



Event-related potential correlates of transient attention shifts to color and location

Martin Eimer

Institut für Psychologie, Universität München, Leopoldstr. 13, 80802, München, Germany

Received 15 August 1994; accepted 28 June 1995

Abstract

Effects of selectively attending to specific combinations of stimulus location and color were measured by means of event-related brain potentials in a trial-by-trial cueing paradigm. A symbolic precue was presented at the beginning of each trial indicating the response-relevant position and color of an upcoming imperative stimulus. Responses were required to infrequent target stimuli of the relevant color appearing at the cued location. Stimuli at attended locations elicited enhanced posterior N1 components as well as enhanced negativities at midline electrodes. No P1 enhancement was found for stimuli at the attended location. Attended color stimuli elicited a broad negativity starting about 220 ms that tended to be larger for stimuli presented at attended locations. These results show that transient attention shifts to non-spatial features like color are reflected by event-related potential (ERP) effects comparable to the effects measured under sustained attention conditions. Transient spatial attention yields earlier and larger ERP effects than transient attention to color and may modulate the ERP effects of non-spatial attention.

Keywords: Attention; Colour; Spatial; Event-related Potential; NI; PI

1. Introduction

The mechanisms underlying selective visual attention have been studied by numerous experiments that used electrophysiological measurements. The time course and functional properties of attentional selection processes can be investigated by comparing event-related potential (ERP) waveforms elicited by attended and unattended stimuli. One general finding has been that selection based on spatial position yields earlier and qualitatively different ERP effects than selection based on other stimulus

* Corresponding author. E-mail: eimer@mip.paed.uni-muenchen.de.

attributes. Stimuli at attended locations elicit enhanced posterior P1 and N1 components when compared to stimuli at unattended locations (Eason, 1981; Mangun, Hansen & Hillyard, 1986; Mangun & Hillyard, 1987; Neville & Lawson, 1987; Rugg, Milner, Lines & Phalp, 1987). These effects start as early as 80–90 ms following stimulus onset. On the basis of these results, Mangun & Hillyard (1990) have proposed that spatial attention may consist of ‘sensory gating’ processes that modulate sensory processing in afferent visual pathways. In contrast, attending to non-spatial attributes like color, orientation, contour, or spatial frequency results in an enhanced negativity elicited by attended stimuli that starts beyond 150 ms and may extend up to 300 ms post-stimulus (Harter & Previc, 1978; Harter & Guido, 1980; Harter, Aine & Schroeder, 1982; Previc & Harter, 1982; Aine & Harter, 1984; Wijers, Mulder, Okita, Mulder & Scheffers, 1989; Wijers, Mulder, Okita & Mulder, 1989; Wijers, Lammain, Slopsema, Mulder & Mulder, 1989; Kenemans, Kok & Smulders, 1993). The fact that attending to various non-spatial attributes results in qualitatively similar ERP modulations is in line with the general assumption that different non-spatial stimulus features are processed within a common visual sub-system, the so-called ‘ventral pathway’ (Ungerleider & Mishkin, 1982).

Not only do ERP effects of non-spatial attention occur later than ERP modulations due to spatial attention, they also appear to be hierarchically dependent on the prior selection of the relevant spatial location. This was demonstrated in a study by Hillyard & Münte (1984) where subjects had to attend to a conjunction of stimulus features (location and color) in order to detect infrequent target stimuli having both the attended color and location. Hillyard & Münte (1984) compared the ERP waveforms elicited by non-targets with the relevant color, the relevant location, both relevant properties, or neither of the two relevant features. Stimuli appearing at the attended location elicited enhanced P1, N1 and N2 components as compared to the stimuli at unattended locations. These effects of spatial attention were unaffected by stimulus color. Relevant-color stimuli elicited a broad negativity starting about 150 ms and an enhanced positivity in the P2 time range at frontal electrodes. These ERP effects of color selection were found to be larger for stimuli at the attended location than for stimuli at unattended locations. On the basis of these results, Hillyard & Münte (1984) argued that the selective processing of color may be contingent upon the selection of stimuli on the basis of their location. Stimuli at irrelevant positions were not processed as deeply with respect to their non-spatial attributes as were stimuli at attended locations¹.

All ERP studies on selective attention reported so far employed a sustained attention paradigm where subjects were instructed to attend to a specific stimulus feature, or a combination of features, for an entire experimental block and to detect infrequent target stimuli containing these relevant features. This procedure is rather dif-

¹ No ERP evidence for the priority of spatial attention was obtained in another condition of the Hillyard & Münte (1984) experiment where both possible stimulus locations were in close proximity. In this ‘location-hard condition’, ERP effects of color selection preceded the effects of spatial selectivity. This indicates that the timing of the ERP effects of spatial and non-spatial attention may depend on the discriminability of the stimulus attributes relevant for attentional selection.

ferent from cueing paradigms of visual-spatial attention. In such experiments, the relevant stimulus location is indicated by a centrally presented symbolic cue at the beginning of each trial, and subjects have to respond both to correctly cued stimuli (valid trials) and to less frequent stimuli occurring at uncued locations (invalid trials). Under these conditions, RTs are faster in valid than in invalid trials (Posner, Nissen & Ogden, 1978). When attention is focused on a single location for an entire experimental block, however, these RT effects become considerably smaller (Posner, Snyder & Davidson, 1980). On the basis of this finding, Posner (1980) has argued that visual-spatial attention should not be regarded as a passive filter, but rather as an active process that is more effective in transient attention situations, in which the attentional focus has to be constantly shifted between different locations, than under sustained attention conditions.

Given these considerations, it is possible that different selective attention mechanisms are operative under transient and sustained attention conditions. If this was the case, ERP modulations different from those observed in sustained attention experiments are to be expected for transient attention. The results of a recent study by Friedman-Hill & Mangun (1993) support this assumption. These authors measured ERPs elicited by precues (colored arrows) that preceded the imperative stimulus and indicated either the to-be-attended location or the to-be-attended color. They found significant differences between the ERPs elicited in the cue-target interval by location cues and by color cues. However, this study did not directly address the question how transient selective attention affects the processing of imperative stimuli. With respect to this issue, a number of specific questions have to be answered: can we find differential attention effects on ERP waveforms elicited by imperative stimuli for sustained and for transient spatial attention conditions? Are there differential ERP effects for transient and for sustained non-spatial attention? And finally, can we find electrophysiological evidence for a hierarchical dependence of non-spatial attention upon the selection of location in a transient attention situation?

A number of recent ERP studies have tried to answer the first question by investigating ERP effects of spatial attention in trial-by-trial cueing paradigms. Mangun & Hillyard (1991), for instance, found enhanced P1 and N1 components for valid trials as compared with invalid trials. Because these effects were similar to the attentional enhancements of sensory-evoked components found with the sustained attention paradigm, they argued that functionally similar 'sensory gating' mechanisms may be activated under both conditions. However, recent studies by Eimer (1993, 1994b), in which the direction of spatial attention was also cued on a trial-by-trial basis, showed that the presence of these effects depends upon specific experimental circumstances. When discrimination requirements were high or overt responses were required in valid trials only, the P1 and N1 components were enhanced in valid trials compared to invalid trials. When responses could be selected on the basis of easily discriminable stimulus attributes or had to be executed in valid and in invalid trials, no systematic effects of spatial attention on P1 amplitude could be observed. In contrast, all experimental conditions resulted in an enhanced negativity for valid trials compared to invalid trials that started about 150 ms with an initial

parietal maximum (Nd1), and was followed by a second, more broadly distributed peak between 220 and 280 ms (Nd2). Similar effects were obtained in experiments in which the to-be-attended location was indicated by a peripheral cue (Eimer, 1994a) and in which auditory stimuli were used instead of visual stimuli (Schröger, 1993, 1994; Schröger & Eimer, 1993). Because these latter effects differed from the ERP patterns obtained in most studies employing the sustained attention paradigm, one may assume that the mechanisms underlying transient and sustained spatial attention are not the same.

Only scarce empirical evidence has been collected with respect to ERP modulations related to transient non-spatial attention. In a study by Aine & Harter (1986), subjects were required to respond to a colored patch when it matched the color of a previously presented patch. The ERPs elicited by relevant color patches were compared to the ERPs elicited by irrelevant color stimuli. Relevant color stimuli elicited an enhanced negativity at posterior leads (between 229 and 318 ms) followed by a frontal positivity. Though delayed, these effects were similar to those obtained in experiments in which the sustained attention paradigm was used, suggesting that similar mechanisms of color selection may be operative in sustained and transient attentional situations. However, the results from Aine & Harter (1986) were obtained by directly comparing trials where overt responses were elicited with trials where no overt response was given, thereby possibly confounding attentional and motor effects on the ERP waveforms. Moreover, all stimuli were presented at identical positions, which may have led to sensory refractoriness effects in the case of same-color targets. Thus, the results from Aine & Harter (1986) need to be validated by additional ERP studies of transient non-spatial attention. No electrophysiological evidence has yet been collected with respect to the interrelation of spatial and non-spatial transient attention.

The present experiment was conducted to further investigate transient visual selective attention to spatial and non-spatial stimulus features. Attention was simultaneously directed to color and location on a trial-by-trial basis. Subjects had to attend to a specific combination of color and location that was indicated by a precue in order to detect infrequent targets with the relevant properties. The procedure used here closely parallels the experimental paradigm used by Hillyard & Münte (1984), except that attention to color and location was cued anew at the beginning of each trial instead of being constant for a complete experimental block. Because of this similarity, the results of the present study may be compared to the results obtained by Hillyard & Münte (1984) in order to study the differences of selective attention to color and location under transient and sustained attention conditions.

Three specific questions were addressed by the present study. Are there ERP effects of transient visual-spatial attention in a situation where a precue contains both spatial and non-spatial information, and are these effects similar to the effects found in experiments that used a simple trial-by-trial cueing paradigm? Are there systematic ERP effects of attending to color when the relevant color changes from trial to trial? Are these ERP effects of transient non-spatial attention modulated by spatial attention, that is, are the effects of attending to stimulus color attenuated or even absent for stimuli at unattended locations?

2. Methods

2.1. Subjects

Eleven paid volunteers participated in the experiment. Three subjects had to be excluded because of poor eye fixation control in the cue-target interval (see below), so that eight subjects (three female), aged 23–35 years (mean age: 29 years) remained in the sample. All subjects were right-handed and had normal or corrected-to-normal vision.

2.2. Stimuli and apparatus

Subjects were seated in a dimly lit, electrically shielded and sound-attenuated cabin, with response buttons under their left and right hands. A computer screen was placed 100 cm in front of the subject and carefully positioned so that the stimuli appeared on the subject's horizontal meridian. Each trial began with a 200 ms presentation of a central arrow cue that subtended a visual angle of $1.5^\circ \times 0.6^\circ$. The arrow was either red or blue and pointed randomly to the left or to the right visual field. Seven hundred ms after the offset of the arrow, an imperative stimulus was presented in the left or right visual hemifield at a horizontal distance of 6° from the screen center, subtending an angle of approximately $1^\circ \times 1^\circ$. This stimulus was either a square (non-target) or a circle (target) that could be either red or blue. The intertrial interval between target offset and onset of the next arrow was 2 s.

2.3. Procedure

Twelve experimental blocks were run. Each block consisted of 60 trials and had a duration of approximately 3 min. On 48 trials per block, a square was presented as imperative stimulus (non-target trials), while on the remaining 12 trials, a circle was presented (target trials). Subjects were instructed to press a response button with their right hand whenever they detected a circle that matched the color of the precue and was presented at the indicated side. Target and non-target trials were delivered in random sequence. Only ERP waveforms obtained for non-target trials were analyzed. These trials were classified with respect to whether the attributes (color and location) of the non-target stimuli were correctly indicated by the precue. Trials where both stimulus location and stimulus color were correctly indicated by the precue were termed L+C+. This was the case when a red or blue square was preceded by a red or blue arrow that pointed in the direction of the upcoming square. On L+C- trials, the square position was correctly indicated by the cue, but the square was of the uncued color. On L-C+ trials, the colors of the arrow cue and the square matched, but the square was presented at the side opposite to the arrow's direction. On L-C- trials, neither the square location nor its color matched the attributes of the precue. Each of these four trial types appeared 12 times per block, and all combinations of non-target color and location were equiprobable.

The 12 remaining trials where the target stimulus (the circle) was presented were chosen randomly from a larger pool where all target color and location combinations were equiprobable. As a result of the random selection of the target trials, the absolute number of trials requiring an overt response (i.e., trials where a target stim-

ulus was presented that had both properties indicated by the precue) varied across blocks. The minimum number of Go trials per block was two, the maximum number was five.

Subjects were instructed to respond as quickly and accurately as possible while maintaining fixation throughout the trial. To make subjects familiar with these specific task requirements, two or three training blocks were run at the beginning of the experiment.

2.4. Recording and data analysis

The EEG was recorded with Ag-AgCl electrodes from Fz, Cz and Pz (according to the 10–20 system), from C₃' and C₄' (1 cm in front of C₃ and C₄), from PL and PR (located halfway between Pz and each ear canal), and from OL and OR (located halfway between O₁ and T₅, and O₂ and T₆, respectively). All electrodes were referenced to the right earlobe. The horizontal EOG was recorded bipolarly from electrodes at the outer canthi of both eyes, and the vertical EOG was recorded bipolarly from electrodes above and below the right eye. Electrode impedance was kept below 5 k Ω . The amplifier bandpass was 0.10–40 Hz. EEG and EOG were sampled with a digitization rate of 200 Hz, and stored on disk. Reaction times were recorded for each trial.

EEG and EOG were sampled off-line into epochs of 1800 ms, starting 100 ms prior to the onset of the precue, and ending 800 ms after the onset of the imperative stimulus. Trials with eyeblinks, horizontal eye movements, response errors, or overt responses in non-target trials were excluded from analysis. About one-third of the overall number of trials had to be excluded. After artifact removal, the computer-averaged horizontal EOG for each subject was scored for systematic deviations of eye position in the cue-target interval following left-pointing and right-pointing arrows. If the maximal residual EOG deviation exceeded $\pm 2 \mu\text{V}$, the subject was disqualified. EEG epochs obtained in non-target trials were averaged separately for all combinations of conditions (spatial attention: L+/L-; color attention: C+/C-; square color: red/blue; square location: left/right), resulting in 16 average waveforms for each subject and electrode site. All ERP amplitude measures were taken relative to the mean voltage of the 100 ms interval preceding the onset of the square stimulus.

Effects of experimental variables on the ERP evoked by the imperative stimulus were determined separately for the three lateral electrode pairs (C₃'/C₄', PL/PR and OL/OR) as well as for midline recording sites (Fz, Cz and Pz). Separate repeated measures analyses of variance were performed on ERP mean amplitude measures within different time windows (see Table 1) for the following variables: spatial attention, color attention, square color, and square location. For the lateral electrode pairs, electrode side (left vs. right) was included as an additional factor.

3. Results

Behavioral performance. Mean reaction time to relevant target stimuli was 471 ms. Subjects missed relevant target stimuli on 4.5% of all Go trials. The overall rate of False Alarms was 0.15%, with a False Alarm rate of 0.6% for irrelevant target stimuli and 0.07% for non-target stimuli.

Table 1

Measurement windows for different components and electrodes. Mean amplitude measures were taken for all components and measurement windows

Component	Electrodes	Measurement window (ms)
P1	OL/OR	95–145
N1	PL/PR, OL/OR	150–210
Nd1	Fz, Cz, Pz, C3'/C4'	140–190
Nd2	Fz, Cz, Pz, C3'/C4', PL/PR, OL/OR	220–300
P3	Fz, Cz, Pz	350–500

ERP waveforms. Fig. 1 shows the ERP waveforms elicited by non-target stimuli in L+C+, L+C-, L-C+, and L-C- trials at lateral occipital electrodes, and Fig. 2 shows the ERPs elicited under these conditions at all other recording sites. As illustrated in the figures, the ERPs were most prominently characterized by a broad positivity that overlapped with all components and was largest at lateral central (C3', C4') and at midline electrodes. This positive shift was generally more pronounced for L- trials than for L+ trials.

ERP effects of spatial attention. The ERP modulations related to spatial attention were obtained by comparing the ERP waveforms elicited by stimuli at cued locations (regardless of their color) with the ERPs to stimuli presented at the non-cued locations (regardless of their color). The resulting (L+)-(L-) difference waveforms are displayed in Fig. 3 (solid line). No effect of spatial attention was present for the P1 component at lateral occipital electrodes. In contrast, the posterior N1 component was strongly influenced by spatial attention (see also Fig. 1). An enhanced N1 for L+ trials was found both at lateral occipital and at lateral parietal electrodes ($F(1,7) = 10.17, p < 0.015$, and $F(1,7) = 24.29, p < 0.002$; for occipital and parietal electrode pairs, respectively).

Spatial attention also had a highly significant effect on mean amplitudes in the Nd1 interval (140–190 ms). Enhanced negativities for L+ compared to L- trials were present at all midline electrodes as well as at lateral central electrodes (all $F_s > 12$; all p -values < 0.01). In the Nd2 range (220–300 ms), stimuli at attended locations also elicited enhanced negativities when compared to stimuli at unattended locations. As shown in Table 2, this effect was highly significant at all recording sites. In addition, stimuli at attended locations elicited an enhanced positivity in the P3 time range that was significant at Cz ($F(1,7) = 5.74, p < 0.048$) and Pz ($F(1,7) = 6.24, p < 0.041$).

No significant differences were found when the ERP effects of transient visual-spatial attention obtained in the N1, Nd1 and Nd2 time windows for relevant-(C+) and irrelevant-color stimuli (C-) were compared. However, there were interactions between color attention and spatial attention in the P3 time interval, indicating the existence of a differential effect of spatial attention for relevant and irrelevant color stimuli. These interactions were significant at Pz ($F(1,7) = 7.21, p < 0.031$) and ap-

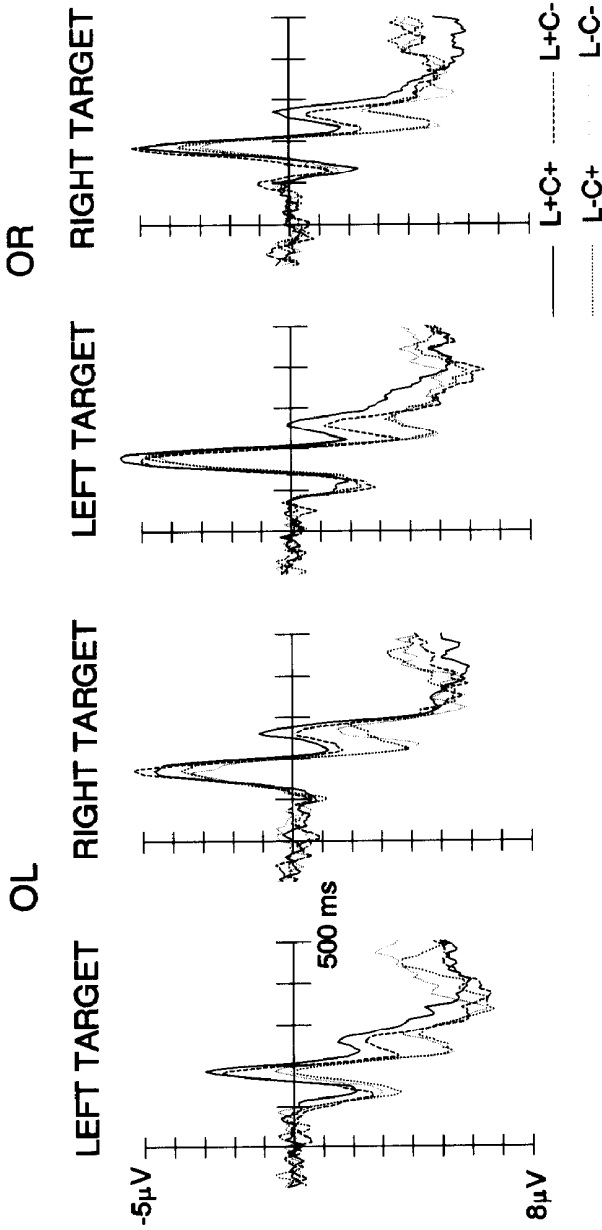


Fig. 1. Grand-average ERPs at lateral occipital electrodes for L+C+, L+C-, L-C+ and L-C- trials. Left side: ERP waveforms recorded from OL. Right side: ERP waveforms recorded from OR. Waveforms are displayed separately for targets presented in the left and in the right visual field.

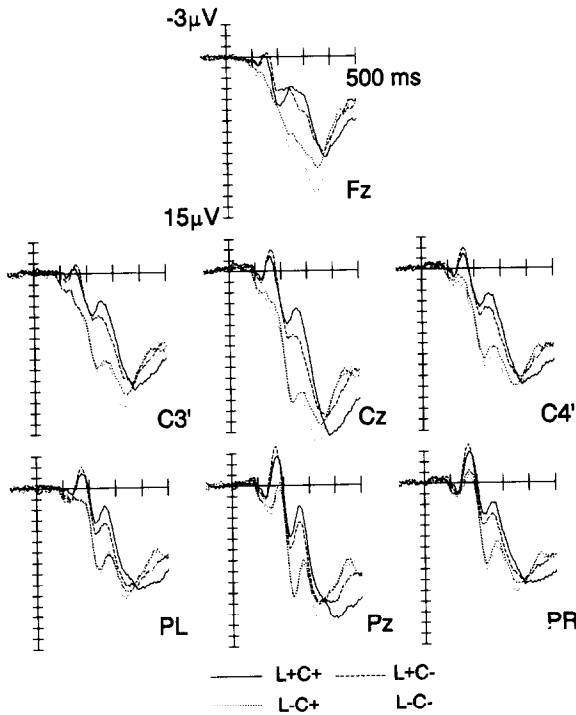


Fig. 2. Grand-average ERPs at Fz, Cz, Pz, C3', C4', PL and PR for L+C+, L+C-, L-C+ and L-C- trials.

proached significance at Fz and Cz ($F(1,7) = 4.94$, $p < 0.062$; $F(1,7) = 5.03$, $p < 0.060$, respectively), and were presumably due to the fact that the late positivity elicited by L+ trials was larger for attended color stimuli than for unattended color stimuli (see Fig. 2).

ERP effects of color attention. ERP effects of color attention were obtained by comparing the waveforms elicited by C+ stimuli (collapsed over L+C+ and L-C+) to the ERPs elicited by C-stimuli (L+C- and L-C-). As can be seen from the difference in waveforms in Fig. 3, the effects of attending to a specific stimulus color (dashed lines) were of much smaller magnitude than the ERP effects of spatial attention (solid lines). Moreover, they started considerably later than the spatial attention effects, that is, beyond 200 ms post-stimulus. This latter observation was confirmed by the finding that color attention failed to influence both P1 amplitude at occipital electrodes as well as N1 amplitude at lateral parietal and occipital sites. Likewise, no effect of color attention was present at midline and lateral central electrodes in the Nd1 interval.

In contrast to its absence during the first 200 ms following stimulus onset, effects of attention to stimulus color were clearly present in the Nd2 interval, with an enhanced negativity elicited by C+ stimuli. This effect was significant at lateral cen-

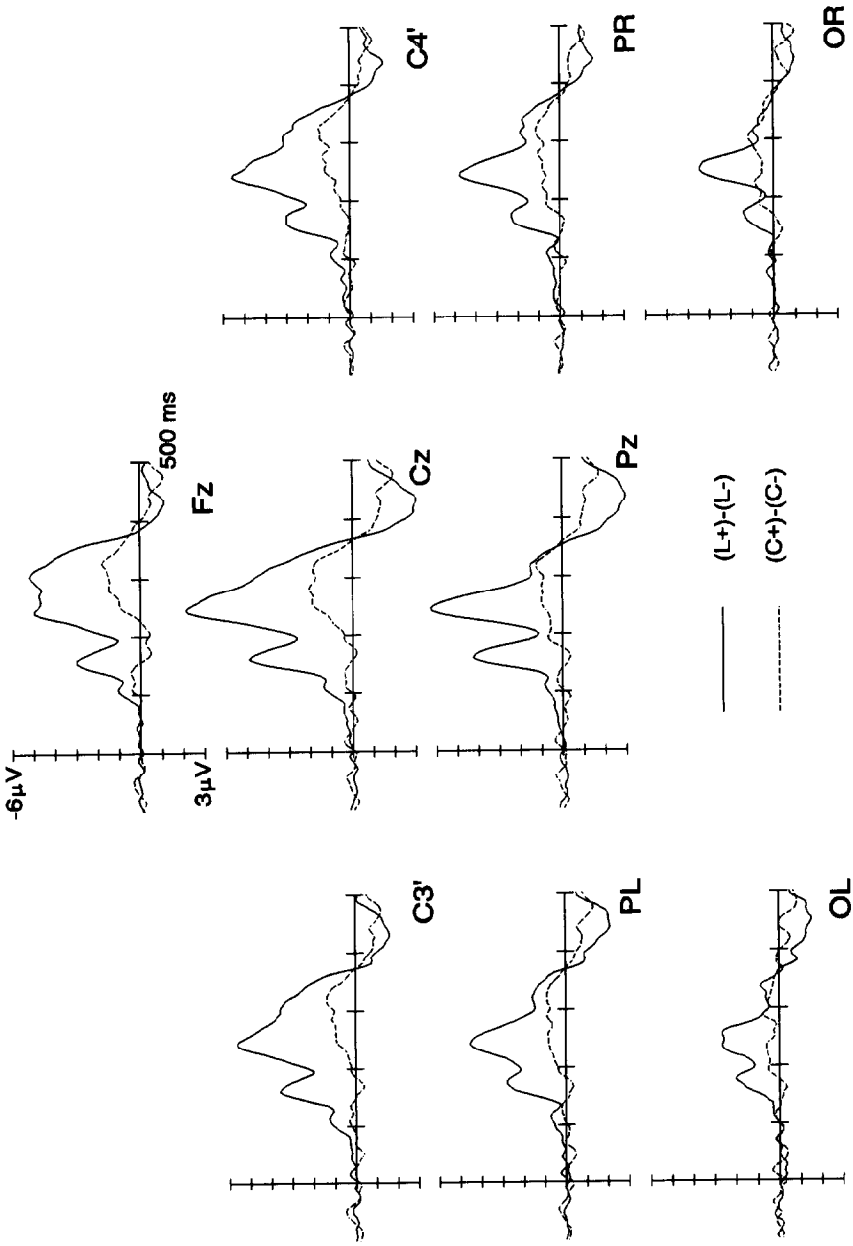


Fig. 3. Difference in waveforms reflecting spatial attention effects (solid lines), obtained by subtracting ERPs elicited by L- trials from ERPs elicited by L+ trials are contrasted with difference waveforms reflecting color attention effects, obtained by subtracting ERPs to C- trials from ERPs to C+ trials (dashed lines).

Table 2

Mean ERP difference amplitudes and ANOVA effects in the Nd2 interval (220–300 ms) for stimuli at attended and unattended locations (L+–L–; left side) and stimuli of attended and unattended color (C+–C–; right side) for midline electrodes Fz, Cz, Pz and for lateral and central (C3'/C4'), parietal (PL/PR), and occipital (OL/OR) electrodes.

	(L+)–(L–) (μ V)	<i>F</i> (1,7)	<i>p</i> -value	(C+)–(C–) (μ V)	<i>F</i> (1,7)	<i>p</i> -value
FZ	–4.58	51.22	<i>p</i> < 0.001	–0.76	4.56	ns
CZ	–6.78	53.56	<i>p</i> < 0.001	–1.71	11.82	<i>P</i> < 0.01
PZ	–4.59	42.22	<i>p</i> < 0.001	–0.97	4.67	ns
C3'/C4'	–4.68	98.18	<i>p</i> < 0.001	–1.01	26.90	<i>p</i> < 0.001
PL/PR	–3.57	47.09	<i>p</i> < 0.001	–0.89	11.56	<i>p</i> < 0.011
OL/OR	–2.37	23.91	<i>p</i> < 0.002	–0.58	1.95	ns

ns: not significant, *p* > 0.05.

tral and parietal electrode pairs (C3'/C4', PL/PR) and at Cz, and approached significance at Fz and Pz (see Table 2). In the P3 time range, attended-color stimuli elicited an enhanced positivity at Cz and Pz (Fig. 2). This effect was almost significant at Pz ($F(1,7) = 5.30$, *p* < 0.055).

As can be seen from Fig. 4, where the ERP effects of attending to color are plotted separately for attended location stimuli (L+) and unattended location stimuli (L–), the Nd2 effects of color attention tended to be larger for L+ than for L– stimuli. Additional analyses revealed that for stimuli presented at cued locations, the effects of attending to color were significant at Cz, C3'/C4' and at PL/PR. In contrast, no significant negative enhancement for C+ stimuli was present at any electrode when these stimuli were presented at unattended locations. However, these differences were not reflected in significant interactions between spatial attention and color attention (*p* > 0.10 at all electrodes). In addition, Fig. 4 seems to reveal the existence of an enhanced positivity for L+ stimuli as compared with L– stimuli at attended locations that is elicited about 200 ms at midline electrodes (most notably at Fz). This was further investigated by conducting repeated measures ANOVAs for the ERP mean amplitudes at Fz, Cz and Pz in the 160–190 ms time interval. No significant interactions between color attention and spatial attention could be obtained.

4. Discussion

The present study was conducted to investigate ERP correlates of spatial and non-spatial selective attention in a situation where attention had to be directed to a particular combination of color and location on a trial-by-trial basis. Three specific questions were raised. How does transient spatial attention influence the ERPs elicited by imperative stimuli? Are there ERP effects of transient attention to color? Is there evidence that non-spatial selection processes depend on a prior selection by location in a transient attention situation?

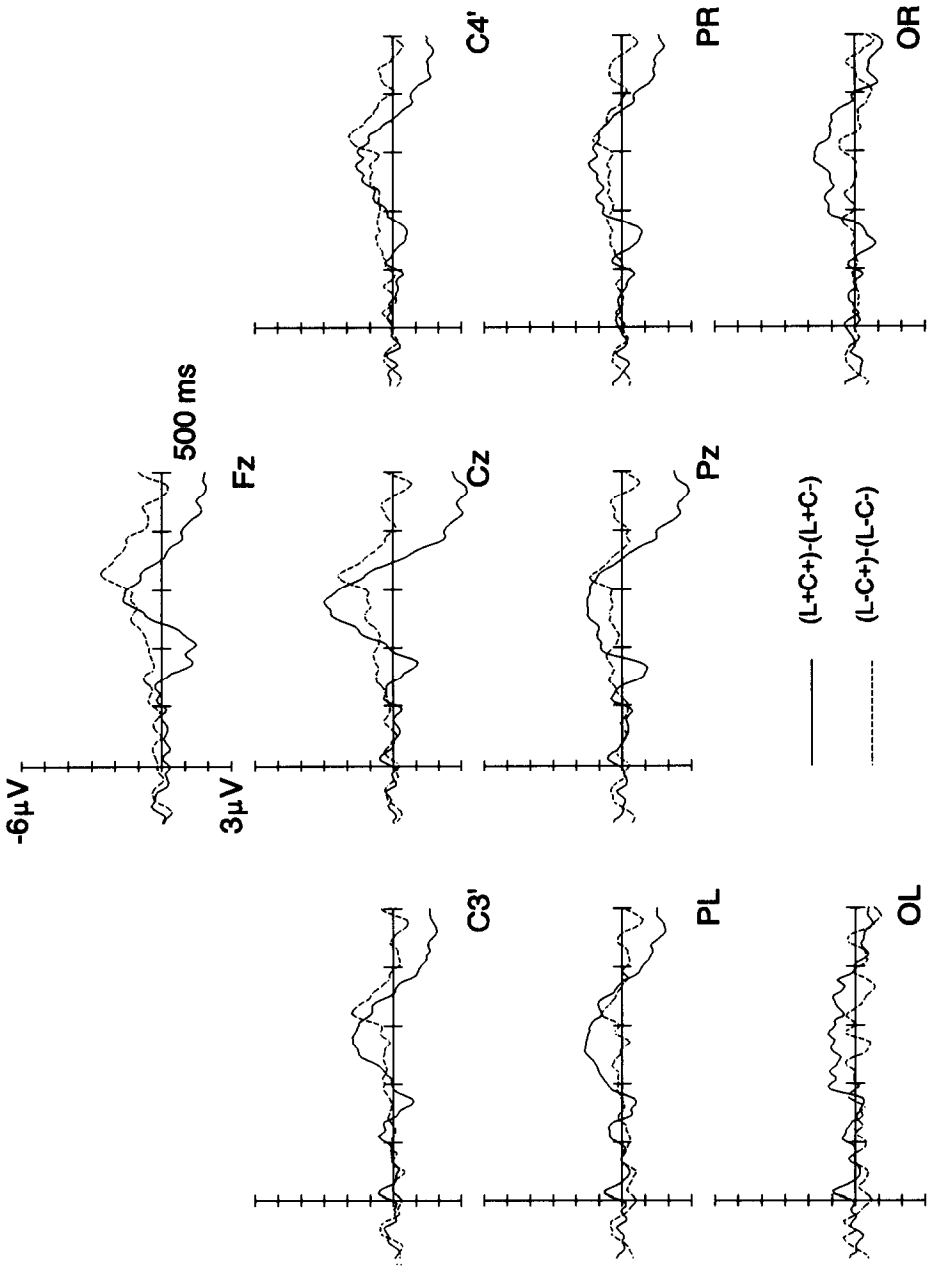


Fig. 4. Difference waveforms reflecting ERP effects of color attention, obtained by subtracting ERPs to C- trials from ERPs to C+ trials, are shown separately for L+ stimuli (solid lines) and for L- stimuli (dashed lines).

A major effect of spatial attention was an enhanced negativity elicited by L+ stimuli compared to L- stimuli (Fig. 3). This effect was characterized by a bimodal pattern that was already observed in previous trial-by-trial cueing studies (Eimer, 1993, 1994b): an initial negative peak was observed in the (L+)-(L-) difference waveforms between 140 and 200 ms post-stimulus. Unlike in previous studies, in which the Nd1 effect was maximal parietally, here Nd1 was broadly distributed over all midline electrodes. A second negative peak was present in the Nd2 range between 220 and 300 ms that was broadly distributed over all recording sites. Furthermore, enhanced N1 amplitudes were found at lateral posterior electrodes for L+ stimuli. In contrast, no effect of spatial attention was observed for the P1 component (Fig. 1). As attentional modulations of the P1 component are usually interpreted as evidence for the existence of 'sensory gating' processes as a prominent mechanism underlying visual-spatial attention (Mangun & Hillyard, 1990), this negative finding could be regarded as evidence that spatial selection did not influence early stages of perceptual processing in the present experiment. It has already been shown that effects of transient spatial attention on P1 amplitude are highly sensitive to the specific circumstances of the experimental task (Eimer, 1993, 1994b). In contrast to previous trial-by-trial cueing studies that reported P1 attention effects, both precues and targets carried spatial as well as non-spatial information in the present study. When spatial and non-spatial attentional processes are active simultaneously, spatial attention may be less focused than under conditions where only location is relevant for stimulus selection, resulting in the absence of electrophysiological indices of 'sensory gating'. These considerations should be taken with caution, however, since the effects of spatial attention on P1 are usually quite small and may have gone unnoticed due to the relatively small number of subjects included in this experiment.

Before interpreting the negative enhancements found for L+ trials as a result of transient spatial attention, two possible objections have to be ruled out. First, it is conceivable that these ERP effects are due to systematic lateral eye movements in the direction of the cue that were not detected by the artifact rejection routines. In Fig. 5 (left side), grand averaged horizontal EOGs are displayed that were recorded in the cue-target interval in response to left-pointing and right-pointing arrow cues. The maximum difference between these two HEOG waveforms is less than 1 μ V throughout the cue-target interval, thereby ruling out this first objection. Second, it is possible that the ERP differences observed between L+ and L- trials are due to differential ERP modulations in the interval between cue and imperative stimulus, where a CNV was elicited in response to the cue. However, as can be seen in Fig. 5 (right side), there were no systematic differences in CNV amplitudes between L+, L-, C+ and C- trials. Therefore, the second objection can also be ruled out. However, the fact that a CNV developed in response to the cue may have contributed to the amplitude differences between L+ and L- trials as shown in Fig. 3. In L- trials, where stimuli were presented at irrelevant locations, response preparation may have been aborted earlier than in L+ trials, resulting in an earlier onset of CNV resolution, and thus an enhanced negativity for L+ as compared to L- trials. Thus, the negativity found in the (L+)-(L-) difference waveforms may reflect both processes related to selective spatial attention as well as differential CNV resolution onsets for L+ and L- trials.

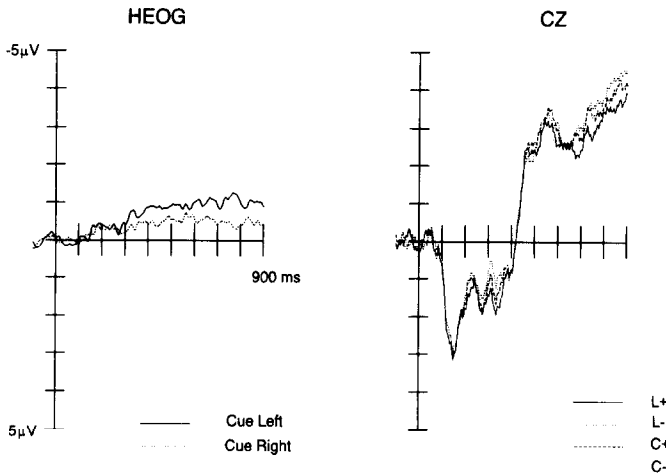


Fig. 5. Left side: Grand-average horizontal electrooculogram (HEOG) in the interval between cue onset and the onset of the imperative stimulus, displayed separately for trials with left-pointing and right-pointing arrow cues. Right side: Grand-average ERPs in the interval between cue onset and the onset of the imperative stimulus at Cz, displayed separately for L+, L-, C+, and C- trials.

In addition to the ERP effects of transient spatial attention, transient attention to color was also found to have an influence on the ERP waveforms. However, while spatial attention effects were clearly visible around 140 ms post-stimulus, ERP modulations due to selectively attending to stimulus color could only be observed starting beyond 200 ms. This temporal delay is comparable to the results of Hillyard & Münte (1984) who found that ERP effects of sustained spatial attention preceded the effects related to color attention by about 50 ms. The (C+)–(C-) difference wave revealed a broad negativity for C+ as compared to C- stimuli that was reflected in significant or nearly significant effects of color attention in the Nd2 time range at all electrodes, except lateral occipital sites. A broad negativity elicited by attended color stimuli was also found in the Hillyard & Münte (1984) study. This may indicate that color selection is based on similar mechanisms under transient and under sustained attention conditions. However, the effect of attending to color found by Hillyard & Münte (1984) started about 50 ms earlier and were also larger than in the present experiment. Two explanations may be considered to explain these differences. First, it may be assumed that attentional selectivity for non-spatial features like color is diminished when the to-be-attended feature varies from trial to trial. Alternatively, the fact that attention had to be directed to two distinct features (location and color) of a single stimulus on each trial may have delayed the onset of each feature-specific attention effect in the present study. As noted before, this second explanation could possibly also account for the absence of a P1 modulation due to spatial attention.

Was there any evidence for a hierarchical dependence of non-spatial upon spatial

attention? The ERP effects of attending to stimulus color in the Nd2 interval were found to be larger for stimuli presented at attended locations (Fig. 4). Thus, it seems that in the present study selective attention to color was in part hierarchically dependent upon the previous selection of location. However, since none of the relevant location attention \times color attention interactions were significant, this conclusion has to remain tentative.

In addition, interactions between spatial attention and color attention were present in the P3 time range. These were due to the fact that an enhanced positivity was elicited most notably in L+C+ trials. In these trials, non-target stimuli were presented that possessed two response-relevant features. It is therefore likely an enlarged P3 was elicited under these conditions.

In summary, the present study shows that in a situation where attention is simultaneously cued to a spatial and a non-spatial stimulus attribute, the ERP can be used to monitor both spatial and non-spatial selection processes. Both transient shifts of visual-spatial attention as well as transient attention to non-spatial (color) attributes had an effect on the ERP waveforms. However, the ERP effects of spatial attention were considerably larger, and preceded the ERP effects of color attention. In addition, the present results suggest that spatial selectivity may exert a modulatory influence on non-spatial selection.

Acknowledgments

This research was supported by the Max-Planck-Institute for Psychological Research and by a grant from the Deutsche Forschungsgemeinschaft (No. Ei 266/2-2). The author wants to thank Erich Schröger, Dagmar Endres and an anonymous reviewer for helpful comments on earlier drafts of this article, and Desiree Schön and Doris Koschubatz for their help in conducting the experiment.

References

- Aine, C.J., & Harter, M.R. (1984). Event-related potentials to stroop stimuli: Color and word processing. In R. Karrer, J. Cohen & P. Tueting (Eds.) *Brain and Information: Event-Related Potentials*. Annals of the New York Academy of Sciences (Vol. 425, pp. 154–156).
- Aine, C.J., & Harter, M.R. (1986). Visual event-related potentials to colored patterns and color names: Attention to features and dimension. *Electroencephalography and Clinical Neurophysiology*, 64, 228–245.
- 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. (1994a). An ERP study on visual-spatial priming with peripheral onsets. *Psychophysiology*, 31, 154–163.
- Eimer, M. (1994b). 'Sensory gating' as a mechanism for visual-spatial orienting: Electrophysiological evidence from trial-by-trial cueing experiments. *Perception and Psychophysics*, 55, 667–675.
- Friedman-Hill, S.R., & Mangun, G.R. (1993). Selective attention to location and color: Electrophysiological evidence for separate neural processes. *Society for Neuroscience Abstracts*, 19, 563.
- Harter, M.R., & Guido, W. (1980). Attention to pattern orientation: Negative cortical potentials, reaction time, and the selection process. *Electroencephalography and Clinical Neurophysiology*, 49, 461–475.

- 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.
- Harter, M.R., Aine, C., & Schroeder, C. (1982). Hemispheric differences in the neural processing of stimulus location and type: Effects of selective attention on visual evoked potentials. *Neuropsychologia*, *20*, 421–438.
- Hillyard, S.A., & Münte, T.F. (1984). Selective attention to color and location: An analysis with event-related brain potentials. *Perception and Psychophysics*, *36*, 185–198.
- 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. *Electroencephalography and Clinical Neurophysiology*, *88*, 51–63.
- Mangun, G.R., & Hillyard, S.A. (1987). The spatial allocation of visual attention as indexed by event-related brain potentials. *Human Factors*, *29*, 195–211.
- Mangun, G.R., & Hillyard, S.A. (1990). Electrophysiological studies of visual selective attention in humans. In A. Scheibel & A. Wechsler (Eds.) *The Neurobiological Foundations of Higher Cognitive Function* (pp. 271–294). New York: Guilford Press.
- Mangun, G.R., & Hillyard, S.A. (1991). Modulations of sensory-evoked brain potentials indicate changes in perceptual processing during visual-spatial priming. *Journal of Experimental Psychology: Human Perception and Performance*, *17*, 1057–1074.
- Mangun, G.R., Hansen, J.C., & Hillyard, S.A. (1987). 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.
- Neville, H.J., & Lawson, D. (1987). Attention to central and peripheral visual space in a movement detection task: An event-related potential and behavioral study. I. Normal hearing adults. *Brain Research*, *405*, 253–267.
- Posner, M.I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, *32*, 3–25.
- Posner, M.I., Nissen, M.J., & Ogden, W.C. (1978). Attended and unattended processing modes: The role of set for spatial location. In H.L. Pick & E.J. Saltzman (Eds.) *Modes of perceiving and processing information* (pp. 137–157). Hillsdale, NJ: Erlbaum.
- Posner, M.I., Snyder, C.R.R., & Davidson, B.J. (1980). Attention and the detection of signals. *Journal of Experimental Psychology: General*, *109*, 160–174.
- Previc, F.H., & Harter, M.F. (1982). Electrophysiological and behavioral indicants of selective attention to multifeature gratings. *Perception and Psychophysics*, *32*, 465–472.
- Rugg, M.D., Milner, A.D., Lines, C.R., & Phalp, R. (1987). Modulation of visual event-related potentials by spatial and non-spatial visual selective attention. *Neuropsychologia*, *25*, 85–96.
- Schröger, E. (1993). Event-related potentials to auditory stimuli succeeding transientshifts of spatial attention in a Go/NoGo task. *Biological Psychology*, *36*, 183–207.
- Schröger, E. (1994). Human brain potential signs of selection by location and frequency in an auditory transient attention situation. *Neuroscience Letters*, *173*, 163–166.
- Schröger, E., & Eimer, M. (1993). Effects of transient spatial attention on auditory event-related potentials. *NeuroReport*, *4*, 588–590.
- Ungerleider, L.G., & Mishkin, M. (1982). Two cortical visual systems. In Ingle, D.J., Goodale, M.A. & Mansfield, R.J.W. (Eds.) *Analysis of Visual Behavior* (pp. 549–586). Cambridge: MIT Press.
- Wijers, A.A., Lamain, W., Slopsema, S., Mulder, G., & Mulder, L.J.M. (1989). An electrophysiological investigation of the spatial distribution of attention to colored stimuli in focussed and divided attention conditions. *Biological Psychology*, *29*, 213–245.
- Wijers, A.A., Mulder, G., Okita, T., & Mulder, L.J.M. (1989). An ERP-study of memory search and selective attention to letter size and conjunctions of lettersize and color. *Psychophysiology*, *26*, 529–547.
- Wijers, A.A., Mulder, G., Okita, T., Mulder, L.J., & Scheffers, M.K. (1989). Attention to color: An analysis of selection, controlled search, and motor activation, using event-related potentials. *Psychophysiology*, *26*, 89–109.