



Electrophysiological correlates of early attentional feature selection and distractor filtering



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ABSTRACT

Using electrophysiology, the attentional functions of target selection and distractor filtering were investigated during visual search. Observers searched for multiple tilted line segments amidst vertical distractors. In different conditions, observers were either looking for a specific line orientation (“feature-based” selection), or for any tilted line (“saliency-based”). The search array could contain both left- and rightward tilted lines simultaneously (requiring spatial filtering) or only one line type (no filtering). The amplitude of the P1 event-related potential component was reduced during feature-based selection, compared to saliency-based selection. The N1 showed a similar effect, at least when filtering was required. Amplitudes were also somewhat reduced when competing nontarget stimuli required filtering. Interactions between selection and filtering became stronger on the N2a and P3. When both feature-based selection and filtering were required, N2a amplitude was highest, and P3 amplitude was lowest. The results support an early locus of feature-based attentional selection in multi-item search.

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1. Introduction

The deployment of attention toward a target stimulus across the visual field is a classic field of research in psychology. One particularly influential theory of human visuospatial attention was proposed by Duncan and Humphreys (1989). One of its most important contributions was that it considered both the relation of the visual environment and the search target object, and aspects related to other, distracting objects also present in the visual field. According to the theory, search speed, that is, attentional efficiency, is reduced when targets are similar to and difficult to discern from distractors, but also when distractors are dissimilar from each other. Of importance to the present study, the theory thus implies there might be a functional division between processes involved in selection of targets and filtering of distractors, both of which however contribute to the deployment of attention.

Selection in this sense may be understood as the specification of the search object or location, as well as the associated enhancement of incoming sensory information that fits this target template. This enhancement might also be understood as the result of a more

relative gain function that takes input from the (dis-) similarity of targets and distractors to achieve the desired target amplification (Navalpakkam and Itti, 2007; Reynolds and Chelazzi, 2004). *Filtering* however reflects the rejection of task-irrelevant objects (nontargets, distractors) and locations, which is associated with the suppression of their (sensory) representations. It is important to note that neither function should be understood as being exclusively top-down (i.e., goal-directed) or bottom-up (stimulus-driven; for a review see Corbetta and Shulman, 2002, see also He et al., 2004); bottom-up and top-down control can both affect selection and filtering. Selection and filtering aspects of attention have been incorporated in several models to date, and are generally believed to operate side-by-side (Bundesen, 1990; Bundesen et al., 2005; Desimone and Duncan, 1995; Duncan and Humphreys, 1989).

Previous functional imaging studies have provided a tentative framework specifying the functional neuroanatomy of selection and filtering. The first finding of interest is the link between attention and the parietal cortex, in particular the intraparietal sulcus (IPS) and the junction of the intraparietal and transverse occipital sulcus (IPTO; Wojciulik and Kanwisher, 1999). The critical factor in the involvement of these regions seemed to be the presence of distractors, which had to be suppressed across a range of attentional tasks. The role of the parietal cortex thus seemed related to the inhibition of distractors, which again may also be understood as the relative enhancement of task-related information (Desimone

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and Duncan, 1995). The results led Wojciulik and Kanwisher (1999) to conclude that the parietal involvement might be viewed as a filtering function.

The second relevant finding concerns the involvement of the (pre-) frontal cortex in attention (e.g., Corbetta, 1998). The anterior cingulate in particular seems to be involved in target detection (Posner and Petersen, 1990). Because the pre-frontal cortex is not only implicated in (top-down) control over attention, but also the organization and control of working memory (Bor et al., 2003; Dosenbach et al., 2008), a functional common ground seems plausible. Such could be found if one assumes the specification and maintenance of an attentional target template is one of the functions of working memory. Close links between attention and working memory have indeed been reported in a variety of paradigms (e.g., Akyürek et al., 2010a; Downing, 2000; Kuo et al., 2012). Regardless of whether control is indeed initiated through working memory, it seems fair to interpret the involvement of frontal areas as a selection function (but see also the General Discussion for an alternative interpretation).

1.1. Multi-item search

Studies of spatial attention have mostly used tasks that require observers to look for a single target item. Although these tasks are certainly representative of many aspects of search behavior, they may underestimate others. In particular, one of the defining aspects of single target search is that search can terminate as soon as the target has been found, allowing any possible remaining (distractor) locations or objects to escape inspection altogether. However, if the task requires finding more than a single target item in the display, and if the number of potential targets varies between trials, then search cannot stop once one target has been found. Instead, participants have to search through the entire display and inspect all single items before they can terminate their search. This requirement of multi-item search arguably enables a more comprehensive examination of search behavior across all items of interest; including any distractors within that set.

Recently, Akyürek et al. (2010b) attempted to characterize the hypothesized division between selection and filtering functions in a functional magnetic resonance imaging (fMRI) study, using a multi-item search task designed for this purpose. In this task, a number (2–4) of 45°-tilted line segments appeared in an array of vertical distractor lines, and observers were asked to count (subitize) the number of targets. Target selection criteria were varied so that in one condition observers were looking for either only left- or only rightward tilted lines, and in the other condition for tilted lines regardless of their direction (i.e., both left- and rightward tilted lines). Thus, observers were either performing a feature-specific, “feature-based”, or a feature-unspecific, “saliency-based” selection task. This selection variable was crossed with a manipulation of filtering requirements (cf. Fig. 1). In one condition, both directions of tilt were presented simultaneously in the search arrays, while in the other only one direction was present within any one array (but both directions were still used between arrays). In the former condition, simultaneous spatial filtering between the two directions of tilt was required, whereas it was not in the latter condition.

The behavioral results of the Akyürek et al. (2010b) study showed that both variables interactively affected performance, so that feature-based selection and the need to perform filtering resulted in the slowest responses and the most errors. The physiological results furthermore showed that selection and filtering differentially activated distinctly different regions in the brain. Briefly summarized, the contrasts between feature- and saliency-based selection principally revealed differences in the involvement of the medial frontal gyrus, while the contrasts

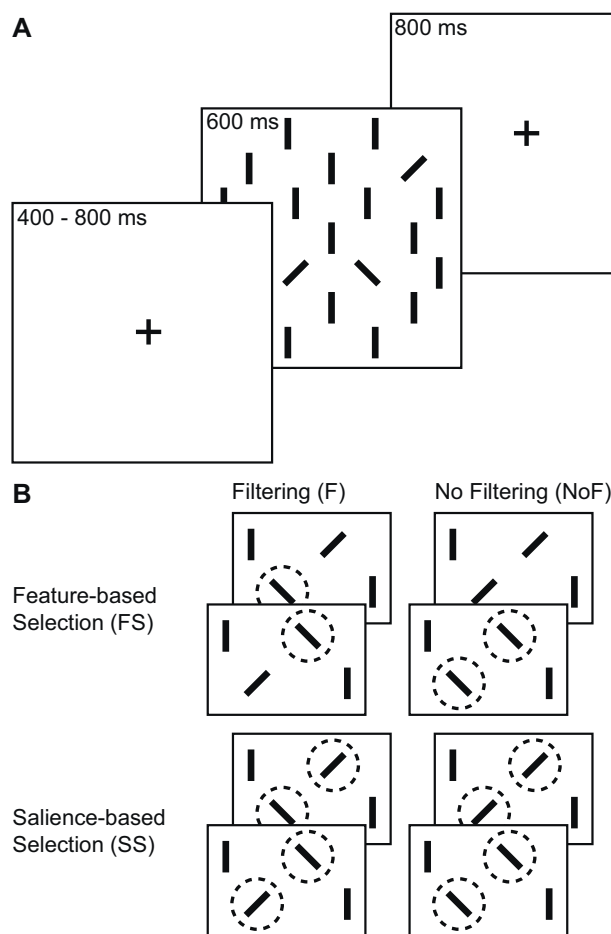


Fig. 1. The experimental procedure. Panel A shows trial structure and the full search array, which consisted of 21 line segments arranged in a circular fashion. Two, three or four of these lines were tilted, and these could appear at any position in the array. The experimental conditions are illustrated in panel B by means of two overlaid exemplars per condition. Dashed circles indicate targets. In feature-based selection trials (upper panels), participants were instructed to attend to one specific orientation (in this case leftward tilted lines), while in saliency-based selection trials (lower panels) they were attending to any orientation. In filtering trials (left panels) both left- and rightward tilted lines were presented simultaneously, in no-filtering trials (right panels) only one orientation was shown in each individual search array. The actual orientation of the lines in the array was random in both filtering and no-filtering conditions.

between filtering and no filtering implicated occipital and parietal loci. The authors concluded that these results supported the idea that areas in the frontal cortex are involved in specification of the target template, and that parietal and occipital areas are involved in the processing of distraction. However, because of the limited temporal resolution of fMRI, the temporal dynamics of these purported attentional functions remain unknown. The present study sought to investigate these dynamics, by measuring the event-related potential (ERP), which affords the required temporal resolution.

Although previous ERP studies have not always strictly dissociated between selection and filtering, and have not addressed multi-item search specifically, some data are available that relate to the present topic. A study by Luck et al. (1994) in particular provided evidence that suggested that filtering and selection may have different temporal loci. The authors observed that, in a cued search task, unattended stimuli were suppressed (filtered) at an early stage, corresponding with an amplitude reduction of the P1 component of the ERP, in comparison to target-absent ERPs.

Conversely, attended (selected) stimuli elicited an N1 component of enhanced amplitude.

However, such early modulation of the ERP seems to be closely coupled with the type of task that is used, in particular whether the task requires spatial (location-based), or feature-based visual attention. When the task requires location-based selection, attentional modulation of the ERP has been shown to start very early in general, at around 100 ms after stimulus onset (e.g., Hillyard and Münte, 1984; Luck et al., 1994). In such cases, increased P1 and N1 amplitude is observed for stimuli appearing at attended locations compared to unattended locations (for an overview, see Hillyard et al., 1998). By contrast, and of particular interest for the present study is the finding that feature-based attention (e.g., attention toward a color rather than a location) in uncued visual search tasks can seemingly only modulate the P1 component when filtering is also required, and/or when critical stimulus features are presented in direct competition with each other (Nobre et al., 2006; Valdes-Sosa et al., 1998; Zhang and Luck, 2009).

Direct competition in these studies entailed that the target stimuli were to be selected, while nontargets (or nontarget features) were to be ignored simultaneously at competing (overlapping) spatial locations, and the nontarget stimuli possessed features that were task-relevant on half of the trials. In other words, while one thing was to be attended to, others were not, calling for the interplay between amplification of target-related information and suppression of distractor-related information. Thus, arguably, this kind of direct competition requires not only featural selection, but also some process of (spatial) filtering to successfully select the target(s). It is important to distinguish this type of competition from cases in which distractor stimuli possess no task-relevant features throughout the experiment, or cases in which distractors or distractor features do not co-occur or interfere spatially with actual targets, as target-nontarget similarity is high in the former case, but low in the latter (cf. Duncan and Humphreys, 1989).

Using such direct competition paradigms, Valdes-Sosa et al. (1998) found suppression of the P1 and N1 for the nontarget stimuli, while Zhang and Luck (2009) found an enhanced P1 for features that matched the search template even when these appeared in unattended locations. Both of these results support the notion that feature-based selection can start relatively early in visual perception (i.e., at the P1, or even in early visual cortex; Müller et al., 2006), but only as long as direct competition in the search displays necessitates filtering.

Without the need to perform (spatial) filtering, feature-based attention seems to be slower, arising only at the N1, approximately 150 ms post-stimulus (Hopf et al., 2004), or beyond, and continuing over the P2 and N2 components (called the “selection negativity”; Hillyard and Münte, 1984; Anllo-Vento and Hillyard, 1996). Broader selection criteria, such as selection on the basis of an entire feature dimension (e.g., any color), have also resulted in relatively late modulation of the ERP in search tasks. The anterior N2 at beyond 250 ms has been reported as a component to be modulated by feature dimension-based attention in a task that required ongoing switching of the search template between various dimensions like color and orientation (Gramann et al., 2007).

By contrast, location-based selection is inherently linked to spatial filtering, as it involves the selection of one location over others. It might thus be speculated that if the presence of competition is a prerequisite for the P1 effect to appear during feature-based selection in visual search, then that P1 effect may simply be due to spatial filtering, rather than to selection itself. However, this hypothesis has not been tested explicitly to date. The present study sought to do so, and to compare the time course of attentional feature selection and distractor filtering in the brain.

1.2. The present study

The design of the present experiment was adapted from Akyürek et al., 2010b, which may be compared for reference, and is illustrated in Fig. 1. As mentioned, the present design was aimed specifically at examining the temporal aspects of attentional selection and filtering functions and their respective ERP correlates in a multi-item search task. Observers were asked to report the number of target stimuli (0–4 tilted line segments) that appeared in search arrays consisting of vertical lines mostly. Thus, all searches were carried out on the basis of stimulus features (i.e., orientation), rather than stimulus location. Filtering and selection were systematically manipulated by varying the criterion for selection (one specific orientation, or any non-vertical orientation) and the number of line orientations that were simultaneously present in the search array (one or two). Filtering was expected to have an early locus and accordingly to modulate P1 amplitude, with commensurate carry-forward effects on the N1, N2, and P3 components. Specifically, higher amplitude was expected to be associated with easier conditions (i.e., only one orientation shown). Selection, on the other hand, was expected to start later, that is, at the N1, and to continue similarly onto the N2 and P3, with higher amplitude reflecting easier search.

2. Methods

2.1. Participants

Sixteen students (11 female, 5 male) at the Ludwig Maximilian University Munich participated for monetary compensation. Informed written consent was obtained prior to the experiment. Participants were unaware of the purpose of the experiment and reported normal or corrected-to-normal vision. Mean age was 24.4 years (range 20–39 years).

2.2. Apparatus and stimuli

Participants were individually seated in a dimly lit and sound attenuated testing chamber at a distance of approximately 100 cm from the screen. The 20" CRT screen was driven by a Core 2 Duo computer running Windows XP, with a discrete graphics card, and refreshed at 100 Hz with a resolution of 1024 by 768 pixels in 16 bit color. The experiment was programmed in E-Prime 1.2. Responses were recorded with a USB keyboard (125 Hz polling rate). A white background was maintained throughout the experiment. The fixation cross (“+”) was drawn in bold 18 pt. New Courier font.

The stimulus arrays consisted of 21 black line segments, each 30 pixels in length and 5 in width, which were arranged in a circular fashion, centered on the screen, as shown in Fig. 1. This virtual circle was composed of 7 rows, of 2, 3, 4, 3, 4, 3, and 2 line segments each, from top to bottom. The rows were separated from each other by a distance of 50 pixels (vertically). Between line segments in each row, a horizontal distance of 100 pixels was used, but the lines in each row were displaced by ± 50 pixels compared to the neighboring rows. The lines were thus separated by 50 pixels on both the horizontal and vertical axes. Additionally, each individual line segment was displaced randomly between 0 and 7 pixels (x, y). All but 2–4 lines (evenly distributed and randomly chosen in each condition) had a vertical orientation. These other lines were tilted 45 degrees leftward or rightward. On half of the trials both left- and rightward tilted lines were presented in the search array simultaneously, on the other half of trials only one orientation was shown in each individual search array (i.e., only leftward tilted lines, or only rightward tilted lines, randomized across trials). The number of tilted lines was the same (2–4) in all conditions, so that the “set size” remained comparable (cf. Horowitz and Wolfe, 2001). Consequently, the number of actual targets that could be found within the full set of tilted lines did vary between the two selection conditions (explained further below). This choice was motivated by two considerations: First, we were interested in possible modulations of the ERP as a consequence of the full set of stimuli, both when they were targets and when they were not (and mixtures thereof). In our view, this is more indicative of processing in multi-item search than strictly target-related comparisons. Second, the number of tilted lines is arguably the most salient aspect of the search display to the observers, so that keeping this the same should keep the overall appearance of the trials across conditions as similar as possible.

2.3. Procedure and design

There were 864 experimental trials, preceded by a practice block of 54 trials that were excluded from analysis. Each individual trial started with a fixation cross, lasting 400–800 ms. Participants were asked not to move their eyes and to fixate the cross during the trial. The search array then followed for 600 ms. After offset of

the search array, the fixation cross was shown again for 800 ms before the next trial commenced. Participants were asked to enter the number of target line segments (0–4) they had seen, and they were informed they had to make a response before the next trial started for it not to be considered missing and excluded from analysis. Responses were made on the numeric keypad of a standard keyboard with the fingers of the right hand.

The experiment consisted of three identical parts of 288 trials each, with optional breaks in-between. These 288 trials were presented in eight blocks of 36 trials each. The presentation order of the blocks was randomized. In four out of these eight blocks, participants were asked to attend to one specific line orientation only. In two of these blocks the leftward tilted lines were to be attended to, and in the other two blocks the rightward tilted lines. In the remaining four blocks, participants were asked to attend to both directions of tilt. Thus, half the trials required feature-specific selection, while the other half required only salience-based selection (i.e., attend to anything not-vertical). The selection instructions were given at the start of each block, and remained on screen for two seconds, followed by a two second blank interval, to minimize costs related to setting up the search template (Wolfe et al., 2004). These selection conditions were crossed (again, block-wise) with the filtering manipulation, so that half the blocks contained trials in which both left- and rightward tilted lines appeared simultaneously in the search arrays, and the other half contained trials in which only one direction of tilt was shown in each individual search array. In the former trials, spatial filtering between left- and rightward tilted lines was required, while in the latter trials it was not. Note that this is not to say that no spatial filtering was needed at all in the search arrays that contained but one direction of tilt, as the vertical distractor lines were always present, but for reasons of brevity only the direct competition between targets and tilted nontargets is referred to here.

In this design, the need to filter when two directions of tilt are present in the search array is much reduced when a salience-based selection criterion is used, as any tilted line was denoted a target. However, even in this case there were still different kinds of stimuli to be processed, at various locations in the visual field, compared to the conditions in which only one direction of tilt was shown, so that a limited degree of filtering may still have been necessary. One reason to assume that limited filtering matters even when selection is salience-based is the effect of target-target similarity; when targets are all identical they may be grouped more easily (Duncan and Humphreys, 1989). Such grouping was prevented by simultaneous presentation of both types of target.

Mean accuracy and reaction time were analyzed in a repeated measures analysis of variance (ANOVA) with one variable for the selection instruction (selection; feature-based or salience-based), and one for the level of spatial filtering required (filtering; present or absent). Planned comparisons between selection and filtering conditions were carried out when appropriate (i.e., when significant interaction terms were found). Please note that the terms “feature-based” and “salience-based”, used in the context of the present paradigm are strictly meant to refer to the search template used to find the targets. Thus, the search is either performed on the basis of a specific feature (e.g., rightward tilted; feature-based), or on the basis of any deviant feature that dissociates the targets from the vertical lines (i.e., anything that stands out in the search array; salience-based). In the present paradigm, the latter condition entailed both left- and rightward tilted lines, no other features were used. Thus, these terms are certainly not meant to imply that stimulus salience matters in one condition, but not another. They also do not refer to the nature of the task itself; search was performed on the basis of featural information in all cases – as opposed to location-based search in which a spatial coordinate is used for search.

2.4. Electrophysiological recording and data analysis

EEG was recorded with Ag-AgCl electrodes from 64 electrodes, which were positioned according to the extended International 10–20 System. The electrodes were referenced to Cz and re-referenced offline to the average of both mastoids. The horizontal electro-oculogram (EOG) was recorded from the outer canthi of the eyes and the vertical EOG from above and below the left eye. Electrode impedance was kept below 5 k Ω . The amplifier used a 125-Hz cut-off and a 0.1-Hz high-pass filter, and recorded at a frequency of 500 Hz. The data were filtered off-line with a 40-Hz low-pass filter at –12 dB (48 dB/oct roll-off), and a 0.1-Hz high-pass at –6 dB (24 dB/oct roll-off). EEG was averaged into 1000 ms segments, starting 200 ms prior to the onset of the search array and ending 800 ms afterwards. Ocular artifacts (blinks and eye movements) were corrected using the Gratton-Coles procedure (Gratton et al., 1983).¹ For each electrode, trials with amplitudes exceeding $\pm 80 \mu\text{V}$, voltage steps exceeding $\pm 50 \mu\text{V}$ between two sampling points, and trials with voltage differences lower than $0.10 \mu\text{V}$ for a 100-ms interval were excluded from analysis. Subsequently, a 200-ms interval directly preceding the search array was used for baseline

¹ Statistical analyses based on the data after EOG removal (criteria being EOG steps $> 50 \mu\text{V}$ or absolute differences $> 80 \mu\text{V}$) instead of analyses based on the data after the reported EOG correction produced results highly similar to those reported here. Visual inspection of the waveforms confirmed that the EOG removal and correction approaches showed negligible differences.

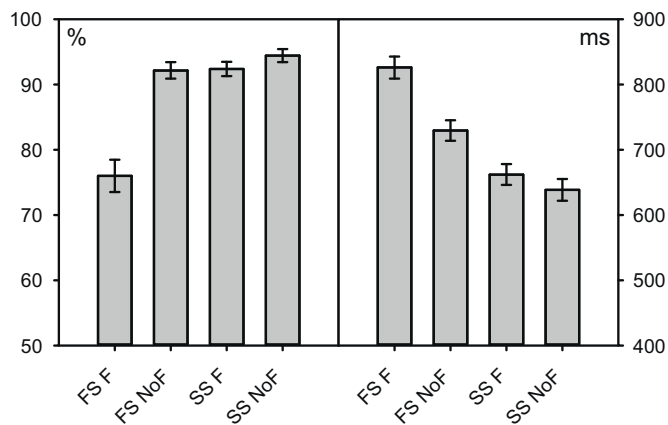


Fig. 2. Response accuracy in percent correct (left panel), and reaction time in ms (right panel) for the experimental conditions: feature-based selection and spatial filtering (FS F), feature-based selection and no spatial filtering (FS NoF), salience-based selection and spatial filtering (SS F), and salience-based selection and no spatial filtering (SS NoF). Error bars represent one standard error of the mean.

correction. Trials were categorized into correct, incorrect, and missing responses. Only the first category was used for the electrophysiological analyses.

Analyses of variance (ANOVA) were performed for mean amplitude values in time windows corresponding to the occipital P1 (70–100 ms after search array onset) and N1 (140–170 ms), the P2 (180–230 ms), the central-frontal N2 (N2a; 280–320 ms), and the parietal P3 (320–500 ms).² No lateral difference-based component such as the N2pc was measured, because of the varying number and random distribution of the target and nontarget stimuli across the visual field. Based on convention and observed component amplitude, the PO7 and PO8 electrodes were selected for the P1 and N1, FCz for the P2 and N2a, and Pz for the P3. The current source density (CSD) plots shown in Figs. 3 and 4 may be compared for reference. Although there seemed to be some positive lateralization in the P2 time window, it did not seem of particular significance in the present paradigm, and the fronto-central electrode was maintained to reflect the overall P2 effect in the analysis. For ANOVA's involving multiple electrodes, electrode was added to the analysis as a variable. Finally, for the earlier components, when the waveforms suggested there might be latency differences between conditions, an analysis thereof was conducted.

3. Results and discussion

3.1. Behavior

Response accuracy was affected by both selection, $F(1, 15) = 29.72$, $MSE = .003$, $p < .001$, $\eta^2 = .67$, and filtering, $F(1, 15) = 60.92$, $MSE = .002$, $p < .001$, $\eta^2 = .8$. The interaction was reliable as well, $F(1, 15) = 56.75$, $MSE = .001$, $p < .001$, $\eta^2 = .79$. Accuracy was low when feature-based selection and filtering were required (78.2%), compared to the same selection without filtering (92.1%), and to the salience-based conditions with (92.4%) and without filtering (93.8%). Comparison of the means showed that selection made a difference when filtering was required, $t = 6.83$, $p < .001$, but not reliably so when filtering was not required, $t = 1.52$. Filtering remained reliable both with feature-based selection, $t = 8.25$, $p < .001$, and with salience-based selection, $t = 2.13$, $p < .05$. The left panel of Fig. 2 shows accuracy in all four conditions.

The analysis of reaction time showed reliable main effects of selection, $F(1, 15) = 308.78$, $MSE = 760.263$, $p < .001$, $\eta^2 = .95$, and filtering, $F(1, 15) = 76.89$, $MSE = 456.33$, $p < .001$, $\eta^2 = .84$, as well as their interaction, $F(1, 15) = 20.91$, $MSE = 879.373$, $p < .001$, $\eta^2 = .58$.

² An anonymous reviewer pointed out that one might assume that mean amplitudes cannot entirely account for differences in latencies of components, which may have caused differences between participants, conditions or recording sites. To control for this possibility, we ran additional analyses of P1, N1 and N2a mean amplitude obtained from the maximum peak value of the respective component ± 5 sample points. These analyses are not reported in detail, but produced virtually identical effects to the main analyses reported in the text.

Reaction time was highest when feature-based selection and filtering were required at 817 ms, dropping to 736 ms when no spatial filtering was needed. Saliency-based selection elicited the fastest reaction times, both with filtering (662 ms) and without (649 ms). Further comparisons showed that selection had an effect both when filtering was required, $t = 13.27, p < .001$, and when it was not, $t = 10.54, p < .001$. Filtering likewise affected the means both when feature-based selection was required, $t = 6.72, p < .001$, and, importantly, also when saliency-based selection was required, $t = 2.72, p < .05$. The right panel of Fig. 2 shows reaction time in all conditions.

3.2. Electrophysiology

Fig. 3 shows the ERP recorded in each condition, for both PO7 and PO8. The analysis of the P1 showed a reliable main effect of selection, $F(1, 15) = 10.8, MSE = .131, p < .005, \eta^2 = .42$, but not of filtering or electrode ($F_s < 1$). Mean amplitude was $2.82 \mu\text{V}$ when feature-based selection was required, and $3.03 \mu\text{V}$ when saliency-based selection was required. Selection did not interact with filtering ($F < 1$), and neither with electrode ($F < 1$). The interaction between filtering and electrode failed to reach significance, $p < .1$. The three-way interaction was reliable, however, $F(1, 15) = 5.59, MSE = .078, p < .05, \eta^2 = .27$. The interaction seemed to indicate that the decrease in amplitude from saliency- to feature-based selection was larger on the PO7 electrode ($.49 \mu\text{V}; t = 2.8, p < .05$, although this would just miss the Tukey criterion of $t = 2.88$) than on the PO8 electrode ($.13 \mu\text{V}; t = .98$, not significant), at least when filtering was required.³ When no filtering was required, the differences came to $.05 \mu\text{V}$ at PO7 and $.16 \mu\text{V}$ at PO8, neither of which was reliable. Further comparisons of the means did not reveal significant differences due to filtering on either electrode.⁴ An additional analysis of P1 peak latency across the present conditions did not produce reliable differences between the experimental conditions.

Finally, to ascertain that differences in the number of targets between selection conditions were not responsible for the effects described above, these conditions were plotted for a subset of trials in which the number of targets was the same (but not, as a consequence, the number of tilted lines). As shown in the Appendix, mean P1 (as well as N1 and P3) amplitude showed a pattern very similar to that of the full set of trials. The observed differences between conditions are preserved also for comparisons involving two targets exclusively (e.g., the P1 difference between gray and black lines). An ANOVA of these subsets, including a variable for the number of targets, continued to show a reliable effect of selection, $F(1, 15) = 4.57, MSE = .729, p < .05, \eta^2 = .23$. By contrast, no main effect ($F < 1.7$), and no interactions ($F_s < 1.6$) of the number of targets were observed. It therefore seemed unlikely that the number of targets (and any potentially resultant differences in target grouping) played a tangible role in the emergence of these differences in the overall analysis.

N1 amplitude (see Fig. 3) was affected by selection, $F(1, 15) = 13.01, MSE = .572, p < .005, \eta^2 = .47$, and filtering also, $F(1, 15) = 10.06, MSE = .341, p < .01, \eta^2 = .4$. Amplitude averaged

$-3.75 \mu\text{V}$ during feature-based selection, and $-4.23 \mu\text{V}$ during saliency-based selection. Amplitude was less negative when filtering was required, at $-3.82 \mu\text{V}$, compared to $-4.15 \mu\text{V}$ when it was not. Electrode was unreliable ($F < 2.8$). Neither of the interaction terms involving electrode was significant either ($F_s < 1.1$). By contrast, the interaction between selection and filtering was significant, $F(1, 15) = 7.39, MSE = .418, p < .05, \eta^2 = .33$. The interaction was due to a stronger decrease in component amplitude from saliency- to feature-based selection with filtering (from $-4.22 \mu\text{V}$ to $-3.43 \mu\text{V}; F(1, 15) = 13.71, MSE = .734, p < .005, \eta^2 = .48$), than was observed without filtering (from $-4.24 \mu\text{V}$ to $-4.07 \mu\text{V}, F < 1.8$, not significant). Vice versa, the effect of filtering was unreliable when saliency-based selection was required ($F < 1$), but clearly present when feature-based selection was required, $F(1, 15) = 21.35, MSE = .305, p < .001, \eta^2 = .59$. Finally, the three-way interaction was significant as well, $F(1, 15) = 9.02, MSE = .058, p < .01, \eta^2 = .38$. The selection effect was reliable when filtering was required, both on PO7 ($.69 \mu\text{V}$ difference; $t = 2.85, p < .05$) and on PO8 ($.89 \mu\text{V}; t = 4.01, p < .001$), although the former value was just shy of the Tukey criterion of $t = 2.88$. When no filtering was required, selection was only marginally significant on PO7 ($.33 \mu\text{V}$ difference; $t = 2.02, p < .06$, also below the Tukey level), and far from it on PO8 ($.01 \mu\text{V}$ difference; $t = 1$). Filtering was significant on both electrodes when feature-based selection was required ($.47 \mu\text{V}$ difference on PO7, $t = 3.49, p < .005$, and $.8 \mu\text{V}$ difference on PO8, $t = 5.05, p < .001$), both of which passed the Tukey criterion. When saliency-based selection was required, filtering was unreliable on either electrode ($.11 \mu\text{V}$ difference on PO7, and $.07 \mu\text{V}$ difference on PO8).

The P2 component (see Fig. 4) showed an effect of filtering only, $F(1, 15) = 7.27, MSE = .332, p < .05, \eta^2 = .33$. Amplitude was higher when no filtering was required ($6.83 \mu\text{V}$ vs. $6.44 \mu\text{V}$). Selection did not reliably affect P2 amplitude ($F < 1.6$), and neither did the interaction term ($F < 2.4$).

The anterior N2 (see Fig. 4) also showed a reliable effect of filtering, $F(1, 15) = 8.38, MSE = .826, p < .05, \eta^2 = .36$. Higher component amplitude was elicited by displays that required filtering ($-.88 \mu\text{V}$ compared to $-.22 \mu\text{V}$). Selection did not have a main effect ($F < 1$). However, the two variables did interact, $F(1, 15) = 7.07, MSE = .661, p < .05, \eta^2 = .32$. When filtering was needed, feature-based selection elicited higher amplitude ($-1.31 \mu\text{V}$) than saliency-based selection ($-.45 \mu\text{V}$), a difference that proved only marginally reliable in a direct comparison of the means, $t = 1.92, p < .07$. Without filtering, the differences were unreliable, and if anything in the reverse direction ($-.11 \mu\text{V}$ feature-based and $-.33 \mu\text{V}$ saliency-based). Filtering did affect the means, as long as feature-based selection was required ($1.2 \mu\text{V}$ difference, $t = 3.08, p < .01$). When saliency-based selection was required, the difference was unreliable ($.12 \mu\text{V}$). An additional analysis of component latency revealed only a significant effect of filtering, $F(1, 15) = 8.71, MSE = 132.8, p < .01, \eta^2 = .37$, reflecting an earlier N2a onset for displays that did not require filtering (194 ms, compared to 202 ms for filtering).

Finally, on the P3 (see Fig. 4) a main effect of filtering was observed as well, $F(1, 15) = 11.9, MSE = 1.592, p < .005, \eta^2 = .44$. Trials without filtering elicited higher P3 amplitude ($6.45 \mu\text{V}$) than trials with filtering ($5.36 \mu\text{V}$). There was no main effect of selection ($F < 1.9$), but the interaction term was reliable, $F(1, 15) = 7.17, MSE = .639, p < .05, \eta^2 = .32$. While the P3 was slightly larger for feature-based selection compared to saliency-based selection when no filtering was required ($6.57 \mu\text{V}$ compared to $6.33 \mu\text{V}; t = .97$, not significant), the reverse was true for the trials on which filtering was required; saliency-based selection elicited higher amplitude ($5.77 \mu\text{V}$ compared to $4.95 \mu\text{V}; t = 2.49, p < .05$). Filtering had a stronger effect during feature-based than during saliency-based selection ($1.62 \mu\text{V}$ difference; $t = 3.69, p < .005$, and $.55 \mu\text{V}$ difference; $t = 1.89, p < .08$, respectively).

³ Because targets and distractors were not specifically lateralized, differences between PO7 and PO8 electrodes should be interpreted cautiously. None of the conclusions that are drawn from these data rely on differences between these electrodes.

⁴ Partial analyses excluding the interaction between (saliency-based) selection and filtering showed a very similar pattern. A comparison of feature-based search with filtering with saliency-based search produced a reliable effect of selection, $F(1, 15) = 5.79, MSE = .262, p < .05, \eta^2 = .28$. Electrode was unreliable ($F < 1$), and was expressed in a marginal interaction with selection only, $F(1, 15) = 4.19, MSE = .122, p < .06, \eta^2 = .22$. A comparison of feature-based search with and without filtering did not produce significant main effects of filtering or electrode ($F_s < 1$), but their interaction was reliable, $F(1, 15) = 6.18, MSE = .17, p < .05, \eta^2 = .29$.

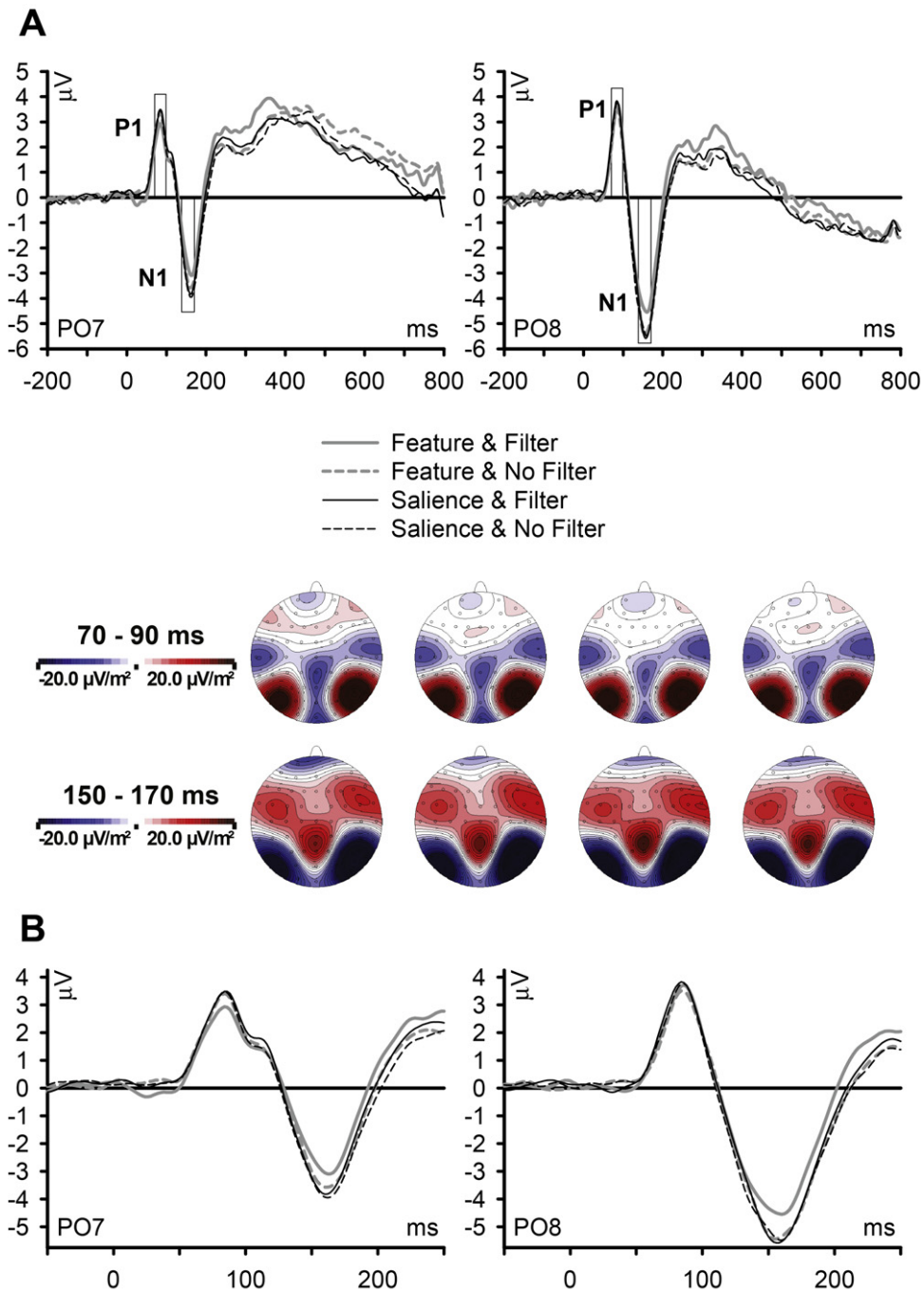


Fig. 3. Mean ERP amplitude (μV) as a function of time in ms. Panel A shows the PO7 and PO8 electrodes. A close-up of the P1 and N1 components on the PO7 and PO8 electrodes is shown in panel B. The onset of the stimulus array is at time zero. Thick lines represent the feature-based selection condition, and thin lines represent the saliency-based selection condition. Solid lines represent filtering trials, and dashed lines represent no-filtering trials. Box outlines delineate analysis windows. Topographical current source density maps are shown for the relevant component peaks. Maps were constructed using spherical spline interpolation and represent a 20 ms average. From left to right the maps represent the FS F, FS NoF, SS F, and SS NoF conditions.

In summary, the present results showed early modulations of the ERP due to selection criteria and distractor filtering, starting at the P1. Remarkably, the effect of selection was strongest at the earliest components (P1 and N1), suggesting that these were primarily modulated by the selection template, with only a secondary effect of the actual complexity of the display, that is, whether it required filtering or not. The P2 component was the only component to show no effect of selection, and it was affected by filtering only. The later components (N2a and P3) were again modulated by selection, but only if the stimulus displays also required filtering.

4. General discussion

The present study provided evidence for feature-based attentional modulation of the earliest components of the ERP in multi-item search. The occipital P1 showed the strongest modulation depending on whether feature- or saliency-based selection was performed, with easier search reflected in increased amplitude, as might have been expected. The data furthermore suggested that the need to filter between different line orientations (in other words, the presence or absence of direct competition between

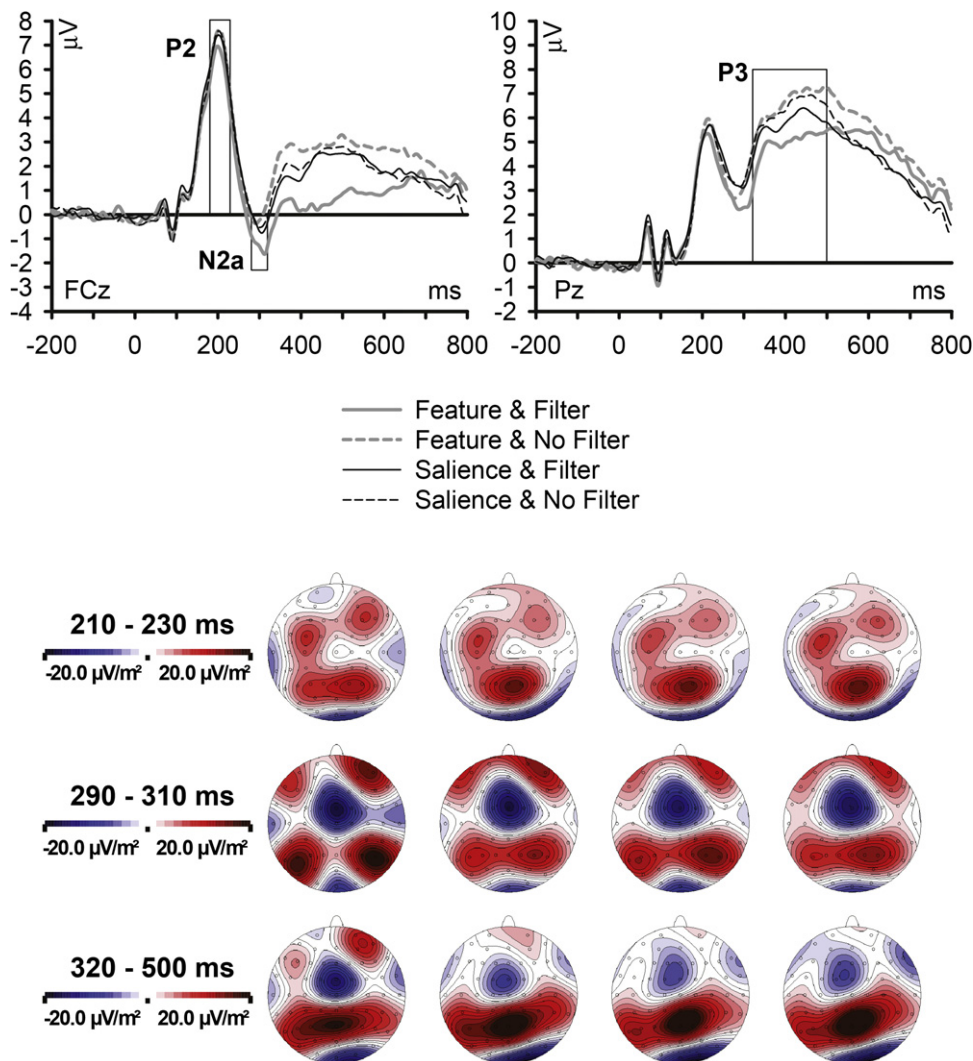


Fig. 4. Mean ERP amplitude (μV) as a function of time in ms. Shown are the FCz electrode (left), and the Pz electrode (right).

stimuli or their locations) only played a secondary role at this stage. Filtering did not reliably affect overall P1 amplitude, and was only expressed in an interaction with selection at the PO7 electrode. The presently observed effect of the selection criterion on the P1 was a noteworthy result, as it expands previous reports of P1 effects of feature-based attention in uncued visual search tasks, which were obtained only when there was direct competition; when the selection of one kind of target stimulus also entailed the filtering of simultaneously presented distractor stimuli or features at competing locations (Nobre et al., 2006; Valdes-Sosa et al., 1998; Zhang and Luck, 2009). Our results demonstrated feature-based selection amplitude effects in the P1 time range independent of filtering requirements, in a paradigm with spatial separation, rather than overlap, between (still simultaneously presented) targets and nontargets, which is arguably a less competitive task.

One might argue that in the comparison between feature-based and saliency-based selection in the present paradigm, the design might still have required some limited degree of filtering in all cases, because the search arrays always contained (neutral) vertical distractor lines. However, this kind of ‘residual’ filtering should be largely effortless. First, unlike the tilted lines, the distractors were never task-relevant, so in this sense targets and distractors were dissimilar, and they were furthermore evenly distributed across the visual field, without interfering with the locations of targets and nontargets. Second, these identical vertical lines essentially

formed little more than a homogeneous background that could be rejected as one (Duncan and Humphreys, 1989; Schubö et al., 2007).

In any case, the conclusion seems warranted that (spatial) filtering, considered to be necessary in order to deal with direct competition between targets and nontargets, does not seem to be required for early effects of feature-based attention. In the present simultaneous, multi-item search paradigm, the P1 effect of selection supported the idea that participants were able to select targets based on a specific target feature without the need to spatially filter targets from nontargets first. Thus, the present results support, but also extend, previously observed early attentional modulation of the P1 component in the context of visual search.

These results are also in line with findings from other paradigms that have shown that the P1 component can be modulated by feature- or dimension-based attentional selection. For instance, in tasks in which a single stimulus is shown at a time, or in which a single stimulus pops out from a search array, P1 amplitude and latency can be modulated by non-spatial features, such as color (Taylor, 2002). Another demonstration of such early effects in the context of a cued search task was given by Gramann et al. (2010), who showed that the amplitude of the P1 increased for a target stimulus that was preceded by a cue at the same location when the cue also matched the feature dimension of the target, although matching the exact feature did not seem to further modulate amplitude.

The occipital N1 component continued to show modulation depending on whether feature- or salience-based selection was needed. As might have been expected from previous reports of modulation in the N1 range by feature-based attention when direct competition was present (Hillyard and Münte, 1984; Anllo-Vento and Hillyard, 1996), the filtering requirements played a more prominent part here, although there was also still a main effect of selection. Similar to the effect observed on the P1, the requirement to perform feature-based selection reduced mean amplitude. Additionally, the requirement to perform spatial filtering now reduced amplitude as well. These suppressive effects on the N1 may reflect a more cautious mode of processing, which instantiates feature-based selection. In this mode, early responses to salient stimuli (i.e., *anything* tilted) might be suppressed in comparison to the salience-based selection mode. Since featural selection is most critical when competing nontargets have to be filtered out, the interaction between selection and filtering was to be expected. This may be interpreted as an instance of early endogenous control of attention, which takes into account not only the selection criteria, but also the configuration of the search array.

The P2 was exclusively sensitive to the filtering requirement. Previous studies have associated increased P2 amplitude with location-based attention (Anllo-Vento and Hillyard, 1996). In the present study, increased amplitude was found when no spatial filtering was required. The P2 effect may thus be interpreted as a facilitation of attentional deployment toward target locations in this condition. It may also be worthwhile to consider potential effects in this time range as an early associate of the selection negativity (Hillyard and Münte, 1984). The selection negativity has been found to increase for attended-location features; which would have decreased the P2 in the present study. However, since selection had no reliable effect on the P2, it seems hard to provide an explanation in terms of selection negativity here. Instead, the present data at least suggested that the P2 is closely linked to the filtering aspect of attention. The fact that the P2 seemed unresponsive to the selection aspect of the task, unlike all the other components reported, is notable but remains hard to account for. Clearly more research into this component is needed to determine its functional significance.

Starting at the central-frontal N2a, the filtering requirement took priority over the selection criterion as a primary determinant of component amplitude. The direction of the effect was furthermore opposite to that observed at the N1; higher N2a amplitude was associated with the need to filter. The interaction with selection similarly showed an increased negativity with feature-based selection, rather than with salience-based selection. The interaction may be related to a similar effect reported by Gramann et al. (2007), who found an increased N2a when selection changed from trial to trial. A possible alternative interpretation of these effects, previously coined by Gramann et al. (2007), is that they are the result of deviance or template mismatch detection. In this framework, increased negativity observed for feature-based selection, compared to salience-based selection, might be attributed to increasing deviance between the specific feature-based target template and the nontargets. Such deviance would not be expected when salience-based (dimensional) selection was required. Similar effects would be expected for the presence or absence of the need to perform spatial filtering. The deviance detection account is largely compatible with the present findings, but may offer a less specific account of the differences observed for the presently used variables of selection and filtering, respectively, because it considers both interactively.

It may also be noted that Gramann et al. (2007) did not present search arrays that required spatial filtering – which seemed a necessary condition for the N2a modulation in the present study, although the direct comparison of the associated means was only marginally significant. The presently observed N2a effects seemed

to mirror task difficulty, as both increased competition (filtering) and feature-specific selection criteria increased amplitude (even though the former effect was larger). The behavioral results similarly showed increased RT and decreased accuracy for filtering compared to no-filtering trials, and to a lesser degree also for feature-based selection compared to salience-based selection. The longest RT and lowest accuracy was associated with the combination of filtering and feature-based selection.

These effects were carried over into the parietal P3 time range, that is, the absolute voltage differences were preserved, rather than component amplitude. Thus, feature-based selection with filtering resulted in the smallest P3 (i.e., amplitude remained most negative). The time windows examined, the observed deflections of the ERP, as well as the CSD plots, did however indicate clearly identifiable N2a and P3 components. At the same time, the modulations of selection and filtering affected these components uniformly. The P3 modulation might thus reflect the ease of the task, with increased amplitude associated with the easier trials. Similar to the effects of the N2a (but in the opposite direction), the modulations were compatible with the behavioral outcome. This view is supported by the idea that the P3 is related to the consequences (or monitoring) of a decision to make a particular response (Verleger et al., 2005; see also Polich, 2007). One caveat with a pure task difficulty interpretation might be that the response set was bigger in the salience-based selection condition (0–4 vs. 2–4) as a side-effect of balancing the total number of target and nontarget stimuli in the search arrays between conditions. It is thus conceivable that differences in response selection might have contributed to the effect on the P3 component. However, comparison of the ERP for equal target numbers (see Appendix) did not suggest such a contribution for the time-window presently examined. Furthermore, although the N2 is less likely to be influenced by response-related factors, the observed effects were congruent between both N2 and P3, supporting the idea that task difficulty played an important role.

The present results may also be related to the fMRI results previously obtained by Akyürek et al. (2010b), who used a virtually identical design. Due caution is warranted with this comparison, of course, because it involves different groups of participants, and because EEG and fMRI measures may not represent the same processes in the brain. Nonetheless, the information gained from both studies can provide a basis for founded speculation, which may direct future research. Two aspects stand out in particular. First, in the fMRI study, the selection criterion modulated the involvement of frontal brain regions, while filtering did so for parietal and occipital regions. In the present study, selection primarily modulated the P1 and N1 components, and was eventually expressed in an interaction with filtering at the N2a and P3 components. This prompts the question of whether and how the early ERP effects might in some way be connected to frontal brain regions. One possibility may be that this connection is realized indirectly through a configuration signal from frontal regions to the extrastriate cortex, from which the P1 and N1 components originate (Hillyard and Anllo-Vento, 1998). Second, the involvement of the parietal and occipital regions seems generally compatible with attentional effects at the N2 range and beyond, without necessarily excluding the possibility that earlier components such as the N1 might also be associated with these brain areas. In sum, it seems clear that the functional patterns revealed by these EEG and fMRI results raise some interesting issues that deserve further investigation.

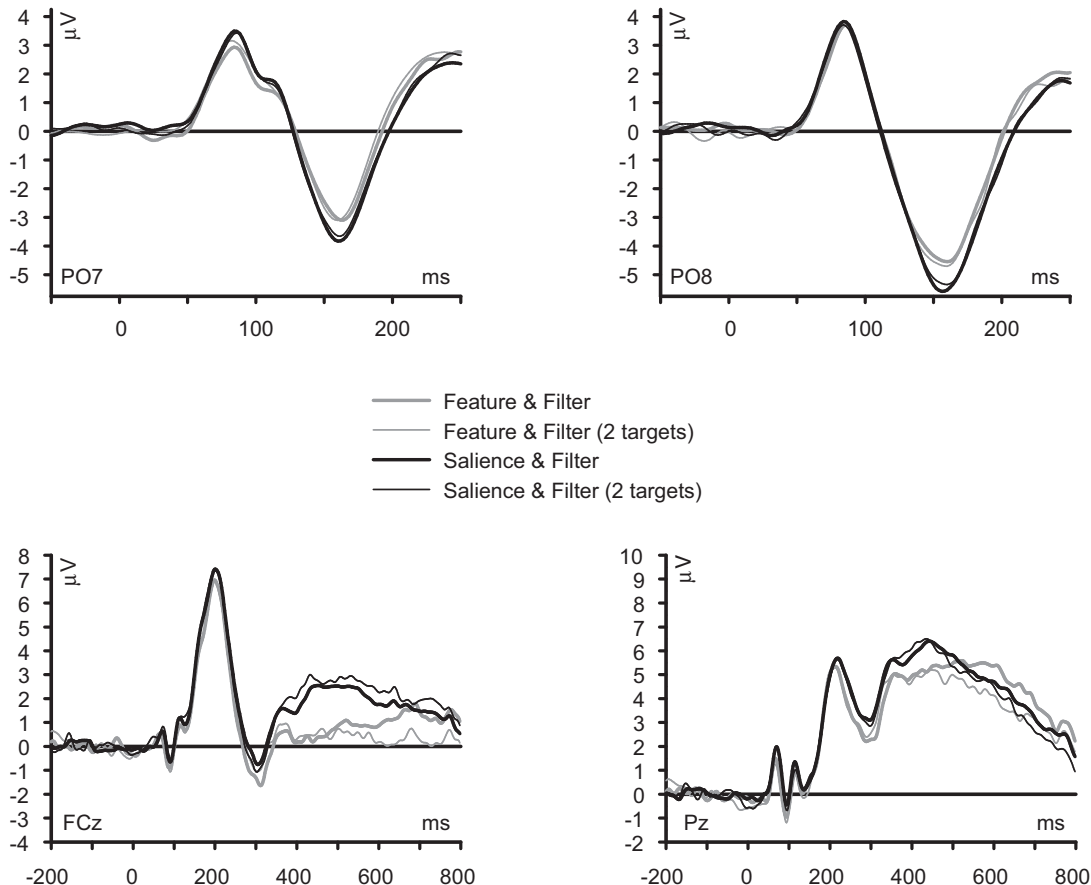
4.1. Conclusion

The results demonstrate that attentional selection and filtering functions can be dissociated in the ERP of a multi-item search task. Feature-based selection was found to modulate early ERP components, starting at the P1, even when only minimal filtering

was required (i.e., rejecting an irrelevant homogeneous background). This suggests that the specification of a search template shapes the earliest stages of perception, and is to a degree independent from the properties of the visual environment in which the search is performed.

Appendix.

Comparison of ERP amplitude in μV between selection conditions, for equal numbers of target elements in the search array. Shown are the PO7, PO8, FCz, and Pz electrodes.



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