

Research Report

The neural processing fate of singleton target and nontarget stimuli

Elkan G. Akyürek*, Angela Dinkelbach, Anna Schubö

Ludwig Maximilian University, Munich, Germany

ARTICLE INFO

Article history: Accepted 2 October 2009 Available online 13 October 2009

Keywords: Event-related potentials (non-)target processing Visual search Distraction P2 N2pc P3

ABSTRACT

The neural processing fate of target and nontarget singleton stimuli was investigated in a series of visual search tasks. The first experiment showed that the ERPs elicited by nontargets defined in the same feature dimension as targets were identical to those of targets until a relatively late divergence in the P3 time range. The second experiment showed that increased stimulus duration allowed slightly faster attentional selection: The ERPs of targets and nontargets now diverged earlier at the N2pc component, although nontargets still elicited a reliable N2pc, which was indicative of the processing of features of these stimuli. It furthermore seemed that task difficulty did not modulate the observed differences between target and nontarget processing. The third experiment investigated the impact of stimulus-response mapping as well as target probability. The former did not modulate the observed differences, and while the latter modulated absolute ERP amplitude, it again did not change the overall pattern of results. No evidence was found in these experiments for differential processing of targets and nontargets defined in the same feature dimension in the time range of the P2 component or before. In a final experiment, targets were compared with nontargets defined in the same or another feature dimension, and for the latter nontargets a clearly much earlier locus of divergent processing was observed, starting at the P2. The N2pc to these nontargets was also strongly suppressed. The relatively late locus of attentional selection between targets and nontargets defined in the same feature dimension suggested that early attentional processes cannot yet fully distinguish between specific within-dimension features.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

One of the hallmarks of the processing efficiency of the human brain is its ability to quickly cast aside irrelevant information in most situations. Still, failures to do so also happen from time to time; for example when a colorful billboard distracts a driver. As is evident from such occasional failures to maintain focus and thereby to become distracted, there are limits to the process of attentional selection. Since the ability to maintain focused attention is so crucial to virtually all cognitive tasks in life, it has been studied intensively by psychologists. One promising line of research has focused on so-called visual search tasks that require the detection (or identification) of a target stimulus amidst other distracting stimuli (e.g., Wolfe and Horowitz, 2004; for an overview of visual search literature see Wolfe, 1998). It is

^{*} Corresponding author. Department of Psychology, Experimental Psychology, University of Groningen, Grote Kruisstraat 2/1, 9712 TS Groningen, The Netherlands.

E-mail address: e.g.akyurek@rug.nl (E.G. Akyürek).

^{0006-8993/\$ –} see front matter © 2009 Elsevier B.V. All rights reserved. doi:10.1016/j.brainres.2009.10.007

commonly assumed that the primary attentional processes in these relatively simple visual search tasks underlie most forms of attentional selection, and that their properties transfer into more complex scenarios.

An important determinant of attentional deployment is the task that the observer currently seeks to fulfill. It has intuitive appeal to assume that the importance of objects in the visual field is weighed according to their task relevance, and this idea has indeed been confirmed by several studies (Folk et al., 2002; Folk and Remington, 1998; Folk et al., 1992, 1994). Using various versions of a cue-target paradigm, Folk and colleagues have demonstrated that attention can be captured by stimuli that are in principle task-irrelevant, as long as they share taskrelevant properties with a target stimulus, or in other words, feature values that are part of a particular attentional set. Thus, when participants are looking for a target defined by color (e.g., a red square amidst black ones), a distractor that is also defined by the same color will capture attention, but a distractor defined by another feature (e.g., a green square, or a black circle) will not. Task-related attentional control settings are also thought to modulate the response to relatively salient objects in the visual field, possibly overriding stimulus-driven saliency, which suggests that such control can affect early perceptual stages of processing. There is at least one study that has related modulation of the N1, an early event-related potential (ERP) component, to such contingent attentional capture (Arnott et al., 2001). Further ERP evidence consistent with an early locus of attentional control has recently been presented by Eimer and Kiss (2008), who showed that the N2pc component (which can be thought of as a marker of attentional processing of selective features in space) is elicited by cue displays containing task-relevant features only, and not by task-irrelevant ones.

The hypothesized task-dependent nature of attention has been labeled the "contingent attentional capture" theory. This particular view is not entirely unchallenged, as others have claimed that attention is captured by salient stimulus properties regardless of top-down control settings, at least under certain circumstances (Theeuwes, 1991, 1992, 1994; Theeuwes and Burger, 1998). The existence of stimulus-driven attentional capture has intuitive appeal as well, since particularly salient events clearly tend to draw immediate attention (imagine the sudden onset of a wailing siren). Contrary to the previously mentioned studies by Folk and others, Theeuwes and colleagues have shown that attention is (initially) drawn towards an irrelevant but salient distractor stimulus in a dual singleton visual search paradigm, even when the salient distractor does not share any target property. A recent electrophysiological study by Hickey et al. (2006) corroborated this view by showing that lateralized attentional deployment as indexed by the N2pc is affected by the presence of such irrelevant distractors. In their study, an N2pc to a distractor was elicited when presented simultaneously with a target on the vertical midline (which precludes a lateralization of target-related components).

The key to the apparent controversy might be the particular search mode that is induced in the participants of these studies (for an overview of the debate see Ruz and Lupiáñez, 2002). According to a proposal by Bacon and Egeth (1994), participants can either engage in a "singleton search mode," in which any salient stimulus is selected, regardless of its particular properties, or in a "feature search mode," in which only task-relevant features are considered. The requirements of the experimental task determine which mode is likely to be used. Thus, in the experiments by Folk and colleagues, participants were searching for a particular feature, while in those by Theeuwes and colleagues any salient feature fitted that role, explaining the discrepancy of their results. Search mode is thus likely to play an important role in attentional deployment. However, the possibility exists that procedural differences between the cue-target paradigm and the simultaneous singleton visual search paradigm have contributed to the seemingly opposite results.

Without taking a particular side in this debate, the present study sought to investigate the onset of task-specific attentional processing by examining the ERP to task-relevant and task-irrelevant stimuli in specific instances of visual search. Participants were asked to detect the presence of singular target stimuli within visual search arrays consisting of line segments. In the first series of experiments, a singular orientation singleton was shown within the search array, which consisted of uniformly vertical distractor lines. Crucially, whether the singleton was task relevant or not was determined by the direction of its tilt (i.e., 45° rightward or leftward). In this design task relevance thus depended on the feature value (i.e., tilt) within one feature dimension, namely line orientation. This approach was intended to create a straightforward visual search task in which the ERP to both target and nontarget singletons could be measured independently, without the potential confound of simultaneous presentation of both target and nontarget singletons, which may induce increased attentional effort simply because two stimuli are more difficult to process than one (cf., filtering costs; Folk and Remington, 1998). This first series of experiments was thus meant to investigate the degree of processing devoted to singleton nontarget stimuli, when these are defined in the same feature dimension as targets. In a subsequent experiment, the same comparison between target and nontarget stimuli was made, but these were now dissociated by being salient on different feature dimensions. In all experiments, the main empirical question was to what extent attention is drawn to a nontarget singleton, as reflected by the evoked potentials to these stimuli, compared to that of targets.

The study was set up to include both early and late components of the ERP, to characterize potential differences between target and nontarget processing during a comprehensive time interval after stimulus onset. Therefore, the earliest components under consideration were the P1 and N1. These components have been shown to be affected by attentional factors (e.g., Luck et al., 1994) and perceptual difficulty in the context of visual search (Handy and Mangun, 2000). If targets and nontargets were to show differential amplitude, this would suggest that already the earliest attentional processes can dissociate between these stimuli.

Continuing in time, the P2 component was considered next. This component has been associated with visual feature discrimination (O'Donnell et al., 1997), and the detection of particular features in various dimensions (e.g., color, orientation, etc.), and has been shown to increase for singleton target stimuli (Luck and Hillyard, 1994a). In Luck and Hillyard's study, the ERPs elicited by homogeneous arrays of line segments and similar arrays that contained a salient singleton stimulus were compared. Singletons were defined by their orientation (orthogonal to the other line segments in the display), their unique color, or their size (enlarged). Crucial to the experimental task, participants were asked to detect the presence of a given type of singleton stimulus, and to ignore the others. This design allowed the comparison of the ERP to homogeneous displays, displays with a nontarget singleton, and displays with a target singleton, thereby aiming to isolate the relevance-induced target selection process from visual singleton detection in the brain. Apart from the P2 component, the N2(pc) and P3 components were also found to be affected by stimulus relevancy (i.e., the selection of stimuli as targets vs. the rejection of nontargets). The aforementioned components were all much more pronounced for targets than for nontargets. These results supported a model of guided search in which attention is directed to task-relevant stimuli by "preattentive" stimulus information (i.e., spontaneous pop-out detection). In accordance with this view, the authors proposed that the early P2 effect could be related to the detection of salient features on separate feature dimensions, such as color, size and orientation. Thus, the findings of Luck and Hillyard (1994a) provide evidence for a very rapid mechanism of dissociating between relevant and irrelevant stimuli. However, it has to be noted that the salient feature dimensions in their study were always unique between targets and nontargets. Attentional processing has been shown to be affected by feature dimension-specific factors (Müller et al., 1995, 2004, 2003). Thus, if the attentional system was indeed driven or configured by their stimuli being salient on uniquely separated feature dimensions, then the early modulations of the ERP observed by Luck and Hillyard (1994a) may have been an effect specific to search between dimensions (as opposed to withindimension search). As mentioned, the first three experiments of our study focused on a paradigm where the factor of multidimensionality was removed from the comparison between task relevant and irrelevant stimuli. In this case then, if early attentional dissociation between target and nontarget stimuli is only possible across feature dimensions and not within, then the P2 should not be different for target and nontarget stimuli in these experiments, since these were singletons in the same dimension regardless of task instructions. Alternatively, if attention can be guided rapidly towards the target stimulus even if it is salient in the same dimension as a nontarget, then modulation of this component should presently be observed as well. In a final experiment, the betweendimension design was replicated, which should produce results similar to those of Luck and Hillyard.

Further components that were examined in the present study were the N2pc and the parietal N2 (N2p). The N2pc component reflects the processing of stimulus features of objects lateralized in the visual field, while the related N2p is sensitive to task relevance (Eimer, 1996; Luck and Hillyard, 1994a; Woodman and Luck, 1999). A modulation of the N2p component may therefore be expected in the present study, as task instructions varied to designate stimuli as targets and nontargets. The N2pc can be thought of as a measure of the degree of attentional selection of lateralized targets, and to reflect a stage of attentional processing beyond covert orienting and spatial attention unspecific to targets (Kiss et al., 2008b). Recall that the N2pc component has furthermore been used as a measure of attentional capture. In the study by Eimer and Kiss (2008), no N2pc was elicited by nontarget stimuli, depending on the current task set. Hickey et al. (2006) also focused on this component and they did observe an N2pc for nontarget stimuli, suggestive of bottom-up capture of attention. With regard to the predictions of the present study, if attentional deployment as reflected by the N2pc is sensitive to the task relevance of the singleton stimuli, then the N2pc may differ for targets and nontargets. Furthermore, if the N2pc is dimension-specific rather than feature-specific, then an N2pc to nontarget stimuli would only be expected when these lie on the same feature dimension as targets, but not when targets and nontargets lie on different dimensions.

Lastly, the P3 component was considered. This component is related to the processing of task-relevant target stimuli leading up to stimulus categorization and full identification (Kok, 2001), as well as memory encoding (context updating; Donchin and Coles, 1988) and consolidation (Vogel et al., 1998). In particular, the P3 is thought to reflect a memory process in which incoming stimulus identities are compared to representations in memory, and subsequently updated. It has also been linked to conscious access to the stimulus (Sergent et al., 2005), and has been implicated in the deployment of executive control. In dual task studies that have shown P3 modulation of attention, this has generally been taken to reflect effects on "late" processes (Luck et al., 2000). Although the primary function underlying the P3 component seems to be related to working memory operations, it is thought to be driven by attention (especially the P3a) and its amplitude is modulated by the cognitive demands of the task (Polich, 2007). As the P3 can be taken to reflect a final phase of attention-related processing, it was expected that this component should be modulated in the present study whenever target stimuli were successfully discriminated from nontargets.

In summary, the present study reports three experiments that aimed to characterize task-dependent processing of singletons within the same feature dimension of line orientation, and a fourth experiment in which two feature dimensions were compared additionally. In Experiment 1, the ERP to physically identical line orientation singletons was compared depending on whether these stimuli were task-relevant or not. In Experiment 2, the effect of task difficulty and that of stimulus duration on the ERPs to target and nontarget stimuli were studied. In Experiment 3, the effect of stimulus-response mapping and that of target probability on the speed of (non-) target processing was investigated. Finally, a fourth experiment made a direct comparison between targets and nontargets when nontargets where were defined in the target feature dimension, and in cases where they were defined on a different dimension.

2. Results

2.1. Experiment 1

In Experiment 1, participants were asked to search for line orientation singleton targets that were presented in arrays of vertical line elements (Fig. 1). Besides trials in which no singleton stimulus was shown (i.e., "blank" trials with vertical lines only), three possible singleton trials were presented in which a leftward tilted, a rightward tilted, or a horizontal line element was embedded in the context of the array of vertical lines. The participant's task was to count the number of target-present displays in each experimental block (a cumulative counting task). The task relevance of the singleton stimuli was determined by instruction. In the first condition, the rightward tilted singletons were relevant to the task and had to be selected, while in the second condition they were not task-relevant and had to be ignored. This was implemented so that in the first condition (TASK variable, "select-all"), participants had to count all singletons irrespective of their actual orientation, while in the second condition (TASK, "select-some") they had to count horizontal and leftward tilted lines only, and not rightward tilted ones. The comparison of the ERP to rightward tilted singletons in the select-all and select-some conditions thus reflected the difference between task-relevant and task-irrelevant stimuli that were physically identical, in the context of a search within one feature dimension.

Behavioral counting performance was recorded for each participant after each block. Performance in the select-all condition averaged 58.9% correct (i.e., correctly counted blocks), and 59.5% correct in the select-some condition. These did not differ statistically $(F < 1)^1$. In essence, the task appeared to have been suitably challenging, and equally so in each TASK condition. The number of correctly counted blocks was used to bin performance based on a median split between "high" and "low" performance. This was done in order to assess a possible modulation of the ERP due to a different deployment of cognitive processes (and resulting error rates) in these two groups. However, these analyses did not reveal any systematic impact on the observed waveforms. The Appendix figure (A) shows the waveforms derived from only those participants who had the highest report accuracy (between 71% and 100% of blocks correct). If errors would have had an effect on the ERP differences reported below, then it should be significantly attenuated when correct report rate was high. As can be seen from the Appendix figure, this plots virtually the same results as the middle panel (right side) of Fig. 2, indicating that the overall ERPs are a good representation of the experimental task.

For the electrophysiological measures, in the P2 timewindow between 180 and 240 ms, the TASK variable was not significant, and neither was its interaction with STIMU-



Fig. 1 – Illustration of the experimental procedure. After a 50-ms fixation dot, the search array is displayed (100 or 500 ms). A singleton stimulus is shown in an otherwise uniform array of vertical line elements. A masking array is shown for 800 ms, followed by the fixation dot for 1500 ms.

LUS (F's<1). There was a main effect of STIMULUS, however, F(1, 19)=19.53, MSE=0.715, p<0.001. The main effect reflected differences between trials that were not due to task relevance, but rather due to physical appearance. Tukey tests proved that leftward tilted lines (5.43 µV) differed from rightward tilted lines (5.06 µV), q(3, 13)=3.73, t=2.96, p<0.05, and from blank trials (4.26 µV), t=4.97, p<0.001. Blank trials furthermore differed from rightward tilted singleton trials, t=4.06, p<0.001. The top panel of Fig. 2 shows the waveforms recorded at the FCz electrode. Topographical scalp maps are shown in Fig. 3.

In the N2pc time range between 170 and 250 ms, the analysis of lateralized activation showed an effect of LATERALITY, F(1, 13)=28.93, MSE=1.927, p<0.001. The LATERALITY effect demonstrated the existence of the N2pc component to the singleton stimuli, and was thus in line with expectations; attention shifted to the location of the singleton stimulus (of any kind), with a more negative amplitude at contralateral electrode locations as a result (.07 μ V compared to 1.48 μ V for ipsilateral stimuli). No other effect was significant, all F's<2.3, which indicated that the

¹ Note that chance level is practically zero for this task and that the performance indicator is quite strict: If a participant missed a single target array in a block, this would result in the total count being classified as incorrect. At the same time, the possibility existed for one error to be compensated by the other (e.g., miss one array, and count one too many at another point). Therefore, these percentages should be taken as a coarse guide only, not fully indicative on the level of single trials. This method of report was used to prevent response-related confounds from affecting the ERP, at the expense of some behavioral detail.



Fig. 2 – (A) Waveforms recorded at FCz (top) and Pz (bottom) electrodes (μ V) in Experiment 1. The left panels represent the select-all condition, and the right panels the select-some condition. Separate lines represent different display conditions; singleton absent (thin line), left-tilted singleton (thick line), right-tilted singleton (thick dashed line), and horizontal singleton (thick dotted line). Stimulus onset is set at 0 ms. In this and subsequent graphs a slightly stronger lowpass filter was used for visual clarity (30 Hz at 48 dB/oct). (B) N2pc contra-minus ipsilateral difference waveforms ($\Delta\mu$ V) in Experiment 1. Panel and figure conventions are as in panel A.

N2pc was not further modulated by the experimental variables. The bottom panel of Fig. 2 shows the lateralized difference waveforms.

The N2p time window (240–300 ms) showed a significant effect of STIMULUS, F(1, 14)=17.33, MSE=7.664, p<0.001. This effect was clearly due to the blank trials, which averaged

2.00 μ V, compared to 4.01 and 3.94 μ V for left-, and rightward tilted singletons. STIMULUS also interacted with electrode SITE, F(1, 17)=5.22, MSE=0.756, *p*<0.05, but not with TASK. The interaction seemed to highlight the absence of increased negativity in the left hemisphere for blank trials. While mean amplitude for blank trials was similar on both left



Fig. 3 – Topographical maps of the brain activity at the three relevant waveform peaks in Experiment 1, organized in columns. The three columns in the left panel show the maps in the select-all condition, and those in the right panel show the same for the select-some condition. Maps represent a 20-ms average centered at the observed waveform peaks.

and right electrode sites (.13 μ V difference), singleton trials were more negative on left sites (0.61 μ V difference on average).

The P3 time window (320-560 ms) showed markedly different effects. Although there was no main effect of TASK (F<1), there was one of STIMULUS, F(1, 14) = 48.57, MSE=9.267, *p*<0.001. Blank trials had strongly diminished P3 amplitude (5.39 µV). Leftward tilted lines furthermore had higher amplitude (10.84 μ V) than rightward tilted ones (10.19 μ V). Importantly, the critical interaction of STIMULUS with TASK was significant, F(2, 26) = 3.70, MSE = 0.761, p < 0.05. The interaction was due to the rightward tilted lines, which elicited lower amplitude in the select-some condition. P3 amplitude was reduced (9.73 μ V) when the singleton stimulus was not relevant for the task (i.e., for a rightward tilted line when instructions were to select only leftward tilted and horizontal lines), compared to when it was relevant (10.85 µV). The middle panel of Fig. 2 shows the waveforms recorded at Pz.

In summary, the P3 component was the first component to differentiate between targets and nontargets. Only during the P3 time window did the ERPs differ, as mean amplitude was reduced for stimuli that were not to be selected. One possible interpretation is that all singletons were processed in a similar way up to processes where consolidation of the relevant targets became necessary: while selection and classification of the stimuli into target and non-target categories may have been the same, only for those singletons that had to be counted according to the task instructions was an enhanced P3 component observed. These P3 differences between task-relevant and task-irrelevant stimuli cannot be attributed to differences in perceptual processing, as the physical appearance of the stimuli was the same (both rightward tilted), and must thus reflect task relevance alone. An early selection of targets and rejection of nontargets (as observed by Luck and Hillyard, 1994a) was not apparent in the present experiment. The present results thus indicated that task relevance was extracted only fairly late in the chain of

processing and suggested that target detection across feature dimensions may be a necessary requirement for attentional modulation of the P2 and N2(pc) components. In other words, it might be the case that the P2 and N2(pc) components are sensitive only to singleton detection between feature dimensions. Since there was no way to select between targets and nontargets on the basis of different dimensional features (e.g., color vs. size singleton) in the present design, this might have caused the lack of a modulation of the P2 and N2(pc) components. Converging evidence for a relatively late locus of selection with stimuli varying within the same feature dimension was recently obtained by Schubö and Müller (2009), who compared singleton processing within and across feature dimensions. Their results showed modulation of the ERP to singleton stimuli in the P3 range when they varied within the same dimension. Only when the stimuli were varied between dimensions were earlier modulations (in the N2 range) observed.

2.2. Experiment 2

Experiment 1 showed ERP differences in the P3 time range for physically identical stimuli dependent on their task-relevance. Experiment 2 was conducted to test whether the relatively late modulation of the ERP that was observed in Experiment 1 could be modulated by the factors of task difficulty and presentation duration. Regarding the first, the more specific nature of the target template in the select-some condition in Experiment 1 might be taken to increase task difficulty. In the select-all condition, any salient stimulus could be selected initially (although identity still had to be established to be able to add either 1 or 2 to the tally). In the select-some condition, the salient nontarget singletons had to be rejected in addition to the selection of the targets. A potential increase in task difficulty may have an effect similar to holding more items in working memory or to doing arithmetic during the task, by loading attentional control processes. It is possible that attentional deployment is impaired when cognitive control functions are taxed. In the temporal attention literature, the attentional blink task is one example of a situation in which a relatively late process associated with a target stimulus (i.e., consolidation in memory) stalls the initial attentional processing of a second target (Dell'Acqua et al., 2006; Jolicœur et al., 2006). To investigate the impact of increased demands on cognitive control, the task requirements in Experiment 2 were changed. The task for the target stimuli was varied between two conditions. In one condition participants were asked to add three to their internal count whenever they saw a target stimulus (difficult condition), and in the other this number was one as before (easy condition). If these two counting conditions modulate the pattern observed in Experiment 1, then task difficulty can be considered to contribute to relatively late target selection.

The second factor of presentation duration was approached by a more or less direct test. In Experiment 2 the presentation duration was increased to 500 ms. The prediction was that if the late divergence of the ERP between targets and nontargets in Experiment 1 was (partially) caused by a lack of visual encoding time, then this should change in Experiment 2, in which ample time to perceive the search displays was available. Behavioral performance in the "add three" condition averaged 66.3% correct, and 75.0% in the "add one" condition, which suggested increased difficulty in the former. However, this was only marginally significant, F(1, 15) = 3.85, MSE = 0.016, p < 0.07. Physiologically, activation in the early time window (180–240 ms) was unaffected by the experimental variables, all F's < 2. Fig. 4 shows the waveforms recorded at FCz (top panel). Note that the activation beyond 600 ms post-stimulus reflects the onset of the mask. Topographical maps are shown in Fig. 5 (top panel).

In contrast to the earliest time window, differences did become apparent in the N2pc range. There was a main effect of STIMULUS, F(1, 15)=19.31, MSE=0.124, p<0.001. Amplitude for leftward tilted lines was more negative than for rightward tilted ones (5.13 and 5.41 μ V, respectively). Note that because stimuli were directly mapped to task categories in this experiment (i.e., leftward lines were targets, and rightward lines nontargets), the STIMULUS variable now contained the factor of task relevance. The main effect may have reflected that the leftward titled stimuli were categorized as relevant targets at this stage already. As expected, LATERALITY also had an effect, F(1, 15)=22.74, MSE=1.176, p<0.001. Contralateral electrode sites showed more negative amplitude (4.81 μ V) compared to ipsilateral ones (5.73 μ V). Importantly, both main effects also interacted, F(1, 15) = 5.29, MSE = 0.085, p < 0.05. The interaction pointed to increased negative amplitude on contralateral electrode sites when a target singleton was shown (1.03 µV difference), which was less pronounced for rightward tilted nontarget singletons (0.80 μ V). No other effects were significant, all F's<1. Closer examination of the involved means with post-hoc Tukey tests showed that the N2pc was significant for both targets, q(4, 15)=4.15, t=4.80, p<0.001, as well as for nontargets, t=4.41, p<0.001. Furthermore, the N2pc's of targets compared to that of nontargets differed significantly; t=3.96, p<0.001. The bottom panel of Fig. 4 shows the difference waveforms.

In the N2p time window (240–300 ms), STIMULUS interacted with SITE, F(1, 15)=8.43, MSE=0.160, p<0.05. This seemed to point to a stronger N2 at left electrode sites (PO3, PO7) for leftward tilted singletons (7.66 μ V) than for rightward tilted ones (8.01 μ V). Tukey tests could not quite confirm this trend, t=2.38, p<0.05. It was somewhat unclear why this trend was only visible in the left hemisphere and not in the right. No other effects were significant in this time window (F's<2.2).

Finally, in the P3 time range (320–560 ms), STIMULUS had a main effect, F(1, 15) = 19.78, MSE = 1.223, p < 0.001. Leftward tilted targets showed larger P3 amplitude (7.45 μ V) than rightward tilted lines (6.36 μ V), which replicated the pattern observed in Experiment 1. Interestingly, neither the main effect of TASK, nor its interaction with STIMULUS was anywhere near significant, F's < 1. The task instructions apparently did not affect the neural processes involved, despite the trend towards increased difficulty in the "Add three", as indicated by the number of blocks that participants counted correctly. Fig. 4 (middle panel) shows the waveforms recorded at Pz.

The results from Experiment 2 revealed two main points. The first point was that ERP components earlier than the P3 were now affected by the experimental task (namely the N2pc and the N2p), showing that the increased presentation



Fig. 4 – (A) Waveforms recorded at FCz (top) and Pz (bottom) electrodes (μ V) in Experiment 2. The left panels represent the Add One condition, and the right panels the Add Three condition. Separate lines represent different display conditions; left-tilted singleton (thick line), and right-tilted singleton (thick dashed line). (B) N2pc contra-minus ipsilateral difference waveforms ($\Delta\mu$ V) in Experiment 2.

duration allowed for earlier attentional dissociation between target and nontarget stimuli. It is important to note here that the modulation of the earlier ERP components did not reflect an absence of those for nontargets. In fact, a reliable N2pc to nontargets was again observed, even though it was attenuated compared to the N2pc for targets. The second main point was that task difficulty clearly did not change the ERP effects observed on the N2pc and P3. The P3 between taskrelevant and task-irrelevant stimuli was modulated similar to Experiment 1 (with physically different stimuli). Since the error rates did not strongly show that the difficult counting condition was indeed more challenging than the easy one, some caution with interpreting this null effect is in order. Still, the hypothesized difference in difficulty between counting one and counting three was supported by a marginal effect on behavior, and subjective reports indicated that the participants felt that the difficult condition was more taxing.



Fig. 5 – Topographical maps of the brain activity at the three relevant waveform peaks in Experiments 2, 3, and 4. In the top panel, the three columns on the left show the maps in the Add One condition, and those on the right show the Add Three condition. In the bottom panel, the three columns on the left show the maps of Experiment 3, and those on the right the ones of Experiment 4.

2.3. Experiment 3

Experiment 3 was designed to investigate whether the relatively late effects on the ERP in Experiment 1, and to a lesser extent Experiment 2 (i.e., no modulation of N1, P1, P2, and a significant N2pc to nontargets), might have been due to a strategic decision by the participants to attend to and identify each stimulus fully before deciding which action to undertake (cf., Bacon and Egeth, 1994). Such a strategy might be modulated by the complexity of the stimulus-response mappings. The data so far are compatible with this idea. In Experiment 1 four stimulus types (leftward tilted, rightward tilted, and horizontal singletons, and uniform displays) were mapped onto three actions (count 1, count 2, and do not count). In Experiment 2 three stimulus types were mapped onto three actions (count 1 or 3, count 2, and do not count). Therefore we simplified the design in Experiment 3 by using only leftward and rightward tilted singletons and uniform displays, which was meant to further discourage the strategy of fully identifying each singleton stimulus. Making the search task more straightforward reduced the appeal of employing a select-then-identify approach, as targets and nontargets could be more easily dissociated from each other at an early stage. In other words, feature search mode was made more feasible.

Related to the previous point, Experiment 3 also probed the effect of target probability. Similar to the response mappings, the data support the idea that a reduced target probability might lead to earlier selection, possibly by making the target event more salient. Target probability can be expressed as the ratio of target trials to all trials, as well as to singleton trials only (i.e., excluding blank trials). Since Experiment 2 had no blank trials, the latter metric is the fairest and is thus used here. A target appeared in 2/3rd of the singleton trials in Experiment 1 (in the select-some condition), and in Experiment 2, 3/5th of the singleton trials were target trials. There is evidence that target probability matters for early components such as the P2; Luck and Hillyard (1994a) did not observe a P2 difference between homogenous and singleton displays when singleton probability was high, but they did when it was low. Similarly, the P3 has been shown to be modulated by stimulus probability (e.g., Verleger and Berg, 1991). Behavioral data from a slightly different paradigm furthermore indicate that (simultaneous) distractor probability interacts with top-down control settings (Müller et al., 2009). One more consideration one might have related to target probability is the probability of a (i.e. any type of) singleton. However, Horstmann and Ansorge (2006) studied the effect of nontarget singleton frequency, and found no evidence for any influence on spatial attention. Taking these considerations together, in order to address both the probability factor as well as the likelihood of employing feature search mode, we designed Experiment 3 to not only have a simplified stimulus-response mapping, but also to have a lower target probability. In Experiment 3, only half of all singleton trials were target trials, so that a bias towards target-presence was avoided.

Finally, Experiment 3 also counterbalanced target identity between participants to control for the possibility that some differences in the ERP might be due to the physical appearance of the stimuli. Half of the participants were asked to look for leftward tilted lines, and the others looked for the rightward tilted ones. Whenever a target stimulus was detected, participants added one to their internal count.

Behavioral performance averaged 89.1% correct, which suggested that the simplification of the design led to decreased difficulty. Physiologically, activation in the early time window (180–240 ms) was once more unaffected by the task, F < 1. Fig. 6 (top left panel) shows the waveforms recorded at FCz. The topographical maps are shown in Fig. 5 (bottom left panel).

In the N2pc window, the first effect of STIMULUS emerged, as evidenced by a significant interaction between STIMULUS and LATERALITY, *F*(1, 15)=5.23, *MSE*=0.076, *p*<0.05. Note that the STIMULUS variable in essence reflected the factor of task relevance, which was now decoupled from the stimulus identity due to the use of counterbalancing. The main effect of LATERALITY was also significant, F(1, 15)=8.04, MSE= 1.837, p<0.05, but the main effect of STIMULUS was not, F<1.9. The N2pc was larger for target singletons (1.12 μ V difference) than for nontarget singletons (0.80 μ V), indicating that attention was drawn more towards lateralized targets than towards nontargets. Both targets and nontargets evoked reliable N2pc's, t=3.23, *p*<0.01, and t=2.33, *p*<0.05, although the latter effect did not quite survive the Tukey criterion (i.e., q(4, 15) = 4.08). Fig. 6 (bottom left panel) shows the difference waveforms.

In the N2p time window (240–300 ms), STIMULUS had a reliable effect, F(1, 16) = 27.07, MSE = 17.698, p < 0.001. Similar to the results of Experiment 1, a stronger N2 was observed for blank trials (3.61 μ V) than for singleton trials (8.36 and 8.54 μ V, for targets and nontargets, respectively). Neither electrode SITE (F<3.1), nor STIMULUS (F<1) had an overall effect on its own.

Finally, in the P3 time window, STIMULUS had a pronounced effect, F(1, 20)=66.54, MSE=2.887, p<0.001. A target stimulus resulted in higher amplitude (12.02 μ V) than a nontarget stimulus (9.86 μ V), and blank trials showed the lowest amplitude (6.39 μ V). Fig. 6 (middle left panel) shows the waveforms recorded at the Pz electrode. Tukey tests showed that targets differed from nontargets, q(3, 15)=3.67, t=7.44, p<0.001, and from blank trials, t=9.20, p<0.001, and nontargets differed from blank trials as well, t=6.70, p<0.001.

The results of Experiment 3 mostly replicated the moderately early effects observed in Experiment 2, with modulations of the ERP due to task relevance emerging at the N2pc component, as well as affecting the N2p and P3 components. Given this similarity, it can be concluded that the simplification of the stimulus-response mapping did not cause a clear shift in the affected components, suggesting that the particular feasibility of search modes did not affect the ERPs. This result supports the view that participants attended to both targets and nontargets to a large degree, even if the task was simple enough to at least encourage feature search mode. The probability of a target stimulus also did not strongly impact the time at which the ERP diverged between targets and nontargets. This was the case despite the obvious change in overall ERP amplitude due to the reduction of target probability, especially in the P3 range.



Fig. 6 – (A) Waveforms recorded at FCz (top) and Pz (bottom) electrodes (µV) in Experiment 3 are shown on the left. Separate lines represent different display conditions; target singleton (thick line), nontarget singleton (thick dashed line), and blank displays (thin line). Waveforms on the right represent the same for Experiment 4. Thin lines represent color nontargets, thin dashed lines represent blank trials, and thick dashed lines represent orientation nontargets. (B) N2pc contra-minus ipsilateral difference waveforms (△µV) in Experiment 3 on the left, and the same in Experiment 4 on the right.

2.4. Experiment 4

Experiment 4 was designed to make a direct comparison between targets and nontargets when they were defined on the same feature dimension (i.e., both orientation), and when they were not (i.e., orientation and color). To this end, color singleton nontarget trials were added to the paradigm. Performance in visual attention tasks has been shown to depend critically on the dimensionality of the stimuli (Müller et al., 1995, 2004, 2003). To capture this aspect of visual attention, Müller and colleagues have proposed a cognitive model called the dimensional weighting account (DWA), which holds that feature dimensions can receive attentional weights that affect the way in which attention is deployed. Behavioral and electrophysiological evidence suggests that the weighting mechanism has a rather early locus in the perceptual system (Gramann et al., 2007; Töllner et al., 2008). Because these weights specifically operate between different feature dimensions, and do not affect feature values within a particular dimension, it was expected that introducing a "dimensional" distinction in the present paradigm would allow earlier detection of the difference between targets and nontargets.

Behavioral performance averaged 77.8% correct. In contrast to the results from all previous experiments, P2 amplitude (180–240 ms) was reliably modulated by task relevance; STIMULUS had a significant effect, F(3, 36)=3.15, MSE=1.415, p<0.05. Orientation target singletons (4.41 µV) and orientation nontargets (4.52 µV) showed more positive amplitude than color nontargets (3.25 µV) and blank trials (3.83 µV). Fig. 6 (top right panel) shows the waveforms recorded at FCz. The topographical maps are shown in Fig. 5 (bottom right panel).

Further early differences were apparent in the N2pc range. There was a main effect of LATERALITY, F(1, 12) = 56.08, MSE=1.137, p<0.001, and although the main effect of STIMU-LUS was unreliable (F < 1), the interaction term was also highly significant, F(1, 14)=33.09, MSE=0.361, p<0.001. Overall, there was a pronounced N2pc towards singletons (3.85 µV compared to 5.66 µV). The N2pc was strongly suppressed for color nontargets, however (0.60 μ V compared to 2.47 μ V for targets and 2.35 µV for orientation nontargets). Post-hoc Tukey tests showed that even so, the color nontargets still elicited a reliable N2pc, q(6, 12)=4.75, t=3.67, p<0.005, as did the targets, t=7.76, p<0.001, and the orientation nontargets, t=7.01, p < 0.001. Directly comparing within and between-dimension conditions showed that N2pc amplitude between color and orientation nontargets was significantly different, t=5.52, p<..001, and this was also true for (orientation) targets and color nontargets, t=6.38, p<0.001. Fig. 6 (bottom right panel) shows the difference waveforms.

The analysis of the N2p continued to show a significant effect of STIMULUS, F(1, 16)=27.81, MSE=17.103, p<0.001. Targets and orientation nontargets averaged 7.95 and 8.36 μ V, compared to 3.74 and 2.89 μ V for color nontargets and blank trials. Targets and color nontargets were reliably different, q(4, 12)=4.20, t=5.45, p<0.001, as well as targets and blank trials, t=5.78, p<0.001, orientation nontargets and blanks, t=5.54, p<0.001, and finally color nontargets and orientation nontargets, t=5.03, p<0.001.

The STIMULUS variable similarly affected the P3, F(1, 16) = 30.10, MSE=11.431, p < 0.001. Post-hoc tests confirmed that targets (11.91 µV) differed from orientation nontargets (9.20 µV), q(4, 12) = 4.20, t = 6.95, p < 0.001, and from color nontargets (5.41 µV), t = 6.08, p < 0.001, as well as from blank trials (4.66 µV), t = 6.99, p < 0.001. Blanks differed from orientation nontargets, t = 4.50, p < 0.001, and color nontargets differed from orientation nontargets, t = 3.72, p < 0.005. Fig. 6 (middle right panel) shows the waveforms recorded at Pz.

Experiment 4 clearly showed that the ERP to targets and nontargets diverges at an earlier stage when these are defined in different feature dimensions. The modulation of P2 and N2pc components closely replicated the study by Luck and Hillyard (1994a) in the context of the present experimental paradigm. By extension, it demonstrated the validity of the present paradigm in its ability to reveal early processing differences in the ERP.

3. Discussion

The present experiments set out to study the ERP components elicited by task relevant and task irrelevant singleton stimuli during visual search. In Experiment 1, the ERPs of relevant and irrelevant stimuli diverged relatively late. The P3 was the only component that was affected by the task relevance of the singletons. This finding suggested that all stimuli were processed in an identical fashion up to the time window of that component, and only separated according to actual task relevance then. The presence of an N2pc for nontargets, equal in size to the one for targets, further confirmed that the former were indeed attended to, before being classified as nontargets. Earlier categorization of targets and nontargets was nonetheless observed in Experiment 2 when stimulus duration was increased. The N2pc component was modulated by task relevance in this experiment, indicating that attentional processing of relevant and irrelevant stimuli began to separate at an earlier point in time. Even so, there was still a clear N2pc to nontargets, which was only slightly attenuated compared to the N2pc elicited by targets. The results of Experiment 3 established that the relatively late modulations of the ERP by task relevance are not likely to be accounted for by a strategy of identifying each stimulus fully before deciding what to do with it: When this was discouraged by simplifying the task design, the results remained comparable. It has to be noted that although feature search mode was purposefully encouraged in Experiment 3, it remained theoretically possible to employ singleton search mode even then. Therefore, a caveat here is that the possibility cannot be totally excluded that singleton search mode at least partially contributed to the relatively late locus of the present effects. Experiment 3 furthermore showed that the observed pattern of modulation remained intact with a reduced target probability. In other words, a target being more infrequent (50% of singleton trials, or 33% of all trials) did not increase the speed of the targetspecific selection process. The pattern of relatively late modulation by task relevance that persisted in Experiments 1-3 was replicated in the within-dimension condition of Experiment 4. By contrast, in the between-dimension condition of that experiment, task relevance modulated the ERP at a clearly earlier point in time. The P2 was the first component to show divergent processing, and the N2pc for nontargets defined in another feature dimension was strongly suppressed. The N2p and P3 components were modulated as well. The qualitative differences that existed between and within feature dimensions were also apparent in the measure of global field power, which is plotted in Appendix (B).

Overall ERP amplitude varied between experiments, most likely as a side-effect of variation in task difficulty and target/ singleton probability. Since all statistical comparisons were confined to single experiments, amplitude changes between experiments did not influence these. It may furthermore be worth mentioning that the design of the present experiments ruled out some trivial accounts of the data. By not requiring any overt responses (until verbal report at the end of a block) in these experiments, response selection biases cannot have blurred the effects. Similarly, task strategies involving exclusive search for singletons on unique dimensions were not feasible, since stimulus parameters, whether relevant or not, were always (also) varied within the same dimension of line orientation. Finally, behavioral errors are unlikely to underlie the observed differences between targets and nontargets. In Experiment 1, error rates were statistically equal between these task conditions and high-performing participants did not show any deviant waveforms in either condition (see also the figure in the Appendix). In Experiment 2, while some difference was (purposefully) observed between difficulty conditions, none was visible in the ERP. Finally, in Experiments 3 and 4 the error rates were relatively low, while the ERP was in line with the previous results.

3.1. Factors affecting attentional selection

The present results provide some evidence for a middle ground in the context of the debate on attentional capture (Folk et al., 2002; Folk and Remington, 1998; Folk et al., 1992, 1994; Theeuwes, 1991, 1992, 1994; Theeuwes and Burger, 1998). On the one hand, there was support for the idea that attention was captured in a stimulus-driven manner by salient singletons, regardless of their task relevance. This was particularly pronounced in Experiment 1, where targets and nontargets elicited identical ERPs up to the P3. On the other hand, there was also evidence for a modulation of early attentional components by task relevance. This was shown in Experiments 2 and 3, in which the N2pc was modulated by task relevance, and particularly in Experiment 4, where the between-dimension condition allowed for rapid attentional selection. It was thus clear that neither only task-contingent capture, nor only stimulus driven capture was observed, but that the configuration of the stimulus displays was crucial. This finding is in line with those from a compound search task studied by Kiss et al. (2008a), who found an N2pc to targets, a slightly attenuated N2pc to nontargets in a task-relevant feature dimension, and (virtually) no N2pc to nontargets in a task-irrelevant dimension. The present results confirm these findings and expand them to relatively simple detection tasks. The evidence thus suggests that the N2pc marks the degree of attentional capture, and discredits the idea that the N2pc might also reflect the degree of attentional processing "further downstream."

It indeed seems likely that the specific configuration of the experimental task and the visual arrangement of the stimuli determine how attention is allocated. Hickey et al. (2006) observed an N2pc to nontargets in a visual search task that featured the simultaneous presentation of both target and nontarget stimuli. It has been argued that such a display incurs "filtering costs" that can be dissociated from attentional capture (Folk and Remington, 1998). Although the N2pc is a relatively early component, the locus of this effect does not strongly reject this possibility. In the present paradigm, there was no simultaneous presentation, yet an N2pc to nontargets did emerge. This provided convincing evidence that attention was indeed capture was however modulated by task relevance, in

line with the results of Eimer and Kiss (2008). However, these authors, similar to a study by Luck and Hillyard (1994b), found no evidence for any N2pc for nontargets (irrelevant cues) at all. Both studies used feature cues from different dimensions (e.g., color versus onset) in cases where early differences were observed. The present results replicated that finding, next to delayed selection for within-dimension conditions. Given the N2pc for nontargets observed in those conditions of the present study, one might conclude that simple feature discrimination within the same feature dimension is not yet fully decisive for target selection at the time range of the N2pc. There was some evidence suggesting that the feature discrimination in the present paradigm took considerable time, since the modulation of the N2pc was only observed when presentation duration was increased substantially.

The N2pc has been shown to be affected by bottlenecks on what have been called "central" attentional processes (Jolicœur, 1999; Jolicœur and Dell'Acqua, 1998), as they occur in the Psychological Refractory Period (PRP) and attentional blink paradigms (Brisson and Jolicœur, 2007; Dell'Acqua et al., 2006; Jolicœur et al., 2006). Such central processes are hypothesized to be involved in the implementation of the current task set and control functions such as memory consolidation and response selection. However, in the present study, there was no evidence for an effect of task difficulty on the locus of target and nontarget dissociation (insofar as our counting manipulation could establish), presumably starting at the N2pc (Experiment 2). The present results thus suggested a qualification of the adaptive capabilities of the selection process that is reflected by the N2pc. Since the N2pc did not seem to be modulated by differences in task difficulty, it may be the case that the sequential nature of dual tasks plays an important role in the interference of central processes with the N2pc. In other words, the difficulty of a single task does not impair the allocation of attention during its course.

Apart from the N2pc, the present study investigated a range of ERP components, to chart potential differences in target-nontarget processing in both early and late phases of attentional deployment. With regard to the former, no modulation of the P2 was observed in the within-dimension conditions of the present study, even though lateralized components in partially overlapping time windows (i.e., the N2pc) did show modulation in Experiment 2 and 3. In contrast, when the ERPs to target and nontarget stimuli were examined in the study of Luck and Hillyard (1994a), differences became apparent relatively early at the time window of the P2 component, with subsequent components similarly affected. The present results underscored the idea that the P2 modulation was due to the nature of the singleton stimuli used by Luck and Hillyard, which varied between unique feature dimensions. This pattern is consistent with the interpretation that the P2 is sensitive to contrasts between dimensions, while the N2pc is more general and may also reflect processes that can use within-dimension stimulus features, which can be modulated by task set (Eimer and Kiss, 2008). It should be noted that the possibility of other factors affecting the P2 component remains open, as target-nontarget modulation of this component in visual feature discrimination tasks within the same feature dimension have been reported (e.g., O'Donnell et al., 1997).

With regard to late ERP components, the modulation of the P3 in the present study was expected, and can be taken as a reflection of eventual (if late) successful dissociation between target and nontarget stimuli. This view does not rule out, and is largely compatible with, the possibility that the ERP in this time range may reflect post-sensory categorization (e.g., Philiastides and Sajda, 2006). The P3 effect, like the earlier ones in Experiment 2, could not have been confounded with response preparation or execution, as the task did not require a direct behavioral response to the stimulus displays. A perhaps somewhat surprising finding was the absence of an effect of task difficulty, which might have been expected in Experiment 2 given the results of García-Larrea and Cézanne-Bert (1998). These authors found an effect of task difficulty in a somewhat comparable task on P3 amplitude and related "positive slow waves" (PSW) latency. In this case, however, the reduction in P3 amplitude was attributed to the increased difficulty associated with doing multiple tasks at once; something which was not manipulated in the present paradigm. The PSW effect is furthermore hard to evaluate in relation to the present study, as the onset of the delayed mask in Experiment 2 disturbed the ERP in the relevant time window. Even so, it was clear that no differential effect was present for neither task difficulty alone, nor for an interaction with task relevancy. A stronger test of task difficulty, with a more decisive behavioral signature, may be a fruitful course for future studies. The relevancy of the singleton stimuli modulated the P3 in all experiments in much the same way.

3.2. Perceptual and cognitive constraints

Studies have shown that the suppression of irrelevant information is less successful when viewing very simple scenes than when viewing complex ones. This phenomenon has been explained by the following hypothesis: While perception has limited capacity, all available stimuli are automatically processed until that limit is reached (Lavie, 1995; Lavie and Cox, 1997; Lavie and Tsal, 1994). In the case of a simple visual scene there is relatively little to process, and therefore the perceptual load is low and remains under the limit. Because of this, any distracting element in a sparse scene is also processed automatically. At the same time, a higher cognitive load, such as involved in working memory operations (although see Woodman and Luck, 2007), also makes it more likely for distractors to be processed, and therefore to cause interference (de Fockert et al., 2001). This suggests that although the visual system may automatically process stimuli as long as the capacity limit is not reached, it also requires cognitive control functions to be available to maintain a distinction between targets and distractors. One caveat that has been mentioned is that this type of control may only be needed when targets appear simultaneously with strong distractors, which therefore require immediate suppression in favor of the target stimulus (Lavie, 2005). Although functional magnetic resonance imaging (fMRI) studies have been conducted on cognitive control in this context (e.g., de Fockert et al., 2004), it is presently not known which ERP components are modulated during attentional selection in these cases.

It may be interesting to relate the present findings to the framework of perceptual and cognitive load. Variations in perceptual load have been shown to affect P1 and N1 components (Handy and Mangun, 2000), yet all of the presently observed modulations of the ERP were clearly later in nature. This confirms that perceptual load was not critically different in any of the conditions of the present study. Given the ease of the visual search task, it seems safe to assume that all of the experiments featured a low perceptual load. In Experiment 1, processing of relevant and irrelevant stimuli was identical up to the P3. The extent of processing that was applied indiscriminately to all singletons supported the idea that low perceptual load results in distractor stimuli getting processed automatically (Lavie and Tsal, 1994; Lavie, 1995). This was furthermore true under conditions of sequential presentation, that is, even though the nontargets were never shown simultaneously with actual targets. At the same time, the divergence between ERP components in Experiment 2 and 3 occurred earlier, from the N2pc time window onwards. It is not clear how this earlier selection between targets and nontargets could be easily explained by perceptual factors. If anything, Experiment 2 had a lower perceptual load than Experiment 1, as the masking stimulus was delayed. Experiment 3 was even further simplified. One might suppose that a change in cognitive load was involved in giving rise to the earlier modulation. Yet, the increased difficulty of the counting task in Experiment 2 did not change the observed modulations of the ERP; even in the most difficult condition the N2pc was different for target and nontarget stimuli. That is, the difficult counting condition should have increased cognitive load (leading to sustained processing of nontarget stimuli), but no evidence for this was obtained.

The overall findings suggested that although all salient stimuli receive initial processing when perceptual load is low, this does not always continue automatically beyond the earlier components (i.e., the P2, N2p, and N2pc), especially when search can rely on comparisons between feature dimensions. The factors influencing the possibility of earlier selection between targets and nontargets in the present paradigm seemed to be related to the properties of the attentional set rather than to cognitive load. It is possible that simultaneous presentation of targets and nontargets would result in a more demanding type of task, and that this in turn may lead to a load effect. This may present a fruitful course for future research.

4. Experimental procedures

4.1. Experiment 1

4.1.1. Participants

Fourteen right-handed students (8 females, 6 males) at the Ludwig Maximilian University Munich participated in this experiment for course credit or monetary compensation. They were paid an extra amount of money as a bonus if they performed well. Visual acuity was tested with a Rodenstock vision tester R12 (stimuli no. 112). Participants were naïve about the purpose of the experiment and had not taken part in a memory or visual search experiment in the lab before. Mean age was 25.6 years (range 21–29 years).

4.1.2. Apparatus and stimuli

Participants were seated in a comfortable chair in a dimly lit, electrically shielded and sound attenuated chamber. All stimuli were presented on an Iiyama 20" computer screen refreshing at 60 Hz, placed 100 cm in front of the participants at their straight-ahead line of sight. Search displays consisted of an array of blue (RGB 0, 0, 161) vertical lines on a white (RGB 255, 255, 255) background. The lines were arranged on four imaginary circles with a diameter of 2.9°, 4.5°, 6.3° and 8.0° centered on the screen. On these four circles 8, 10, 12 and 16 lines were evenly distributed, starting at 10°, 26°, 15° and 5° (respectively) clockwise from the 12-o'clock position.

The arrays consisted either of vertical lines only (singleton absent trials) or contained a single line with a different orientation (singleton present trials); the singleton could be a horizontal, a leftward-tilted or a rightward-tilted line (both tilts of 45°). Line elements were approximately 0.69° in length and approximately 0.09° in width. The singleton element appeared with equal probability on one of four possible target positions on the third circle (with a diameter of 6.3°), one in each quadrant with an eccentricity of 3.1°. A schematic depiction of the experimental trials is shown in Fig. 1.

The masking arrays were constructed by superimposing a vertical line and the three possible deviant orientations for each element on the display, resulting in an array of star-like elements which appeared on the same positions as the search array (covering an area of about $0.69^{\circ} \times 0.74^{\circ}$). A jitter was imposed on the search stimuli and the mask stimuli so that each element was randomly displaced between zero and three pixels in all four directions. The fixation point subtended a visual angle of approximately $0.46^{\circ} \times 0.46^{\circ}$.

4.1.3. Procedure and design

Participants viewed the stimulus arrays in continuous blocks. Within the singleton-present trials, a singular leftward tilted, a rightward tilted, or a horizontal stimulus was shown within the array. On some trials, the array was shown without any singleton stimulus (blank trials). Depending on the task set condition, all the singleton elements were targets (select-all condition), or the rightward tilted singleton was not (selectsome condition). The order of the two conditions was balanced across participants. A separate analysis of the ERP within each subgroup did not reveal any systematic impact of block order. Each condition consisted of 12 blocks with 70 trials each. Trials were randomly distributed across all experimental blocks. Half of the trials were singleton-absent trials, the other half were singleton-present trials (with equal probability of each kind of singleton to occur). At the beginning of each session, three short training blocks (in total 160 trials) were run to familiarize participants with the task. Before the start of the second condition (halfway through), another 64 practice trials were shown. Each trial started with the fixation point, which remained on screen throughout the trial. Participants were instructed to maintain strict fixation on this point. The fixation point was presented alone for 50 ms in the center of the screen, after which the stimulus array consisting of either vertical lines only or

vertical lines and a single singleton also appeared on the screen. This search array was displayed for 100 ms and then covered by the mask array which remained on the screen for 800 ms before disappearing so that only the fixation point remained for 1500 ms, after which the next trial began.

To ensure a clear view of modulation of the ERP components by stimulus processing, rather than stimulus-response translation or motor processing, steps were taken to avoid such potential confounds. Motor preparation and related processes may vary systematically with the experimental task, and thus may influence the ERP independently of stimulus effects. Therefore, participants were instructed not to respond overtly to the relevant targets but to count the targets silently and report the final tally verbally at the end of each block. This way, response preparation was not possible during the recording. Participants started to count from zero at the start of each experimental block. In the select-all condition, they added one to their internal count for both right- and leftward tilted line elements, and in the select-some condition for leftward tilted lines only. In both conditions, they added two for each horizontal line and nothing for blank trials.

4.1.4. Electrophysiological recording and data analysis

EEG was recorded with Ag-AgCl electrodes from 64 electrode positions (according to the extended international 10-20 system). All electrodes were referenced to Cz and re-referenced offline to the average of both mastoids. Horizontal and vertical EOG were recorded from the outer canthi of the eyes and from above and below the left eye, respectively. Electrode impedance was kept below 5 k Ω . The amplifier used a 125 Hz cut-off and a 0.1 Hz highpass filter. EEG was sampled on-line with a frequency of 500 Hz.

EEG was averaged off-line for epochs of 1000 ms, starting 200 ms prior to stimulus onset and ending 800 ms afterwards. Trials with amplitudes exceeding±80 μ V, voltage steps exceeding±50 μ V between two sampling points, and trials with voltages lower than 0.10 μ V for a 100 ms interval were marked and excluded from further analysis. Ocular artifacts (blinks and eye-movements) were corrected according to the Gratton–Coles procedure (Gratton et al, 1983)². The data were filtered off-line with a 30 Hz lowpass filter at -6 dB (24 dB/oct roll-off). Baseline correction was done using a 200-ms pre-stimulus interval.

Repeated measures analyses of variance (ANOVAs) were performed for mean amplitude values obtained in the following time ranges: P2 (180–240 ms after stimulus onset), N2pc (170–250 ms), N2p (240–300 ms), and P3 (320–560). Statistical analyses of the P1 and N1 components are not reported, as the waveforms clearly showed that no early differences existed that could be attributed to task relevance.

For the P2 and the P3 component, analyses were run with the factors TASK (select-all vs. select-some), and STIMULUS

² Although eye movement correction methods such as the Gratton–Coles one may distort the ERP, especially at more frontal electrode sites, the use of the correction procedure does not create an imbalance between the experimental conditions, and carries the benefit of an increased signal to noise ratio in the data. Any potentially induced distortion would be present in all cases, and could not explain differences observed between conditions.

(leftward-tilted, rightward-tilted, and blank trials). Note that horizontal lines were used as filler trials and excluded from the analyses because they differed both by physical appearance from the titled lines, as well as by instruction (i.e., "count two"). The N2pc is a component that is more negative-going in a given hemisphere for targets in its contralateral visual field. To calculate the N2pc, ipsilateral waveforms (i.e., left hemisphere electrode sites and stimulus in the left visual field, and the same for the right hemisphere and visual field) and contra-lateral waveforms (i.e., left hemisphere electrode sites and stimulus in the right visual field, etc.) are compared to each other. Lateralized attention is reflected in the difference between ipsi- and contralateral compound waveforms. Thus, in the analyses of the N2pc, the variable LATERALITY (contra- or ipsilateral) was added to the design matrix. Finally, for the N2p, a variable to reflect electrode SITE (left or right) was used next to those of TASK and STIMULUS to get an index of the hemispheric distribution of this component. For the P2, ERPs were recorded from FCz, as this component has been observed to show enhanced amplitude at frontal electrode sites. The average of PO3+PO7 and that of PO4+PO8 were used for the calculation of the N2pc and the N2p. These electrodes match the lateral occipital distribution of these components. To enhance the detection of potential differences in these relatively small components, the signal to noise ratio was increased by averaging over the aforementioned electrode pairs, which all showed the components of interest. It has to be noted that averaging slightly blurs the spatial localization of the signal, which was however of no concern for the purpose of the present study. Finally, Pz was used for the P3, a component known to have a broad central-parietal distribution.

4.2. Experiment 2

4.2.1. Participants

A new group of sixteen students (11 females, 5 males) at the Ludwig Maximilian University Munich participated in the experiment for course credit or monetary compensation. They answered to the same criteria as in Experiment 1. Mean age was 19.9 years (range 19–31).

4.2.2. Stimuli, procedure and design

Experiment 2 was identical to Experiment 1, with the following exceptions. The search displays were on screen for 500 ms rather than 100 ms. Blank trials were no longer shown to reduce session time; search displays always contained a horizontal, leftward tilted, or a rightward tilted line segment. The tilted singletons appeared on 40% of trials each to maximize the statistical power in these crucial conditions. Horizontal targets were still shown to maintain consistency and thus appeared on the remaining 20% of the trials. As before, participants were instructed to add two to their internal count whenever a horizontal target was shown. Depending on the condition, either one or three had to be added for a leftward tilted target. A rightward tilted singleton always meant nothing should be added. The order of the two conditions was again balanced across participants. Each condition consisted of 10 blocks with 48 trials each. Participants no longer counted from

zero, but were given a separate randomized starting number for each block. This was done to make the behavioral task somewhat less trivial and therefore more engaging. To allow a comparison of both conditions the same starting numbers were used in randomized order in both the easy and difficult counting conditions.

4.2.3. Electrophysiological recording and data analysis

Recording procedure was the same as in Experiment 1. ANOVAs were done on the same electrodes and time windows, using the remapped variables of TASK (add three and add one) and STIMULUS (horizontal, leftward, and rightward tilted lines), in addition to LATERALITY (for N2pc) and electrode SITE (for N2p).

4.3. Experiment 3

4.3.1. Participants

Sixteen new students participated in this experiment (13 females, 3 males). Mean age was 22.1 years (range 19–26).

4.3.2. Stimuli, procedure and design

The experiment was completely identical to the easy counting condition of Experiment 2, with the exception that the horizontal singletons were replaced by uniform displays (i.e., no singleton stimulus was present). The distribution was then balanced so that one third of all trials contained a target, one third contained a nontarget, and one third consisted of uniform arrays. The total number of trials was 576, distributed over 12 blocks of 48 trials each.

The statistical analyses were based on ANOVAs on the same electrodes and time windows as in the previous experiment, using the variable STIMULUS to indicate whether the stimulus display contained a target, a nontarget, or neither. As before, the variables LATERALITY and electrode SITE were added for the N2pc and N2p analyses.

4.4. Experiment 4

4.4.1. Participants

Thirteen new students participated in this experiment (9 females, 4 males). Mean age was 23.7 years (range 21–27).

4.4.2. Stimuli, procedure and design

The experiment was identical to Experiment 3, with the exception that trials containing red color singletons (RGB 255, 0, 0) were added. The distribution of trials changed accordingly, so that one fourth of all trials contained a target, one half contained a nontarget (either color or orientation), and one fourth consisted of uniform arrays. The total number of trials was unchanged at 576.

Acknowledgments

This research was supported by the German Research Foundation (DFG) as part of the excellence cluster "Cognition for Technical Systems" (CoTeSys), project #148, and by the DFG research grant "Temporal dynamics of visual processing" (FOR480, TP5).







Fig. A1 – (A) Waveforms recorded at the Pz electrode (μV) in Experiment 1 for the participants with the highest behavioral performance only. The figure represents the select-some condition. Separate lines represent different display conditions; singleton absent (thin line), left-tilted singleton (thick line), and right-tilted singleton (thick dashed line). (B) Plots of Global Field Power (GFP) for all experiments.

REFERENCES

- Arnott, S.R., Pratt, J., Shore, D.I., Alain, C., 2001. Attentional set modulates visual areas: an event-related potential study of attentional capture. Cogn. Brain Res. 12, 383–395.
- Bacon, W.F., Egeth, H.E., 1994. Overriding stimulus-driven attentional capture. Percept. Psychophys. 55, 485–496.
- Brisson, B., Jolicœur, P., 2007. Electrophysiological evidence of central interference in the control of visuospatial attention. Psychon. Bull. Rev. 14, 126–132.
- Dell'Acqua, R., Sessa, P., Jolicœur, P., Robitaille, N., 2006. Spatial attention freezes during the attentional blink. Psychophysiology 43, 394–400.
- Eimer, M., 1996. The N2pc component as an indicator of attentional selectivity. Electroencephalogr. Clin. Neurophysiol. 99, 225–234.
- Eimer, M., Kiss, M., 2008. Involuntary attentional capture is determined by task set: evidence from event-related brain potentials. J. Cogn. Neurosci. 20, 1423–1433.
- de Fockert, J.W., Rees, G., Frith, C.D., Lavie, N., 2001. The role of working memory in visual selective attention. Science 291, 1803–1806.
- de Fockert, J.W., Rees, G., Frith, C.D., Lavie, N., 2004. Neural correlates of attentional capture in visual search. J. Cogn. Neurosci. 16, 751–759.
- Donchin, E., Coles, M.G., 1988. Is the P300 component a manifestation of context updating? Behav. Brain Sci. 11, 357–374.
- Folk, C.L., Remington, R.W., 1998. Selectivity in distraction by irrelevant featural singletons: evidence for two forms of attentional capture. J. Exp. Psychol.: Hum. Percept. Perform. 24, 847–858.
- Folk, C.L., Remington, R.W., Johnston, J.C., 1992. Involuntary covert orienting is contingent on attentional control settings. J. Exp. Psychol.: Hum. Percept. Perform. 18, 1030–1044.
- Folk, C.L., Remington, R.W., Wright, J.H., 1994. The structure of attentional control: contingent attentional capture by apparent motion, abrupt onset and colour. J. Exp. Psychol.: Hum. Percept. Perform. 20, 317–329.
- Folk, C.L., Leber, A.B., Egeth, H.E., 2002. Made you blink! Contingent attentional capture produces a spatial blink. Percept. Psychophys. 64, 741–753.
- García-Larrea, L., Cézanne-Bert, G., 1998. P3, positive slow wave and working memory load: a study on the functional correlates of slow wave activity. Electroencephalogr. Clin. Neurophysiol. 108, 260–273.
- Gramann, K., Töllner, T., Krummenacher, J., Eimer, M., Müller, H.J., 2007. Brain electrical correlates of dimensional weighting: an ERP study. Psychophysiology 44, 277–292.
- Gratton, G., Coles, M.G., Donchin, E., 1983. A new method for off-line removal of ocular artifact. Electroencephalogr. Clin. Neurophysiol. 55, 468–484.
- Handy, T.C., Mangun, G.R., 2000. Attention and spatial selection: electrophysiological evidence for modulation by perceptual load. Percept. Psychophys. 62, 175–186.
- Hickey, C., McDonald, J.J., Theeuwes, J., 2006. Electrophysiological evidence of the capture of visual attention. J. Cogn. Neurosci. 18, 604–613.
- Horstmann, G., Ansorge, U., 2006. Attentional shifts to rare singletons. Vis. Cogn. 14, 295–325.
- Jolicœur, P., 1999. Concurrent response-selection demands modulate the attentional blink. J. Exp. Psychol.: Hum. Percept. Perform. 25, 1097–1113.
- Jolicœur, P., Dell'Acqua, R., 1998. The demonstration of short-term consolidation. Cogn. Psychol. 36, 138–202.
- Jolicœur, P., Sessa, P., Dell'Acqua, R., Robitaille, N., 2006. On the control of visual spatial attention: evidence from human electrophysiology. Psychol. Res. 70, 414–424.

- Kiss, M., Jolicœur, P., Dell'Acqua, R., Eimer, M., 2008a. Attentional capture by visual singletons is mediated by top-down task set: new evidence from the N2pc component. Psychophysiology 45, 1013–1024.
- Kiss, M., van Velzen, J., Eimer, M., 2008b. The N2pc component and its links to attention shifts and spatially selective visual processing. Psychophysiology 45, 240–249.
- Kok, A., 2001. On the utility of P3 amplitude as a measure of processing capacity. Psychophysiology 38, 557–577.
- Lavie, N., 1995. Perceptual load as a necessary condition for selective attention. J. Exp. Psychol.: Hum. Percept. Perform. 21, 451–468.
- Lavie, N., 2005. Distracted and confused?: selective attention under load. Trends in Cognitive Sciences 9, 75–82.
- Lavie, N., Cox, S., 1997. On the efficiency of visual selective attention: efficient visual search leads to inefficient distractor rejection. Psychol. Sci. 8, 395–398.
- Lavie, N., Tsal, Y., 1994. Perceptual load as a major determinant of the locus of selection in visual attention. Percept. Psychophys. 56, 183–197.
- Luck, S.J., Hillyard, S.A., 1994a. Electrophysiological correlates of feature analysis during visual search. Psychophysiology 31, 291–308.
- Luck, S.J., Hillyard, S.A., 1994b. Spatial filtering during visual search: evidence from human electrophysiology. J. Exp. Psychol.: Hum. Percept. Perform. 20, 1000–1014.
- Luck, S.J., Hillyard, S.A., Mouloua, M., Woldorff, M.G., Clark, V.P., Hawkins, H.L., 1994. Effects of spatial cuing on luminance detectability: psychophysical and electrophysiological evidence for early selection. J. Exp. Psychol.: Hum. Percept. Perform. 20, 887–904.
- Luck, S.J., Woodman, G.F., Vogel, E.K., 2000. Event-related potential studies of attention. Trends Cogn. Sci. 4, 432–440.
- Müller, H.J., Heller, D., Ziegler, J., 1995. Visual search for singleton feature targets within and across feature dimensions. Percept. Psychophys. 57, 1–17.
- Müller, H.J., Reimann, B., Krummenacher, J., 2003. Visual search for singleton feature targets across dimensions: stimulus- and expectancy-driven effects in dimensional weighting. J. Exp. Psychol.: Hum. Percept. Perform. 29, 1021–1035.
- Müller, H.J., Krummenacher, J., Heller, D., 2004. Dimension-specific intertrial facilitation in visual search for pop-out targets: evidence for a top-down modulable visual short-term memory effect. Vis. Cogn. 11, 577–602.
- Müller, H.J., Geyer, T., Zehetleitner, M., Krummenacher, J., 2009. Attentional capture by salient color singleton distractors is modulated by top-down dimensional set. J. Exp. Psychol.: Hum. Percept. Perform. 35, 1–16.
- O'Donnell, B.F., Swearer, J.M., Smith, L.T., Hokama, H., McCarley, R.W., 1997. A topographic study of ERPs elicited by visual feature discrimination. Brain Topogr. 10, 133–143.
- Philiastides, M.G., Sajda, P., 2006. Temporal characterization of the neural correlates of perceptual decision making in the human brain. Cereb. Cortex 16, 509–518.
- Polich, J., 2007. Updating P300: an integrative theory of P3a and P3b. Clin. Neurophysiol. 118, 2128–2148.
- Ruz, M., Lupiáñez, J., 2002. A review of attentional capture: on its automaticity and sensitivity to endogenous control. Psicológica 23, 283–309.
- Schubö, A., Müller, H.J., 2009. Selecting and ignoring salient objects in visual search. Brain Res. 1283, 84–101.
- Sergent, C., Baillet, S., Dehaene, S., 2005. Timing of the brain events underlying consciousness during the attentional blink. Nat. Neurosci. 8, 1391–1400.
- Theeuwes, J., 1991. Cross-dimensional perceptual selectivity. Percept. Psychophys. 50, 184–193.
- Theeuwes, J., 1992. Perceptual selectivity for color and form. Percept. Psychophys. 51, 599–606.

- Theeuwes, J., 1994. Stimulus-driven capture and attentional set: selective search for color and visual abrupt onsets. J. Exp. Psychol.: Hum. Percept. Perform. 20, 799–806.
- Theeuwes, J., Burger, R., 1998. Attentional control during visual search: the effect of irrelevant singletons. J. Exp. Psychol.: Hum. Percept. Perform. 24, 1342–1353.
- Töllner, T., Gramann, K., Müller, H.J., Kiss, M., Eimer, M., 2008. Electrophysiological markers of visual dimension changes and response changes. J. Exp. Psychol.: Hum. Percept. Perform. 34, 531–542.
- Verleger, R., Berg, P., 1991. The waltzing oddball. Psychophysiology 28, 468–477.
- Vogel, E.K., Luck, S.J., Shapiro, K.L., 1998. Electrophysiological evidence for a postperceptual locus of suppression during the

attentional blink. J. Exp. Psychol.: Hum. Percept. Perform. 24, 1656–1674.

- Wolfe, J.M., 1998. Visual search. In: Pashler, H. (Ed.), Attention. Psychology Press, Hove, UK, pp. 13–73.
- Wolfe, J.M., Horowitz, T.S., 2004. What attributes guide the deployment of visual attention and how do they do it? Nat. Rev., Neurosci. 5, 1–7.
- Woodman, G.F., Luck, S.J., 1999. Electrophysiological measurement of rapid shifts of attention during visual search. Nature 400, 867–869.
- Woodman, G.F., Luck, S.J., 2007. Do the contents of visual working memory automatically influence attentional selection during visual search? J. Exp. Psychol.: Hum. Percept. Perform. 33, 363–377.