always to the same stimulus feature. As some directing of attention also occurred on repeat cue trials, this may explain why the posterior effect peaked somewhat later in time in the present study (i.e., after processes that link the cue symbol to its associated feature). In addition, in our earlier study, all types of cues (i.e., attentiondirecting and reference cues) were presented intermixed within the same run, whereas in the present study, tasks differed in the number of stimulus features that could be cued within a run. This might explain why the posterior effect had a different, more dorsal posterior scalp distribution in the present study (i.e., reflecting a greater contribution from areas involved in updating the attentional set). Importantly, together these results may suggest that attentional control is initiated by processes that link the attention-directing cue to its associated stimulus feature, which are followed in time by processes that use this information to update the attentional set.

# Late (580 ms) Left-Lateralized Attentional Control-Related Posterior Positivity

The initial increase in posterior positivity was followed by enhanced parietal slow wave positivity in the mixed versus the transient versus the repeated task from 580 ms onward (see Figures 3 and 4). This late sustained positivity strongly resembles the ERP slow-wave pattern observed in the retention periods of visual and nonvisual working memory tasks (Bosch, Mecklinger, & Friederici, 2001; Ruchkin, Grafman, Cameron, & Berndt, 2003). Ruchkin and colleagues have suggested that this slow-wave posterior positivity may index operations that support recoding from visual to phonological format and/or initiation of retention processes (Ruchkin, Johnson, Grafman, Canoune, & Ritter, 1992; Ruchkin et al., 1997).

It is interesting to note in this respect that results from the separately conducted behavioral experiment indicated that attention was fully directed within 600 ms in all tasks (see Figure 1). This estimate is similar to previous estimates of the time course of attentional orienting (Duncan, Ward, & Saphiro, 1994; Muller, Teder-Salejarvi, & Hillyard, 1998) and supports an interpretation of the late slow wave positivity in terms of processes that occur after information is specified as task relevant, such as

processes related to the persistence of information in working memory. These processes may have been more prominent in the transient and mixed tasks than in the repeated task because of interference from other stimulus features that were possibly task relevant in these tasks.

Notably, the attentional control-related activity was more pronounced over left dorsal posterior scalp regions when color compared to location was behaviorally relevant from 520 ms onward (see Figure 4). The left hemisphere specifically has been implicated in verbal working memory (e.g., Smith & Jonides, 1999) and this effect may accordingly reflect the use of verbal rather than more analog strategies related to the persistence of information in working memory, which may have been more prominent when color was task relevant. This left hemisphere focus is consistent with results from fMRI studies showing activation of a left-lateralized network of frontal and parietal regions in the period between attention-directing cue and test stimulus (Giesbrecht, Woldorff, Song, & Mangun, 2003; Hopfinger, Buenocore, & Mangun, 2000; Shulman, d'Avossa, Tansy, & Corbetta, 2002; Weissman, Mangun, & Woldorff, 2002).

It should be noted that in all tasks (i.e., the repeated, transient, and mixed tasks), one item had to be held on-line until test stimulus presentation. It thus seems not likely that the late slow-wave positivity reflects processes related to pure storage of the task-relevant information. Interestingly, as in our previous study (Slagter et al., 2005), a difference in frontal activity was observed between location and color cues late in the cue—target interval (see Figure 3C). In the present study, however, the amplitude of this effect was not affected by demands on attentional control processes, indicating that this late anterior effect should be attributed to differences in dimension-specific functions that are not related to attentional control, such as storage of the task-relevant information.

# Common Attentional Control Mechanisms or Generalized Task-Preparation Strategies?

Next to examining the nature and temporal dynamics of attentional control, the present study also investigated whether subjects may adopt more general task-preparation strategies when color and location attention-directing cues are presented intermixed in a block compared to in separate blocks. Between 460 and 520 ms post cue, location cues elicited greater positivity over midline posterior scalp locations than color cues in the mixed task, whereas both types of cues elicited similar amounts of positivity in the transient task, as was confirmed by a significant task by dimension interaction (see Figure 3 and Table 2). Hence, contrary to expectation, ERP differences between color and location cues in this time window were actually greater when the two types of cues were presented intermixed within the same block. It should also be noted that interaction effects between task and dimension were not observed at any other time point after cue presentation. All in all, the present data thus indicate that, overall, the intermixed presentation of color and location cues did not lead subjects to adopt generalized task-preparation strategies. The observed overlap in ERPs between color and location cues in the current and our previous studies (Slagter et al., 2005) can therefore genuinely be ascribed to mechanisms that are common to spatial and nonspatial top-down attentional control.

## Effect of Attention on Test Stimulus Processing

As expected, spatial attention modulated the early P1 and N1 components elicited by test stimuli, whereas a frontal selection

positivity was observed in relation to nonspatial attention. These findings confirm that subjects indeed used the cue to direct their attention. Interestingly, the type of task performed affected effects of spatial attention on test stimulus processing in two ways (see Figure 2A). First of all, between 68 and 92 ms post test stimulus, P1 amplitude was modulated more strongly in the mixed task than in the transient and repeated tasks. Secondly, the amplitude of the N1 component elicited by test stimuli was modulated more strongly by spatial attention in the transient task than in the mixed and repeated tasks. These results are indicative of interactions between attentional control processes and modulatory processes that may depend on the number of possibly relevant stimulus features and/or dimensions in a task block. As was shown in the behavioral experiment, the different tasks (i.e., repeated, transient, mixed) differed in the time needed to fully direct attention. It is therefore possible that at the time of test stimulus presentation, the tasks differed in the relative strength of engagement of attention to the task-relevant location and/or suppression of attention to the task-irrelevant location. This may have resulted in the observed differences in modulatory effects of spatial attention on test stimulus processing between tasks. Indeed, it has previously been shown that different attentional selection mechanisms may be operative under transient and sustained spatial attention conditions (Eimer, 1996). It is also possible that differences in the number of possibly relevant stimulus dimensions in a block (i.e., one in the repeated and transient tasks [either color or location] and two in the mixed task [color and location]) affected the feature selection process. In the mixed

task, for example, interference from the other possibly relevant stimulus dimension (i.e., color) may have affected attentional orienting to the cued location. Future studies need to replicate these findings and determine in what way the number of possibly relevant test stimulus features and/or dimension in a task-block can affect the location selection process.

#### Summary and Conclusions

The guiding question to our study was to what extent the processes that direct the focus of attention are dependent on the nature of the feature that is selected. To this aim, both demands on attentional control-related processes and the dimension of the task-relevant feature were varied. This approach proved very useful in isolating both attentional control-related processes that generalize over the dimension of the task-relevant information and attentional-control-related processes that are specific to one dimension relative to the other. Generic processes, likely reflecting the generation of an attentional set, were followed in time by dimension-specific processes, possibly related to the persistence of the task-relevant information in working memory. In addition, the current approach permitted investigation of the effects of the intermixed rather than blocked presentation of color and location attention-directing cues on dimension specificity in attentional control. Effects of dimension on attentional control-related processes were generally not smaller in the mixed task, suggesting that the intermixed presentation of color and location cues did not lead subjects to use generalized taskpreparation strategies.

#### REFERENCES

- Altmann, E. M. (2004). Advance preparation in task switching. *Psychological Science*, 15, 616–622.
- Anllo-Vento, L., Luck, S. J., & Hillyard, S. A. (1998). Spatio-temporal dynamics of attention to color: Evidence from human electrophysiology. *Human Brain Mapping*, 6, 216–238.
- Berg, P., & Scherg, M. (1994). BESA version 2.0 Handbook. Munich: Megis.
- Bosch, V., Mecklinger, A., & Friederici, A. D. (2001). Slow cortical potentials during retention of object, spatial, and verbal information. *Cognitive Brain Research*, 10, 219–237.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Neuroscience Reviews*, 3, 201–215.
- Donchin, E., & Coles, M. G. H. (1988). Is the P300 component a manifestation of context updating? *Behavioral and Brain Science*, 11, 357–374
- Driver, J., & Frith, C. (2000). Shifting baselines in attentional control. Nature Neuroscience Reviews, 1, 147–148.
- Duncan, J., Ward, R., & Saphiro, K. (1994). Direct measurement of attentional dwell time in human vision. *Nature*, 369, 313–315.
- Eason, R. G. (1981). Visual evoked potential correlates of early neural filtering during selective attention. *Bulletin of the Psychonomic Society*, 18, 203–206.
- Eimer, M. (1993). Spatial cueing, sensory gating and selective response preparation: An ERP study on visuo-spatial orienting. *Electroencephalography and Clinical Neurophysiology*, 88, 408–420.
- Eimer, M. (1996). ERP modulations indicate the selective processing of visual stimuli as a result of transient and sustained spatial attention. *Psychophysiology*, 33, 13–21.
- Eimer, M., Van Velzen, J., & Driver, J. (2002). Crossmodal interactions between audition, touch and vision in endogenous spatial attention: ERP evidence on preparatory states and sensory modulations. *Journal of Cognitive Neuroscience*, 19, 254–271.
- 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.

- Harter, M. R., & Aine, C. (1984). Brain mechanisms of visual selective attention. In P. Parasuraman & D. R. Davis (Eds.), *Varieties of attention* (pp. 293–321). New York: Academic Press.
- Harter, M. R., & Anllo-Vento, L. (1991). Visual-spatial attention: Preparation and selection in children and adults. In C. H. M. Brunia & M. N. Verbaten (Eds.), Event-related brain research (pp. 183–194). Amsterdam: Elsevier.
- Harter, M. R., Miller, S. L., Price, N. J., LaLonde, M. E., & Keyes, A. L. (1989). Neural processes involved in directing attention. *Journal of Cognitive Neuroscience*, 1, 223–237.
- Harter, M. R., & Previc, F. H. (1978). Size-specific information channels and selective attention: Visual evoked potential and behavioral measures. *Electroencephalography and Clinical Neurophysiology*, 45, 628–640.
- Hillyard, S. A., & Munte, T. F. (1984). Selective attention to color and location: An analysis with event-related brain potentials. *Perception and Psychophysics*, 36, 185–198.
- Hillyard, S. A., Vogel, E. K., & Luck, S. J. (1998). Sensory gain control (amplification) as a mechanism of selective attention: Electrophysiological and neuroimaging evidence. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 353, 1257–1270.
- Hopf, J. M., & Mangun, G. R. (2000). Shifting visual attention in space: An electrophysiological analysis using high spatial resolution mapping. *Clinical Neurophysiology*, 111, 1241–1257.
- Hopfinger, J. B., Buonocore, M. H., & Mangun, G. R. (2000). The neural mechanisms of top-down attentional control. *Nature Neuro-science*, 3, 284–291.
- Kenemans, J. L., Grent-'t-Jong, T., Giesbrecht, B., Weissman, D. H., Woldorff, M. G., & Mangun, G. R. (2002). A sequence of brainactivity patterns in the control of visual attention. *Psychophysiology*, 39, S77.
- Kenemans, J. L., Lijffijt, M., Camfferman, G., & Verbaten, M. N. (2002). Split-second sequential selective activation in human secondary visual cortex. *Journal of Cognitive Neuroscience*, 14, 48–61.

- Kok, A. (2001). On the utility of the P3 amplitude as a measure of processing capacity. *Psychophysiology*, 38, 557–577.
- Lange, J. J., Wijers, A. A., Mulder, L. J., & Mulder, G. (1998). Color and location selection in ERPs: Differences, similarities and "neural specificity. *Biological Psychology*, 48, 153–182.
- Lehman, D., & Skrandies, W. (1984). Spatial analysis of evoked potentials in man—A review. *Progress in Neurobiology*, 23, 227–250.
- Mangun, G. R. (1994). Orienting attenton in the visual fields: An electrophysiological analysis. In H. J. Heinze, T. F. Munte, & G. R. Mangun (Eds.), *Cognitive electrophysiology* (pp. 81–101). Boston, MA: Birkhauser.
- Mangun, G. R., Hansen, J. C., & Hillyard, S. A. (1986). The spatial orienting of attention: Sensory facilitation or response bias? In R. Johnson Jr., J. W. Rohrbaugh, & R. Parasuraman (Eds.), Current trends in event-related-potential research (pp. 118–124). New York: Elsevier.
- Mayr, U., & Kliegl, R. (2003). Differential effects of cue changes and task changes on task-set selection costs. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 29, 362–372.
- McCarthy, G., & Wood, C. C. (1985). Scalp distributions of eventrelated potentials: An ambiguity associated with analysis of variance models. *Electroencephalography and Clinical Neurophysiology*, 62, 203–208.
- Muller, M. M., Teder-Salejarvi, W., & Hillyard, S. A. (1998). The time course of cortical facilitation during cued shifts of spatial attention. *Nature*, 1, 631–634.
- Nobre, A. C. (2001). The attentive homunculus: Now you see it, now you don't. *Neuroscience and Biobehavioral Reviews*, 25, 477–496.
- Nobre, A. C., Sebestyan, G. N., & Miniussi, C. (2000). The dynamics of shifting visuospatial attention revealed by event-related potentials. *Neuropsychologia*, 38, 964–974.
- Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, 32, 3–25.
- Posner, M. I., Inhoff, A. W., Friedrich, F. J., & Cohen, A. (1987). Isolating attentional systems: A cognitive-anatomical analysis. *Psychobiology*, 15, 107–121.
- Pritchard, W. S. (1981). Psychophysiology of P300. Psychological Bulletin, 89, 506–540.
- Ruchkin, D. S., Berndt, R. S., Johnson, R. Jr., Ritter, W., Grafman, J., & Canoune, H. (1997). Modality-specific processing streams in working memory: Evidence from spatio-temporal patterns of brain activity. Cognitive Brain Research, 6, 95–113.
- Ruchkin, D. S., Grafman, J., Cameron, K., & Berndt, R. S. (2003).Working memory retention systems: A state of activated long-term memory. *Behavioral and Brain Sciences*, 26, 709–777.

- Ruchkin, D. S., Johnson, R. Jr., Grafman, J., Canoune, H., & Ritter, W. (1992). Distinctions and similarities among working memory processes: An event-related potential study. *Cognitive Brain Research*, 1, 53–66.
- Shulman, G. L., d'Avossa, G., Tansy, A. P., & Corbetta, M. (2002). Two attentional processes in the parietal lobe. *Cerebral Cortex*, 12, 1124–1131.
- Slagter, H. A., Kok, A., Mol, N., & Kenemans, J. L. (2005). Spatio-temporal dynamics of top-down control: Directing attention to location and/or color as revealed by ERPs and source modeling. Cognitive Brain Research, 22, 333–348.
- Smith, E. E., & Jonides, J. (1999). Storage and executive processes in the frontal lobes. *Science*, 283, 1657–1661.
- Strayer, D. L., & Kramer, A. F. (1994). Strategies and automaticity: I. Basic findings and conceptual framework. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 20, 318–341.
- Treisman, A. (1993). The perception of features and objects. In A. Baddeley & L. Weiskranz (Eds.), Attention: Selection, awareness and control: A tribute to Donald Broadbent (pp. 5–35). Oxford, UK: Clarendon Press.
- van der Heijden, A. C. H. (1993). The role of position in object selection in vision. *Psychological Research*, *56*, 44–58.
- 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.
- Wright, M. J., Geffen, G. M., & Geffen, L. B. (1995). Event-related potentials during covert orientation of visual-attention: Effects of cue validity and directionality. *Biological Psychology*, 41, 183–202.
- Yamaguchi, S., Tsuchiya, H., & Kobayashi, S. (1994). Electroencephalographic activity associated with shifts of visuospatial attention. *Brain*, 117, 553–562.
- Yamaguchi, S., Tsuchiya, H., & Kobayashi, S. (1995). Electrophysiological correlates of age effects on visuospatial attention shift. Cognitive Brain Research, 3, 41–49.
- Yamaguchi, S., Yamagata, S., & Kobayashi, S. (2000). Cerebral asymmetry of the "top-down" allocation of attention to global and local features. *Journal of Neuroscience*, 20, RC72.
- Yantis, S., & Serences, J. T. (2003). Cortical mechanisms of space-based and object-based attentional control. *Current Opinion in Neurobiol*ogy, 13, 187–193.

(RECEIVED September 8, 2004; ACCEPTED March 23, 2005)