The Gradual Emergence of Spatially Selective Target Processing in Visual Search: From Feature-Specific to Object-Based Attentional Control

Martin Eimer and Anna Grubert University of London

To dissociate feature-based and object-based stages in the control of spatial attention during visual search, we employed the N2pc component as an electrophysiological marker of attentional object selection. Participants searched for a target object that was defined by a conjunction of color and shape. Some search displays contained the target or a nontarget object that matched either the target color or its shape among 3 nonmatching distractors. In other displays, the target and a partially target-matching nontarget object appeared together. N2pc results demonstrated that the initial stage of attentional object selection is controlled by local feature-specific signals. Attention is allocated in parallel and independently to objects with target-matching features during this early stage, irrespective of whether another target-matching object is simultaneously present elsewhere. From around 250 ms poststimulus, information is integrated across feature dimensions, and spatially selective attentional processing becomes object-based. These findings demonstrate that feature-based and object-based stages of attentional selectivity in visual search can be dissociated in real time.

Keywords: selective attention, visual search, event-related brain potentials, feature-based attention, object-based attention

Finding a specific target among irrelevant distractors in crowded visual scenes is a complex achievement that requires top-down attentional control. Visual search for a known target object is guided by information about the features of this object. This information is assumed to be represented in visual working memory, and has been described as an attentional template (e.g., Desimone & Duncan, 1995; Duncan & Humphreys, 1989) or attentional control setting (e.g., Folk, Remington, & Johnston, 1992). Attentional templates can be activated prior to search, and then guide the selection of visual objects that possess target-defining features (e.g., Carlisle, Arita, Pardo, & Woodman, 2011; Eimer, 2014; Olivers, Peters, Houtkamp, & Roelfsema, 2011). In many previous investigations of the control processes involved in attentional target selection, target objects were defined by one specific feature or feature dimension (e.g., "red objects" or "any shape singleton"; see Folk & Anderson, 2010; Folk et al., 1992; Müller & Krummenacher, 2006). However, targets in real-world visual environments usually possess a number of different characteristic features from different dimensions. Visual search for the proverbial needle in the haystack can be based on internal representations of a specific target-defining color (silver), size (small), or shape

(thin). How do attentional control settings guide the selection of conjunctively defined target objects?

A commonly held view is that each target-defining feature guides the allocation of attention independently and in parallel with other target features from different dimensions. In computational models of visual target selection, focal attention is controlled by task-dependent weightings of those visual features or feature dimensions that define target objects (e.g., Müller & Krummenacher, 2006; Wolfe, 1994, 2007; see also Bundesen, 1990, for similar ideas). According to the Guided Search model (Wolfe, 1994, 2007), visual input is initially analyzed in parallel in independent feature channels. Each feature channel is weighted in line with current search intentions, so that channels that code targetmatching features receive a stronger weight. The output of these channels is then sent to a spatiotopic salience map, which determines where focal attention will be allocated. All channels contribute independently to the activity profile on the activation map, with larger contributions from more strongly weighted channels. As a result of these guidance processes, spatial attention is likely to be directed to objects with one or several target-defining features (see also Treisman, 1988, for a related view).

Because the location of target objects is typically unknown in visual search experiments, the location of possible target objects needs to be represented in a spatially global fashion during this attentional guidance stage that operates prior to target selection. A plausible neural correlate of this type of spatially global guidance has been found in neuroscientific studies of feature-based attention. As demonstrated in single-unit recoding studies with monkeys (e.g., Martinez-Trujillo & Treue, 2004), an attentional set for a task-relevant feature (such as a particular direction of motion) produces an enhancement in the neural processing of this feature in ventral visual cortex at the expense of the processing of other features in the same dimension. Importantly, because these feature-based attentional modulations of neural activity operate in

Correspondence concerning this article should be addressed to Martin Eimer, Department of Psychological Sciences, Birkbeck College, University of London, Malet Street, London WC1E 7HX, United Kingdom. E-mail: m.eimer@bbk.ac.uk

This article was published Online First July 7, 2014.

Martin Eimer and Anna Grubert, Department of Psychological Sciences, Birkbeck College, University of London.

This research was supported by a grant from the Economic and Social Research Council (ESRC), United Kingdom. We thank Luc Boutsen, John McDonald, Geoff Woodman, and an anonymous reviewer for comments on an earlier version of this article.

a spatially global fashion across the visual field (e.g., Bichot, Rossi, & Desimone, 2005; see also Saenz, Buracas, & Boynton, 2002, and Serences & Boynton, 2007, for corresponding evidence from human neuroimaging), they could act as guidance signals that bias the subsequent allocation of spatial attention toward objects with target-matching visual features (Bichot et al., 2005; Eimer, 2014).

If spatially global feature-based attentional guidance precedes spatially focal attentional selection during visual search, it is important to understand how the information accumulated during the guidance stage controls target selection. When target objects are defined by a conjunction of features, the presence of one or more target-matching features in the visual field will elicit featurebased attentional modulations, and these will then bias spatial attention toward the location of possible target objects. If featurebased attentional guidance operates independently for different feature dimensions, nontarget objects that match one, but not all, target-defining features should therefore be able to attract attention, in particular when no other target-matching object is simultaneously present in the visual field. During this early featureguided stage of attentional object selection, information about the joint presence of target features from different dimensions at the same location is not yet available. Spatial attention can only become sensitive to the difference between conjunctively defined targets and partially matching nontarget objects once guidance signals start to become integrated across feature dimensions. At this stage, attentional processing becomes object-based (Duncan, 1984), and visual working memory representations can be formed that represent integrated objects rather than individual features (e.g., Luck & Vogel, 1997; but see Wheeler & Treisman, 2002, and Woodman & Vogel, 2008).

A recent study from our lab (Kiss, Grubert, & Eimer, 2013) employed a combination of behavioral and event-related brain potential (ERP) measures to investigate the attentional processing of fully and partially target-matching objects in a task in which targets were defined by a color-size conjunction (e.g., small red bars). Each search display was preceded by a cue display that contained a spatially uninformative task-irrelevant feature singleton, and this singleton cue could match both target-defining features, only the target color or the target size, or neither feature. To assess the ability of fully and partially matching cues to attract attention, we measured N2pc components to cue stimulus arrays prior to the subsequent arrival of a target search array. The N2pc component is an enhanced negativity over posterior scalp electrodes that emerges around 200 ms after the onset of a visual search array contralateral to the side of an attended stimulus, and is linked to the spatial selection of candidate target items among distractors in visual search (Eimer, 1996; Luck & Hillyard, 1994; Mazza, Turatto, Umiltà, & Eimer, 2007; Schubö & Müller, 2009; Woodman & Luck, 1999). N2pc components have also been employed to study the task-set contingent capture of attention by target-matching but task-irrelevant visual events (e.g., Eimer & Kiss, 2008; Eimer, Kiss, Press, & Sauter, 2009; Leblanc, Prime, & Jolicoeur, 2008; Lien, Ruthruff, Goodin, & Remington, 2008). In our recent study (Kiss et al., 2013), reliable N2pc components were triggered not only by fully target-matching cues but also by cues that shared either the target-defining color or size, but not both attributes. This demonstrates that both fully and partially matching cues attracted attention, in line with the hypothesis that

attentional guidance operates independently for different feature dimensions. Importantly, N2pc components were larger for fully target-matching relative to partially matching cues, and the N2pc component elicited by fully matching cues equaled the sum of the two N2pc components to color-matching and shape-matching cues. This observation suggests that guidance signals from different feature channels are combined in an additive fashion during the control of focal spatial attention.

In marked contrast to this N2pc evidence for feature-based guidance of spatial attention, the behavioral results obtained in the same study (Kiss et al., 2013) suggested the presence of objectbased attentional control processes. Fully target-matching cues produced spatial cueing effects on reaction times (RTs) to subsequently presented targets, demonstrating that these cues captured attention in a task-set contingent fashion (Folk et al., 1992). Critically, partially matching cues did not produce any spatial cueing effects, suggesting that attention was no longer focused at the cued location at the moment when the target array was presented (200 ms after the onset of the cue array). To explain the discrepancy between these behavioral and electrophysiological effects, we proposed a two-stage selection scenario (Kiss et al., 2013). During the initial stage of attentional object selection (reflected by the N2pc to the cue array), spatial attention is controlled independently by signals from different feature channels, which results in an allocation of attention to objects that possess some but not all target-defining features. Shortly afterward, attention is withdrawn from partially matching nontargets, but remains focused on fully target-matching objects. This will result in spatial cueing effects on target RTs on trials with fully target-matching cues, and the absence of such effects in trials with partially matching cues. This two-stage selection scenario is based on the distinction between feature-guided and object-based attentional control described earlier. Any de-allocation of attention from nontarget objects that match the target in only one feature dimension has to be based on a registration of the fact that this object lacks a target-defining feature in another dimension, that is, on the integration of feature information about a particular object across dimension-specific input channels.

This hypothesis that feature-guided and object-based spatial selection are separable and successive stages of attentional control clearly requires further independent confirmation. In particular, it is important to determine the time course of these processes. If the attentional selection of candidate target objects in visual search is initially feature-based, when does it start to become affected by feature integration processes? The spatial cueing design employed in our previous study (Kiss et al., 2013) was not optimal to address these issues. In this study, the argument for two successive stages of attentional control was based on different types of measures (N2pc components vs. behavioral spatial cueing effects) that were obtained in response to different stimuli that appeared at different times (cue vs. target displays). The present experiment employed an alternative experimental approach to track the time course of attentional selectivity in visual search, and to obtain more direct evidence for two successive stages in the attentional selection of visual objects.

A single search display with two objects on the horizontal meridian and two objects on the vertical meridian was presented on each trial. Each object had a specific color and shape. To equate the discriminability between different features in the color and shape domains, four distinct shapes (circles, squares, hexagons, and gates) were combined with four perceptually similar colors (green, blue, cyan, and yellow; see Figure 1). Participants' task was to find targets that were defined by a color–shape conjunction (e.g., a blue squares). A target present–absent response was required on each trial. Some displays contained the target object among three distractor items that possessed neither of the two target features (Figure 1A and 1B). Other displays included a nontarget object with one of the two target-defining features (e.g., a blue circle or a yellow square during search for blue squares) and three distractors (Figure 1C through 1F). Trials in which these displays were shown were termed *no-competition trials*, because each display contained only one object with target-matching features.

N2pc components were measured for trials in which a target, a color-matching nontarget, or a shape-matching nontarget appeared on the horizontal meridian (i.e., on the left or right side). If the allocation of attention is initially controlled independently by signals from different feature modules, both targets and partially matching nontarget objects should attract attention, and both should therefore elicit reliable N2pc components. If this early feature-specific guidance of attentional object selection by color and shape information operates in a strictly independent and parallel fashion, the sum of the two N2pc components elicited in response to color-matching and shape-matching nontargets should

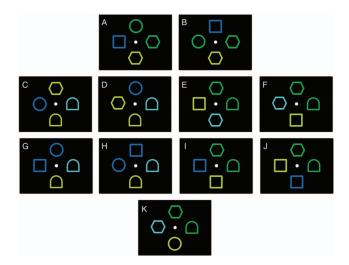


Figure 1. Schematic illustration of the different types of search displays. In the example shown here, the blue square is the target. On no-competition trials (Panels A to F), the target or a partially matching nontarget object were accompanied by three distractor objects without target-matching features. Panels A and B show displays in which the target appeared on the horizontal or vertical meridian. In the displays shown in Panels C to F, a color-matching nontarget (e.g., a blue circle) or a shape-matching nontarget (e.g., a yellow square) were present on the horizontal or vertical meridian. On competition trials (Panels G to J), the target and a partially matching nontarget object appeared in the same display. A horizontal or vertical target could be accompanied by a vertical or horizontal color-matching nontarget (Panels G and H), or by a vertical or horizontal shape-matching nontarget (Panels I and J). On distractor-only trials (Panel K), displays contained four objects without target-matching features. Relative object sizes shown here are larger than in the actual search displays. The color version of this figure appears in the online article only.

initially equal the N2pc component to fully matching target objects. Critically, the moment in which attentional object selection ceases to be purely feature-based should be marked by the point in time in which the N2pc component to target objects becomes larger than the additive contributions of the two N2pc components to partially matching nontargets. At this point, spatially selective attentional processing begins to be affected by the integration of information about visual objects across feature dimensions. We tracked this transition from an early feature-based stage of attentional selectivity to a subsequent object-based selection stage in real time by comparing the N2pc to target objects with the summed N2pc waveforms to color-matching and shape-matching nontarget objects.

In contrast to the no-competition trials used in the present study (Figure 1A through 1F), visual search for conjunctively defined targets is usually studied with displays in which several objects with target-matching visual features are simultaneously present. Under these conditions, targets that possess all task-relevant features have to be distinguished from partially matching nontarget objects that lack at least one of these features. How does attentional target selection operate in displays that contain more than one object with target-matching features? According to featurebased models of attentional object selection, such as guided search (Wolfe, 1994, 2007), information about the presence of candidate target objects from independent feature channels is combined on the salience map. Spatial selection operates serially, with focal attention allocated to a single object at one particular location at a time, and is first directed to the object that triggers the strongest activation on the salience map. Because objects that possess all task-relevant features should produce stronger activation than partially matching objects, targets will usually attract spatial attention, while partially matching nontargets remain unattended. In contrast to this serial selection scenario, an alternative parallel selection account would assume that early feature-guided attentional selection processes operate independently and simultaneously across the visual field, so that focal attention can be allocated at the same time to more than one object with target-matching features (e.g., Eimer & Grubert, 2014). If this was the case, partially matching nontargets may be able to attract attention even when they are accompanied by a target object in the same display.

To test these alternative hypotheses, the current study also included competition trials in which search displays contained both a target and a partially matching nontarget object. One of these objects was always presented on the horizontal meridian, and the other on the vertical meridian (Figure 1G through 1J). On some competition trials, a horizontal target was accompanied by a colormatching or shape-matching nontarget object on the vertical meridian. On other trials, a vertical target appeared together with a horizontal partially matching nontarget. This horizontal-vertical stimulus arrangement allowed us to measure N2pc components to a horizontal target or a partially matching nontarget independently of the attentional processing of the vertical task-set matching object in the same display. Because N2pc components are elicited contralateral to candidate target objects in the left or right visual field, no N2pc will be triggered when these objects appear on the vertical midline (Eimer & Grubert, 2014; Eimer, Kiss, & Nicholas, 2011; Hickey, McDonald, & Theeuwes, 2006; Woodman & Luck, 2003). N2pc components on competition trials exclusively reflect the attentional selection of horizontal objects, irrespective of any simultaneous allocation of attention to a vertical object. This made it possible to investigate whether nontarget objects that possess one target-defining feature attract attention, even when they are accompanied by a target object in the same search display. If focal attention was always directed to target objects, because these objects generate a more potent spatial bias on the salience map, partially matching nontargets on the horizontal meridian should remain unattended and therefore not trigger an N2pc component when a vertical target is simultaneously present. In contrast, if the early feature-guided attentional selection stage operates independently for different target-defining features and in parallel across the visual field, color-matching and shape-matching nontarget objects should trigger reliable N2pc components, even when they are competing with a target on the vertical midline. Similar to no-competition trials, the summed contributions of these two N2pc components should equal the N2pc triggered by target objects during this early parallel stage of feature-guided attentional selec-

Method

Participants

Nineteen paid participants took part in the experiment. Three were excluded because of excessive eye movements or alpha activity, so that 16 participants (aged 26 to 47 years; mean age = 32.8 years; nine female; one left-handed) remained in the sample. All participants had normal or corrected-to-normal vision and reported normal color vision.

Stimuli and Procedure

Stimuli were presented on a 22-in. Samsung SyncMaster 2233 LCD monitor with a resolution of 1280×1024 pixels and a 100 Hz refresh rate. Participants were seated in a dimly illuminated cabin and viewed the screen at a distance of about 100 cm. Manual responses were registered by two purpose-built response keys. Stimulus presentation, timing, and response recording were controlled by a LG Pentium PC running under Windows XP, using the Cogent 2000 toolbox (www.vislab.ucl.ac.uk/Cogent/) for MATLAB (Mathworks, Inc.). On each trial, one search display was presented for 150 ms against a black background, followed by an intertrial interval of 1,650 ms. A central gray fixation point (CIE x/y coordinates, .321/.352; $0.2^{\circ} \times 0.2^{\circ}$) remained continuously present throughout each experimental block. All search displays contained four colored objects $(0.6^{\circ} \times 0.6^{\circ})$. Two of these objects were presented on the horizontal meridian (to the left and right of fixation), and the other two on the vertical meridian (above and below fixation), at an eccentricity of 1.9° from fixation (see Figure 1). Objects were outline shapes (circles, gates, squares, or hexagons; 0.1° line width) that could appear in one of four equiluminant colors (9.8 cd/m²). These colors were green (CIE x/y coordinates, .262/.572), blue (.185/.188), cyan (.212/.347), and vellow (.342/.477).

Participants' task was to detect a target that was defined by a specific combination of color and shape (e.g., a blue square), and to report its presence or absence in a search display by pressing one of two vertically aligned response keys with their left or right index finger (top key = target present; bottom key = target

absent). The hand-to-key mapping was swapped after eight of the 16 experimental blocks. The identity of the target was fully counterbalanced across the 16 participants. Each of them searched for a different combination of one of the four object shapes and four object colors, and this target definition remained the same throughout the experiment for each participant. Figure 1 illustrates the different types of search displays that appeared in random order in each experimental block. In the examples shown here, the target was the blue square. A target was present on half of all trials, and absent in the other half. On some trials, a target appeared on the horizontal or vertical meridian together with three distractor objects that possessed neither of the two target-defining features (Figure 1A and 1B). On other trials, a nontarget object that matched the target color or the target shape was present on the horizontal or vertical meridian (Figure 1C through 1F). These trials were termed no-competition trials because only one object with target-matching features was present in each display. On competition trials (Figure 1G through 1J), a target was presented together with one nontarget object that matched either the target color (e.g., a blue circle) or the target shape (e.g., a yellow square) and two nonmatching distractors. A horizontal target could be accompanied by a vertical color-matching nontarget (T&CMNT; Figure 1G) or by a vertical shape-matching nontarget (T&SMNT; Figure 11). A vertical target could be accompanied by a horizontal colormatching nontarget (CMNT&T; Figure 1H) or by a vertical shapematching nontarget (SMNT&T; Figure 1J). On distractor-only trials, all four objects were distractor objects without any targetdefining feature (Figure 1K).

On each trial, the colors and shapes of the nonmatching distractor objects were assigned randomly, with two constraints. First, to avoid the presence of feature singletons (e.g., one blue object among three green objects), each search display included three different colors and three different shapes. Second, no search display was allowed to contain two physically identical objects (e.g., two green circles as distractors). Each block contained 48 target-present and 48 target-absent trials. There were eight trials per block for each of the six possible types of target-present trials (Figure 1A, 1B, 1G through 1J). There were also eight trials per block for the four possible types of target-absent trials with a partially matching nontarget object (Figure 1C through 1F). In the remaining 16 target-absent trials, search displays contained four nonmatching distractor objects (Figure 1K). Participants completed 16 experimental blocks, resulting in 1,536 experimental trials in total. Prior to the first experimental block, participants completed one practice block containing 48 trials.

EEG Recording and Data Analysis

The continuous EEG was DC-recorded from 23 scalp electrodes, mounted in an elastic cap at sites Fpz, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3, Pz, P4, P8, PO7, PO8, and Oz. EEG was sampled at a rate of 500 Hz and was digitally low-pass filtered at 40 Hz. No other filters were applied offline. All channels were online referenced to the left earlobe and rereferenced offline to the average of both earlobes. Trials with artifacts (eye movements exceeding $\pm 30~\mu V$ in the HEOG channels; eyeblinks exceeding $\pm 60~\mu V$ at Fpz; muscular movements exceeding $\pm 80~\mu V$ in all other channels), and trials with incorrect, anticipatory (faster than 200 ms), very slow (slower than 1,200

ms), or missing responses were excluded from EEG analyses. The EEG on the remaining trials was segmented into epochs from 100 ms prior to 400 ms after search array onset, relative to a 100 ms prestimulus baseline. Averaged ERP waveforms were computed for each of the seven search displays that contained a target or a partially target-matching nontarget on the horizontal meridian (Figure 1A, 1C, 1E, and 1G through 1J), separately for trials in which this object was presented in the left or right visual field. N2pc components were quantified at lateral posterior electrodes PO7 and PO8 on the basis of ERP mean amplitudes obtained in the 200- to 300-ms time window after stimulus onset. N2pc onset latencies were determined on the basis of difference waveforms (contralateral minus ipsilateral ERPs at PO7/8) with a jackknifebased procedure (Miller, Patterson, & Ulrich, 1998). Sixteen grand-average difference waves were computed, each excluding one different participant from the original sample. N2pc onset latencies for different search displays were determined on the basis of these difference waves with an absolute onset criterion of -1μV. N2pc onset latency differences between search display were assessed with paired t tests, with t values corrected according to the formula described by Miller et al. (1998). All t tests were twotailed, with Bonferroni-corrected p values when necessary.

Results

Behavioral Performance

Figure 2 shows RTs on trials with correct responses (top panel) and error rates (bottom panel), separately for trials in which a target object was present and for target-absent trials. Trials with very fast (<200 ms) or slow (>1,200 ms) responses were excluded from analysis (0.1% of all trials). Target-present

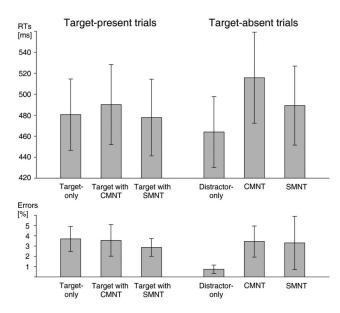


Figure 2. Mean correct response times (RTs; top panel) and error rates (bottom panel) on target-present and target-absent trials, shown separately for target-only and distractor-only displays, and for displays that contained a color-matching nontarget (CMNT) or a shape-matching nontarget (SMNT). Bars represent 95% confidence intervals of the means.

RTs differed between target-only trials and competition trials in which the target was accompanied by a color-matching or shape-matching nontarget, F(2, 30) = 7.8, p < .01, $\eta_p^2 = .34$. RTs on target-only trials were faster than on trials in which a color-matching item was simultaneously present (481 ms vs. 490 ms), t(15) = 2.9, p < .01, but did not differ from trials that also included a shape-matching item (478 ms), t(15) = 1.0. The RT difference between target-present trials with color-matching and shape-matching nontargets was also significant, t(15) =3.3, p < .02. Error rates on these three types of target-present trials did not differ significantly (3.7% on target-only trials, 3.6% on trials with an additional color-matching object, 2.9% on trials with an additional shape-matching object), F(2, 30) =1.6, p = .22, $\eta_p^2 = .10$. Performance on target-absent trials was strongly affected by the presence versus absence of a partially target-matching object (Figure 2, right panels). Target-absent RTs differed between trials with a color-matching or shapematching nontarget and distractor-only trials in which no such object was present, F(2, 30) = 24.9, p < .001, $\eta_p^2 = .62$. RTs were faster on distractor-only trials (464 ms) compared with trials with color-matching or shape-matching nontargets (516 ms and 489 ms, respectively), both t(15) > 5.2, both ps < .001. The RT difference between trials with color-matching and shape-matching nontargets was also reliable, t(15) = 2.8, p <.02. Error rates differed between the three types of target-absent trials, F(2, 30) = 3.7, p < .04, $\eta_p^2 = .20$. False alarm rates on trials with partially matching nontargets (3.4% and 3.3% for color- and shape-matching objects) were larger than on distractor-only trials (0.7%), t(15) = 4.2, p < .01.

N2pc Components in No-Competition Trials

Figure 3 (top panel) shows ERPs measured at lateral posterior electrodes PO7/PO8 contralateral and ipsilateral to the side of a target or a partially matching nontarget object on no-competition trials in which no additional task-set matching object was present in the search display. Target displays (Figure 1A) triggered larger N2pc components than displays with a color-matching nontarget (CMNT; Figure 1C) or shape-matching nontarget (SMNT; Figure 1E). However, partially matching nontargets also triggered sizable N2pc components. This was assessed in an ANOVA on N2pc mean amplitudes obtained in the 200- to 300-ms poststimulus time window for the factors display type (target, CMNT, SMNT) and laterality (electrode contralateral vs. ipsilateral to the target or partially matching nontarget object). A main effect of laterality was obtained, F(1, 15) = 41.7, p < .001, $\eta_p^2 = .74$, reflecting the presence of reliable N2pc components. There was a Display Type × Laterality interaction, $F(2, 30) = 15.6, p < .001, \eta_p^2 = .51$. N2pc mean amplitudes were larger for targets compared with color-matching and shape-matching nontargets, both t(15) > 4.7, both ps < .001, but did not differ reliably between color-matching and shape-matching nontargets, t(15) = 2.0, p = .180. Follow-up comparisons of contralateral and ipsilateral ERPs revealed that reliable N2pc components were present not only in response to targets, t(15) = 6.4, p < .001, but also for color-matching and shape-matching nontargets, t(15) = 4.8 and 3.8, both ps < .003, respectively.

To determine whether, and up to which point in time, the target N2pc equaled the summed contributions of the two N2pc compo-

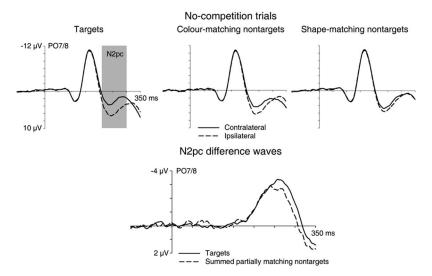


Figure 3. Top panel: Grand-average event-related brain potentials (ERPs) measured on no-competition trials in the 350-ms interval after search display onset at posterior electrodes PO7/8 contralateral and ipsilateral to the location of a target, a color-matching nontarget, or a shape-matching nontarget on the horizontal meridian. Bottom panel: Difference waveforms obtained by subtracting ipsilateral from contralateral ERPs for target displays (solid line), and summed difference waves for displays with color-matching and shape-matching nontargets (dashed line).

nents to partially matching nontarget objects, contralateral and ipsilateral average ERP waveforms measured on CMNT and SMNT trials were added, and N2pc difference waves were computed by subtracting the resulting ipsilateral ERP waveforms from contralateral ERPs. Figure 3 (bottom panel) shows the summed N2pc components for color-matching and shape-matching nontargets (dashed line), together with the N2pc difference waveform for target objects (solid line). The combined N2pc response to both partially matching targets emerged at the same point in time as the target N2pc, and these two N2pc waveforms remained virtually identical until approximately 250 ms after stimulus onset. Beyond 250 ms, the N2pc to target objects was larger than the summed N2pc to partially matching nontargets. A jackknife-based comparison of N2pc onset latencies with an absolute onset criterion of -1μV revealed no onset differences between these two N2pc difference waveforms. N2pc onset latencies were 197 ms and 195 ms poststimulus for targets and summed partially matching nontargets, $t_c(15) < 1$.

To estimate when the target N2pc started to become larger than the summed N2pc component for partially matching nontargets (as shown in Figure 3, bottom panel), summed N2pc difference waveforms for partially matching nontargets were subtracted from N2pc difference waves for targets, separately for each participant. The resulting grand-averaged double subtraction waveform is shown in Figure 4 (solid line). N2pc differences between targets and summed partially matching nontargets, as measured with a jackknife-based analysis performed for individual double subtraction waveforms with a fixed onset criterion of $-0.5~\mu\text{V}$, emerged at a poststimulus latency of 251 ms. Additional analyses of N2pc mean amplitudes to targets and summed partially matching nontargets measured during the first and second half of the original N2pc time window (200 to 250 ms and 250 to 300 ms poststimulus, respectively) confirmed this observation. During the earlier

time window, there was no interaction between laterality and condition (target vs. summed partially matching nontargets), F(1, 15) < 1, $\eta_p^2 = .00$, suggesting that N2pc components to target-matching features combined in an additive fashion during this time period. Between 250 and 300 ms, this interaction was significant, F(1, 15) = 5.4, p < .04, $\eta_p^2 = .27$, as the N2pc component to target objects was now larger than the summed contribution of the N2pc components to partially matching nontargets.

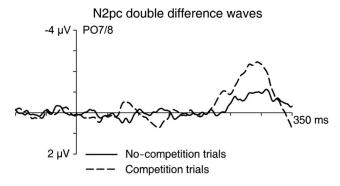


Figure 4. N2pc double difference waveforms obtained by subtracting N2pc difference waves for summed partially matching nontargets from N2pc difference waves for targets, separately for no-competition and competition trials. The waveform for no-competition trials (solid line) represents the difference between the N2pc waveforms to targets and partially matching nontargets shown in Figure 3 (bottom panel). The waveform for competition trials (dashed line) represent the difference between target and partially matching nontarget N2pc waveforms shown in Figure 5 (bottom panel). The point in time at which the target N2pc started to become larger than the summed N2pc to partially matching nontargets emerged earlier in competition trials relative to no-competition trials.

N2pc Components in Competition Trials

Figure 5 (top and middle panels) shows ERPs measured at posterior electrodes PO7/PO8 contralateral and ipsilateral to the side of a horizontal target or partially matching nontarget object on competition trials in which an additional item with target-matching features was present on the vertical midline. The top panel shows ERPs triggered to horizontal target objects that were accompanied by a vertical color-matching nontarget (T&CMNT; Figure 1G) or by a vertical shape-matching nontarget (T&SMNT trials; Figure 1I). The middle panel shows ERPs to horizontal color-matching or shape-matching nontarget objects that were presented together with a target on the vertical midline (CMNT&T trials and

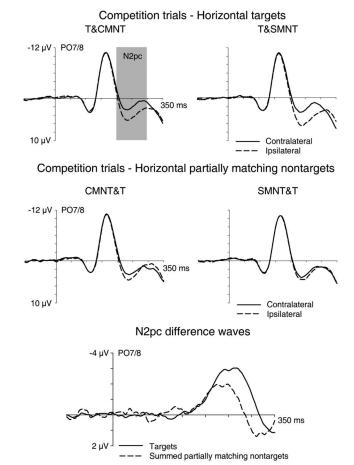


Figure 5. Top and middle panels: Grand-average event-related brain potentials (ERPs) measured on competition trials in the 350-ms interval after search display onset at posterior electrodes PO7/8 contralateral and ipsilateral to a horizontal target or partially matching nontarget. ERPs are shown separately for displays with a horizontal target and a vertical color-matching nontarget (T&CMNT), a horizontal target and a vertical shape-matching nontarget (T&SMNT), a horizontal color-matching nontarget and a vertical target (CMNT&T), and a horizontal shape-matching nontarget and a vertical target (SMNT&T). Bottom panel: N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs, for displays with horizontal targets (averaged across displays with a vertical color-matching and shape-matching nontarget; solid line), and for displays with horizontal partially matching nontargets and vertical targets (summed across displays with color- and shape-matching nontargets; dashed line).

SMNT&T trials; Figure 1H and 1J). N2pc components were larger for targets relative to color- or shape-matching nontargets. However, partially matching nontarget objects also appeared to trigger N2pc components, despite the fact that they were accompanied by a target in the same display.

N2pc components for displays with a horizontal target and a vertical partially matching nontarget were analyzed in an ANOVA of ERP mean amplitudes obtained in the 200-to 300-ms poststimulus time window. A main effect of laterality, F(1, 15) = 58.3, p <.001, $\eta_p^2 = .80$, confirmed the presence of reliable target N2pc components. There was an interaction between laterality and nontarget type (color match vs. shape match), F(1, 15) = 11.4, p <.005, $\eta_p^2 = .43$, with smaller target N2pc amplitudes on T&CMNT trials compared with T&SMNT trials. However, N2pc components were reliably present for both types of trials, both t(15) > 6.5, both ps<.001. In the corresponding analysis of N2pc components for displays with a horizontal partially matching nontarget and a vertical target, a significant main effect of laterality, F(1, 15) =9.5, p < .01, $\eta_p^2 = .39$, confirmed that these nontarget objects did indeed elicit reliable N2pc components. There was no interaction between laterality and nontarget type, F(1, 15) < 1, $\eta_p^2 = .03$, indicating that N2pc components of similar size were elicited on color-matching and shape-matching nontarget objects. Follow-up t tests confirmed that N2pc components were reliable for both color-matching and shape-matching nontargets, t(15) = 2.2 and 4.5, p < .05 and .001, respectively.

To address the question whether, and for how long, the summed contributions of the N2pc components to color- and shapematching nontargets matched the target N2pc on competition trials, contralateral and ipsilateral ERPs measured on CMNT&T and SMNT&T trials were added, and the resulting contralateralipsilateral difference waveforms were compared with corresponding N2pc difference waves for competition trials with horizontal targets (averaged across T&CMNT and T&SMNT trials; see Figure 5, bottom panel). Results were similar to the pattern observed for no-competition trials. The summed N2pc components to partially matching nontargets emerged at the same time as the target N2pc, and these two N2pc waveforms remained closely aligned until about 230 ms poststimulus. A jackknife-based N2pc onset latency comparison confirmed that the onset latency of target and summed nontarget N2pc waveforms (201 ms vs. 197 ms) did not differ reliably, $t_c(15) < 1$. To estimate the point in time at which the target N2pc became larger than the summed N2pc component for partially matching nontargets, N2pc difference waveforms for partially matching nontargets were subtracted from N2pc difference waves for targets, separately for each participant. Figure 4 (dashed line) shows the resulting grand-averaged double subtraction waveform. In a jackknife-based analysis of individual double subtraction waveforms with an onset criterion of $-0.5 \mu V$, N2pc differences between targets and summed partially matching nontargets were estimated to start 226 ms after display onset.

Analyses of N2pc mean amplitudes to targets and summed partially matching nontargets conducted separately for the first and second half of the N2pc time window revealed a significant interaction between laterality and stimulus type (target vs. summed partially matching nontargets) for the 250- to 300-ms interval, F(1, 15) = 13.5, p < .005, $\eta_p^2 = .47$, with larger N2pc components to target objects. During the earlier 200- to 250-ms time window, this interaction was not reliable F(1, 15) = 2.3, p = .151, $\eta_p^2 = .13$.

As can be seen in Figure 4, larger N2pc components to targets compared with summed partially matching nontargets emerged earlier in competition trials than in no-competition trials. A jackknife-based onset latency comparison of these two double subtraction waveforms (based on a $-0.5~\mu V$ onset criterion) confirmed that the onset of the superadditive target N2pc differed significantly between competition and no-competition trials (251 ms vs. 226 ms), $t_c(15) = 2.9$; p < .02.

Median-Split Analysis of N2pc Components in Competition Trials

The presence of reliable N2pc components to horizontal partially matching nontargets that appeared together with a vertical target object suggests that spatial attention was allocated independently and in parallel to targets and nontargets in the same display. However, the possibility remains that targets and partially matching nontargets attracted attention on different trials, and that the N2pc observed for horizontal nontarget objects on competition trials was generated on a subset of trials in which attention was allocated incorrectly to these objects and not to vertical targets (see McDonald, Green, Jannati, & Di Lollo, 2013, for an analogous argument about target and nontarget N2pc components in the additional singleton paradigm). If this was the case, nontarget N2pc components should be primarily found on trials with slow responses to targets, because slow target RTs would indicate that spatial attention is directed incorrectly to a partially matching nontarget object. In contrast, no nontarget N2pc should be present on trials with fast target RTs, as rapid responses should be the result of efficient target selection.

To test these predictions, N2pc components to targets and partially matching nontargets in competition trials were computed separately for trials with fast and slow responses to targets, based on RT median splits performed for each individual participant and display type. Figure 6 shows N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs on competition trials with a horizontal target and a vertical partially matching nontarget (solid lines), and with a horizontal nontarget and a vertical target (dashed lines), separately for trials with fast or slow target RTs (summed across color-matching and shape-matching nontargets). The pattern of N2pc effects was very similar regardless of whether responses to targets were fast or slow. Most importantly, horizon-

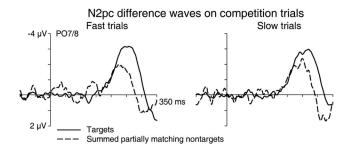


Figure 6. N2pc difference waveforms obtained on competition trials by subtracting ipsilateral from contralateral event-related brain potentials for horizontal targets or summed partially matching horizontal nontargets, shown separately for trials with fast and slow reaction times (RTs) to targets (as determined by RT median splits).

tal partially matching nontarget objects triggered N2pc components not only on trials with slow responses, but also on fast response trials. Analyses of N2pc amplitudes on CMNT&T and SMNT&T trials, conducted separately for trials with fast and slow target RTs, revealed no interaction between laterality and response speed, both F(1, 15) < 1, both $\eta_p^2 < .06$. Follow-up t tests confirmed that reliable N2pc components to color-matching or shape-matching nontarget objects were reliably present on slow as well as on fast response trials, all ps < .05. A jackknife-based onset latency comparison of summed N2pc components to partially matching nontargets between trials with fast and slow RTs for showed no reliable difference (195 ms vs. 198 ms), $t_c(15) < 1$. Likewise, target N2pc components emerged at the same point in time on fast and slow trials (198 ms vs. 204 ms), $t_c(15) = 1.3$, p =.214. Moreover, the point in time when target N2pc components started to become larger that the summed N2pc to partially matching nontargets did not differ reliably between fast and slow response trials (see Figure 6). A jackknife-based onset comparison of N2pc double subtraction waveforms (target N2pc minus N2pc to summed partially matching nontargets) between fast and slow RT trials showed no significant latency difference (222 ms vs. 228 ms), $t_c(15) < 1$, based on a $-0.5 \mu V$ onset criterion.

Discussion

The current study employed the N2pc component as a marker of attentional object selection during visual search to dissociate an early feature-based stage of attentional control that is guided by independent signals from different feature dimensions and a subsequent object-based stage in which these signals are integrated. Participants searched for targets that were defined by a specific combination of color and shape. On no-competition trials, displays included a single object with target-matching features, which could either be the target or a partially target-matching nontarget object. On competition trials, target and partially matching nontarget objects appeared in the same display.

On no-competition trials, reliable N2pc components were elicited not only by targets but also by color-matching or shapematching nontarget objects, demonstrating that these objects were able to attract attention. The fact that target-absent RTs were slower and error rates were higher when displays contained a partially matching nontarget object relative to distractor-only displays (see Figure 2) provides further evidence that these objects could not be completely ignored. The presence of N2pc components to partially target-matching objects demonstrates that some aspects of attentional selection in visual search operate in a feature-based fashion, in the sense that they are controlled independently by guidance signals from different feature dimensions. N2pc components elicited by partially matching nontargets on no-competition trials were smaller than the N2pc to target objects. In fact, the sum of the two N2pc components to color-matching and shape-matching nontargets was virtually identical to the N2pc component to targets during the early phase of spatially selective attentional processing until around 250 ms poststimulus (Figure 3, bottom panel). This finding strongly suggests that the spatial bias produced by signals from color and shape modules affects the initial allocation of spatial attention in the visual field independently and in an additive fashion. Importantly, from about 250 ms after search display onset, the target N2pc became larger than the summed N2pc components to partially matching nontargets. This emergence of a superadditive target N2pc highlights the point in time when spatially selective attentional processing is no longer guided exclusively by signals from independent feature-specific channels, and attentional control begins to be integrated across feature dimensions. In other words, it marks the transition from the initial feature-based guidance of spatial attention to a second stage in which the allocation of focal attention is controlled in an object-based fashion.

The question of whether the difference between target and nontarget N2pc amplitudes observed beyond 250 ms poststimulus is the result of a selective enhancement of target processing or of a selective disengagement of spatial attention from partially matching nontargets cannot be decided on the basis of the present results. Our previous observation that partially target-matching cues elicited reliable N2pc components, but failed to trigger behavioral spatial cueing effects in response to subsequent targets (Kiss et al., 2013), suggest that attention is rapidly withdrawn from partially matching nontargets. The attentional inhibition of nontarget objects is known to trigger a contralateral positivity (PD component) at posterior electrodes (Gaspar & McDonald, 2014; Hickey, Di Lollo, & McDonald, 2009; Sawaki & Luck, 2010), and the reduction of summed N2pc components to partially matching nontargets relative to targets could reflect the emergence of an inhibition-related P_D component around 250 ms after search array onset. This possibility needs to be assessed in future research. Irrespective of whether the second object-selective stage of attentional selectivity operates via the enhancement of target processing or distractor inhibition, the pattern of N2pc results observed on no-competition trials provides new evidence for successive feature-based and object-based stages of attentional control, and new insights into when feature integration processes in visual search emerge in real time: From around 250 ms poststimulus, target objects have become more than the sum of their featural

The N2pc results from competition trials in which a target and a partially matching nontarget object were presented simultaneously provide evidence that the initial feature-based stage of attentional object selection operates in parallel for multiple locations in the visual field. On these trials, color-matching and shapematching nontarget objects triggered reliable N2pc components (see Figure 5), demonstrating that these objects were able to attract spatial attention, despite the fact that they were accompanied by a target object in the same display. This observation appears to be at odds with the predictions of the guided search model (Wolfe, 1994, 2007), which assumes that focal attention is directed serially to one object at a time (see also Jans, Peters, & De Weerd, 2010), and is first allocated to the object that produces the strongest spatial bias on the salience map. If this was correct, partially matching nontarget objects should not attract attention when a stronger competitor for attentional selection (i.e., the vertical target) is present in the same display. The fact that these nontarget objects triggered reliable N2pc components suggests instead that attention was initially allocated in parallel and simultaneously to targets and to color-matching or shape-matching nontarget objects (see also Eimer & Grubert, 2014, for further N2pc-based evidence for the parallel spatial selection of multiple objects). Furthermore, and analogous to the results observed for no-competition trials, the summed N2pc amplitudes to color-matching and shape-matching

nontargets were identical to the target N2pc during the early phase of the N2pc component on competition trials (Figure 5, bottom panel), indicating that the parallel selection of target-matching features operated independently and in an additive fashion for different feature dimensions.

The alternative possibility that target and nontarget N2pc components were triggered on different subsets of competition trials (e.g., McDonald et al., 2013) was ruled out by an additional analysis that separated N2pc components obtained on these trials on the basis on RT median splits. If nontarget N2pc components had been generated only on trials in which attention was incorrectly allocated to the partially matching nontarget object rather than to the target, these components should have been large on trials with slow target RTs, but small, or entirely absent, on trials with fast RTs. In fact, N2pc components to partially matching nontargets emerged at the same point in time and were of similar size regardless of whether responses to targets were slow or fast (see Figure 6). Furthermore, the point in time in which target N2pc waveforms became superadditive also did not differ between these two types of trials. These observations provide strong additional support for the hypothesis that attention was directed in parallel and simultaneously to targets and partially matching nontargets on competition trials.

Our finding that the summed N2pc components to partially matching nontargets perfectly matched the early N2pc to target objects both on no-competition and competition trials indicates that the initial stage of attentional selection in visual search is controlled by local signals from independent feature-specific modules, which trigger spatially specific modulations of visual processing at particular locations in the visual field, regardless of whether another target-matching object is simultaneously present at another location. However, the point in time at which target N2pc amplitudes started to become larger than the summed N2pc components to partially matching nontargets emerged significantly earlier on competition relative to no-competition trials (226 ms vs. 251 ms after search display onset; see Figure 4). This difference is likely to reflect the impact of spatially global competitive interactions between targets and partially matching nontargets in the same display. When a horizontal partially matching nontarget object is accompanied by a target on the vertical meridian, attention may be withdrawn more rapidly from this object relative to displays that do not contain a competing target. This will result in an attenuation of the N2pc component to partially matching nontargets, and, thus, in an earlier onset of a superadditive target N2pc on competition relative to no-competition trials.

Although the N2pc results obtained in this study suggest the existence of successive feature-based and object-based stages during the spatially selective perceptual processing of visual stimuli, an alternative hypothesis is that the emergence of a superadditive N2pc to targets versus partially matching nontargets reflects the encoding and maintenance of target stimuli in visual working memory. Working memory maintenance is known to be associated with sustained negative ERP components at contralateral posterior electrodes (e.g., Jolicoeur, Brisson, & Robitaille, 2008; Mazza et al., 2007; Vogel & Machizawa, 2004). Instead of marking the transition from feature-based to object-based control in perceptual attention, the temporal pattern of N2pc modulations observed in this study could therefore reflect the transition from perceptual selection to working memory processing. Because search display

duration was very brief (150 ms), sensory representations of selected objects may have been transformed into more durable working memory representations within 250 ms after display onset, and this transformation could have been responsible for the N2pc differences between target and partially matching nontarget objects observed within this time window.

To investigate this alternative interpretation, we ran a follow-up ERP experiment with 16 new participants (aged 20 to 36 years; mean age = 28.6 years) that was identical to the experiment described earlier in this article, except that search displays now remained visible until a manual response was registered. The pattern of N2pc results observed in this new experiment was very similar to the pattern of results found when display duration was limited to 150 ms. Figure 7 (top panel) shows grand-averaged contralateral and ipsilateral ERP waveforms on no-competition trials for displays with horizontal targets, color-matching nontargets, or shape-matching nontargets, together with N2pc difference waveforms for targets and summed partially matching nontargets

(bottom left panel). N2pc components were reliably elicited both by targets and partially matching nontargets (all ps < .003), and the summed N2pc to partially matching nontargets was initially identical to the target N2pc. A jackknife-based analysis conducted on N2pc double subtraction waveforms (using the same onset criteria as in the main experiment) revealed that the target N2pc started to become larger than the sum of the two nontarget N2pc components at 262 ms poststimulus. Figure 7 (middle panel) shows contralateral and ipsilateral ERPs on competition trials for search displays with horizontal targets (collapsed across trials with vertical color-matching or shape-matching nontargets), and with horizontal color-matching or shape-matching nontargets that were accompanied by a vertical target, together with N2pc difference waveforms for horizontal targets and summed partially matching nontargets (bottom right panel). N2pc components were reliably present in response to both targets and partially matching nontargets (all ps < .004). Target N2pcs and summed N2pc waveforms to partially matching nontargets were initially aligned, and the

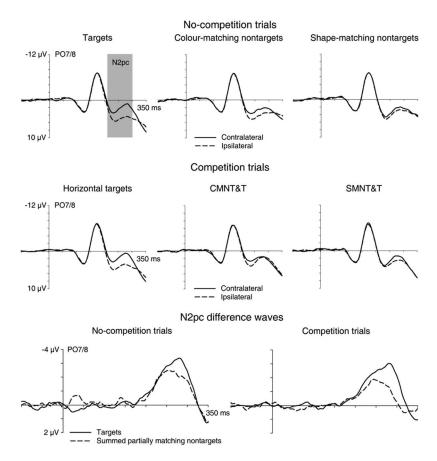


Figure 7. ERP results obtained in a control experiment in which search displays remained visible until a response was executed. Top and middle panels: Grand-average ERPs measured on no-competition and competition trials in the 350-ms poststimulus interval at posterior electrodes PO7/8 contralateral and ipsilateral to a horizontal target or partially matching nontarget. ERPs are shown separately for displays with horizontal targets and displays with horizontal color-matching or shape-matching nontargets. Bottom panel: N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs for no-competition trials (left panel) and competition trials (right panel). N2pc waveforms are shown separately for displays with horizontal targets (averaged across displays with a vertical color-matching and shape-matching nontarget; solid lines), and for displays with horizontal partially matching nontargets and vertical targets (summed across displays with color-and shape-matching nontargets; dashed lines).

target N2pc became larger than the summed nontarget N2pc at 247 ms poststimulus. A jackknife-based comparison showed that the superadditive target N2pc emerged earlier on competition versus no-competition trials (247 ms vs. 262 ms), $t_c(15) = 1.9$, p < .04(one-tailed), as was the case in the main experiment. These findings confirm the N2pc evidence for successive feature-based and object-based attentional control processes and for the parallel operation of feature-based attentional selectivity across different locations in the visual field that was obtained in our main experiment. They also demonstrate that these mechanisms are not specific to data-limited situations with brief search displays, but are also activated when the temporal demands on attentional selectivity are less extreme (see Kiss, Grubert, Petersen, & Eimer, 2012, for the existence of other qualitative differences of attentional control processes under conditions of high vs. low temporal task demands). The similarity in the N2pc results observed in these two experiments suggests that this pattern reflects the operation of successive feature-based and object-based stages of spatially selective perceptual processing rather than the transition from perceptual attention to working memory maintenance.

The observation that summed contributions of the N2pc to color-matching and shape-matching nontarget objects matched the target N2pc during the early phase of attentional object selection suggests that signals from different feature dimensions control the allocation of spatial attention in a parallel and independent fashion (see also Andersen, Hillyard, & Müller, 2008, for corresponding electrophysiological evidence from steady-state visual-evoked potentials). This conclusion is based on the assumption that the processes that generate N2pc components to color- and shapematching targets are indeed independent and therefore combine in an additive fashion. An analogous assumption has been made in ERP research on crossmodal integration, in which summed ERP waveforms to unimodal auditory and visual stimuli were compared with ERPs to bimodal audiovisual stimuli in order to identify superadditive effects indicative of multisensory interactions (e.g., Giard & Peronnet, 1999). Critics of this approach have pointed out that any ERP activity that is common to all conditions (e.g., activity related to stimulus expectations or sensory preparation) will be included twice in the summed ERP waveforms to unimodal events, which makes their comparison with ERPs to bimodal stimuli problematic (e.g., Teder-Sälejärvi, McDonald, Di Russo, & Hillyard, 2002). Although this argument is relevant for nonlateralized ERP components, it does not apply to the N2pc, which reflects the difference between contralateral and ipsilateral ERPs. When contralateral and ipsilateral ERPs are subtracted, nonlateralized ERP activity that is common to all task conditions is eliminated. In properly designed ERP experiments on visual search, N2pc components therefore exclusively reflect spatially selective attentional processes triggered by target-matching features or objects. The current findings show that these processes combine additively during a feature-based stage of attentional selection.

Our results demonstrate that visual search for conjunctively defined targets can be guided in an independent and parallel fashion by signals from different feature dimensions when these signals are equally effective in distinguishing targets from nontarget objects. In the present study, target and nontarget colors were perceptually similar, in order to equate target—nontarget discriminability in the color and shape dimensions, and to encourage

participants to use information from both dimensions in the control of spatial attention. With more distinctive stimulus colors, the discrimination between target and nontarget features would have been easier in the color relative to the shape domain. In this case, the feature-based stage of attentional selectivity may have been guided primarily by color, so that shape-matching nontarget objects would not have attracted attention and elicited N2pc components. Behavioral evidence suggests that such subset search strategies (e.g., select all red items, and then determine whether one of these items possesses the other target-defining feature) can be applied during conjunction search (Egeth, Virzi, & Garbart, 1984). The relationship between target—nontarget similarity within a given dimension, and the role of this dimension for feature-guided attentional control, needs to be investigated in future studies.

Unlike feature integration theory (Treisman, 1988; Treisman & Gelade, 1980) and guided search (Wolfe, 1994, 2007), which assume that attentional selection operates in a strictly serial fashion, the current findings suggest that during the early stage of feature-based spatial selection, focal attention can be allocated in parallel to target-matching features at different locations in the visual field (see also Eimer & Grubert, 2014). This observation is in line with a different model of selective attention, which also emphasizes successive stages in the attentional selection of visual objects. According to Boolean map theory (Huang & Pashler, 2007), visual scenes are partitioned into selected and nonselected regions (selection), and selected information can then be consciously apprehended (access). Selection operates through the creation of Boolean maps, which specify selected and nonselected areas of visual space on the basis of one particular feature value from one dimension (e.g., all red items in a display). In this model, targets defined by a combination of features from different dimensions are selected by generating Boolean maps for each of these features, and then using an intersection operation between these maps to generate a new Boolean map that only includes objects that match all target-defining features. Within the framework described by Huang and Pashler (2007), the early feature-based stage of spatial selectivity identified in the present study could represent the creation of Boolean maps based on color and shape information, whereas the subsequent object-based selection stage might reflect the generation of a new Boolean map by applying an intersection procedure to the color-based and shape-based maps. However, although our N2pc results suggest that spatial selection is guided in parallel by different feature dimensions, Boolean map theory assumes that only one feature-selective Boolean map can be generated at a time, and that conjunction search is therefore always based on a sequential subset search strategy (e.g., Egeth et al., 1984).

Instead of providing evidence that focal spatial attention is directed independently and simultaneously to targets and partially matching nontarget objects in the same display, the pattern of N2pc results observed in competition trials could, in principle, also reflect processes at the earlier stage of feature-based attention, which are known to operate in a spatially global fashion (e.g., Bichot et al., 2005; Martinez-Trujillo & Treue, 2004; Serences & Boynton, 2007). However, previous ERP experiments have reported effects of feature-based attention at poststimulus latencies of 100 ms (Zhang & Luck, 2009) or 140 ms (Hopf, Boelmans, Schoenfeld, Luck, & Heinze, 2004), well before the typical onset of the N2pc component, suggesting that feature-based attention

modulates early feedforward stages in the visual processing hierarchy (e.g., Zhang & Luck, 2009). In contrast, the N2pc is assumed to be generated at a subsequent stage in which spatially selective processing is triggered by recurrent feedback that signals the presence of target-matching features that are detected during the rapid feedforward analysis of visual information (e.g., Luck & Hillyard, 1994). In this scenario, spatially global feature-based attention precedes and guides spatially focal attentional selection during visual search (see also Eimer, 2014), and the N2pc component is generated during the later spatially selective phase of visual processing.

Overall, the current study provides new insights into the topdown control and temporal organization of attentional object selection during visual search for targets defined by feature conjunctions. By comparing N2pc components with targets and partially matching nontarget objects, we were able to dissociate an early feature-based stage of spatially selective processing that is controlled in a parallel and local fashion by signals from independent feature modules, and a subsequent object-based stage in which these signals are integrated across feature dimensions. During the early stage, the target N2pc exclusively reflects the sum of its component parts (i.e., the N2pc components to color- and shapematching nontargets). During a later stage, spatially selective attentional processing is sensitive to the presence of feature conjunctions, and the target N2pc becomes superadditive. The idea that attentional object selection involves a feature-based stage that is followed by a subsequent stage in which integrated object representations are generated is a central part of influential models of visual attention such feature integration theory, guided search, or Boolean map theory. The current study demonstrates that the transition between these stages can be tracked in real time with the help of electrophysiological measures.

References

- Andersen, S. K., Hillyard, S. A., & Müller, M. M. (2008). Attention facilitates multiple stimulus features in parallel in human visual cortex. *Current Biology*, 18, 1006–1009. doi:10.1016/j.cub.2008.06.030
- Bichot, N. P., Rossi, A. F., & Desimone, R. (2005). Parallel and serial neural mechanisms for visual search in macaque area V4. *Science*, 308, 529–534. doi:10.1126/science.1109676
- Bundesen, C. (1990). A theory of visual attention. *Psychological Review*, 97, 523–547. doi:10.1037/0033-295X.97.4.523
- Carlisle, N. B., Arita, J. T., Pardo, D., & Woodman, G. F. (2011).
 Attentional templates in visual working memory. *The Journal of Neuroscience*, 31, 9315–9322. doi:10.1523/JNEUROSCI.1097-11.2011
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. Annual Review of Neuroscience, 18, 193–222. doi:10.1146/ annurev.ne.18.030195.001205
- Duncan, J. (1984). Selective attention and the organization of visual information. *Journal of Experimental Psychology: General*, 131, 501– 517. doi:10.1037/0096-3445.113.4.501
- Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review*, 96, 433–458. doi:10.1037/0033-295X .96.3.433
- Egeth, H. E., Virzi, R. A., & Garbart, H. (1984). Searching for conjunctively defined targets. *Journal of Experimental Psychology: Human Perception and Performance*, 10, 32–39. doi:10.1037/0096-1523.10 .1.32
- Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography & Clinical Neurophysiology*, 99, 225–234. doi:10.1016/0013-4694(96)95711-9

- Eimer, M. (2014). The neural basis of attentional control in visual search. *Trends in Cognitive Sciences*. doi:10.1016/j.tics.2014.05.005
- Eimer, M., & Grubert, A. (2014). Spatial attention can be allocated rapidly and in parallel to new visual objects. *Current Biology*, 24, 193–198. doi:10.1016/j.cub.2013.12.001
- Eimer, M., & Kiss, M. (2008). Involuntary attentional capture is determined by task set: Evidence from event-related brain potentials. *Journal of Cognitive Neuroscience*, 20, 1423–1433. doi:10.1162/jocn.2008 20099
- Eimer, M., Kiss, M., & Nicholas, S. (2011). What top-down task sets do for us: An ERP study on the benefits of advance preparation in visual search. *Journal of Experimental Psychology: Human Perception and Performance*, 37, 1758–1766. doi:10.1037/a0024326
- Eimer, M., Kiss, M., Press, C., & Sauter, D. (2009). The roles of feature-specific task set and bottom-up salience in attentional capture: An ERP study. *Journal of Experimental Psychology: Human Perception and Performance*, 35, 1316–1328. doi:10.1037/a0015872
- Folk, C. L., & Anderson, B. A. (2010). Target-uncertainty effects in attentional capture: Color singleton set or multiple attentional control settings? *Psychonomic Bulletin & Review*, 17, 421–426. doi:10.3758/ PBR 17 3 421
- Folk, C. L., Remington, R. W., & Johnston, J. C. (1992). Involuntary covert orienting is contingent on attentional control settings. *Journal of Experimental Psychology: Human Perception and Performance*, 18, 1030–1044. doi:10.1037/0096-1523.18.4.1030
- Gaspar, J. M., & McDonald, J. J. (2014). Suppression of salient objects prevents distraction in visual search. *Journal of Neuroscience*, 34, 5658–5666. doi:10.1523/JNEUROSCI.4161-13.2014
- Giard, M. H., & Peronnet, F. (1999). Auditory-visual integration during multimodal object recognition in humans: A behavioral and electrophysiological study. *Journal of Cognitive Neuroscience*, 11, 473–490. doi: 10.1162/089892999563544
- Hickey, C., Di Lollo, V., & McDonald, J. J. (2009). Electrophysiological indices of target and distractor processing in visual search. *Journal of Cognitive Neuroscience*, 21, 760–775. doi:10.1162/jocn.2009.21039
- Hickey, C., McDonald, J. J., & Theeuwes, J. (2006). Electrophysiological evidence of the capture of visual attention. *Journal of Cognitive Neu*roscience, 18, 604–613. doi:10.1162/jocn.2006.18.4.604
- Hopf, J. M., Boelmans, K., Schoenfeld, A., Luck, S. J., & Heinze, H.-J. (2004). Attention to features precedes attention to locations in visual search: Evidence from electromagnetic brain responses in humans. *The Journal of Neuroscience*, 24, 1822–1832. doi:10.1523/JNEUROSCI .3564-03.2004
- Huang, L., & Pashler, H. (2007). A Boolean map theory of visual attention. Psychological Review, 114, 599-631. doi:10.1037/0033-295X.114.3 .599
- Jans, B., Peters, J. C., & De Weerd, P. (2010). Visual spatial attention to multiple locations at once: The jury is still out. *Psychological Review*, 117, 637–682. doi:10.1037/a0019082
- Jolicoeur, P., Brisson, B., & Robitaille, N. (2008). Dissociation of the N2pc and sustained posterior contralateral negativity in a choice response task. *Brain Research*, 1215, 160–172. doi:10.1016/j.brainres.2008.03.059
- Kiss, M., Grubert, A., & Eimer, M. (2013). Top-down task sets for combined features: Behavioural and electrophysiological evidence for two stages in attentional object selection. *Attention, Perception, & Psychophysics*, 75, 216–228. doi:10.3758/s13414-012-0391-z
- Kiss, M., Grubert, A., Petersen, A., & Eimer, M. (2012). Attentional capture by salient distractors during visual search is determined by temporal task demands. *Journal of Cognitive Neuroscience*, 24, 749– 759. doi:10.1162/jocn_a_00127
- Leblanc, É., Prime, D. J., & Jolicoeur, P. (2008). Tracking the location of visuospatial attention in a contingent capture paradigm. *Journal of Cognitive Neuroscience*, 20, 657–671. doi:10.1162/jocn.2008.20051

- Lien, M.-C., Ruthruff, E., Goodin, Z., & Remington, R. W. (2008). Contingent attentional capture by top-down control settings: Converging evidence from event-related potentials. *Journal of Experimental Psychology: Human Perception and Performance*, 34, 509–530. doi: 10.1037/0096-1523.34.3.509
- Luck, S. J., & Hillyard, S. A. (1994). Spatial filtering during visual search: Evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception and Performance*, 20, 1000–1014. doi: 10.1037/0096-1523.20.5.1000
- Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature*, 390, 279–281. doi:10.1038/36846
- Martinez-Trujillo, J. C., & Treue, S. (2004). Feature-based attention increases the selectivity of population responses in primate visual cortex. *Current Biology*, 14, 744–751. doi:10.1016/j.cub.2004.04.028
- Mazza, V., Turatto, M., Umiltà, C., & Eimer, M. (2007). Attentional selection and identification of visual objects are reflected by distinct electrophysiological responses. *Experimental Brain Research*, 181, 531– 536. doi:10.1007/s00221-007-1002-4
- McDonald, J. J., Green, J. J., Jannati, A., & Di Lollo, V. (2013). On the electrophysiological evidence for the capture of visual attention. *Journal of Experimental Psychology: Human Perception and Performance*, 39, 849–860. doi:10.1037/a0030510
- Miller, J., Patterson, T., & Ulrich, R. (1998). Jackknife-based method for measuring LRP onset latency differences. *Psychophysiology*, 35, 99– 115. doi:10.1111/1469-8986.3510099
- Müller, H. J., & Krummenacher, J. (2006). Locus of dimension weighting: Pre-attentive or post-selective? *Visual Cognition*, 14, 490–513. doi: 10.1080/13506280500194154
- Olivers, C. N. L., Peters, J., Houtkamp, R., & Roelfsema, P. R. (2011). Different states in visual working memory: When it guides attention and when it does not. *Trends in Cognitive Sciences*, 15, 327–334.
- Saenz, M., Buracas, G. T., & Boynton, G. M. (2002). Global effects of feature-based attention in human visual cortex. *Nature Neuroscience*, 5, 631–632. doi:10.1038/nn876
- Sawaki, R., & Luck, S. (2010). Capture versus suppression of attention by salient singletons: Electrophysiological evidence for an automatic attend-to-me signal. Attention, Perception, & Psychophysics, 72, 1455– 1470. doi:10.3758/APP.72.6.1455
- Schubö, A., & Müller, H. J. (2009). Selecting and ignoring salient objects within and across dimensions in visual search. *Brain Research*, 1283, 84–101. doi:10.1016/j.brainres.2009.05.077

- Serences, J. T., & Boynton, G. M. (2007). Feature-based attentional modulations in the absence of direct visual stimulation. *Neuron*, 55, 301–312. doi:10.1016/j.neuron.2007.06.015
- Teder-Sälejärvi, W. A., McDonald, J. J., Di Russo, F., & Hillyard, S. A. (2002). An analysis of audio-visual crossmodal integration by means of event-related potential (ERP) recordings. *Cognitive Brain Research*, 14, 106–114. doi:10.1016/S0926-6410(02)00065-4
- Treisman, A. (1988). Features and objects: The fourteenth Bartlett memorial lecture. *The Quarterly Journal of Experimental Psychology A: Human Experimental Psychology, 40,* 201–237. doi:10.1080/02724988843000104
- Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. Cognitive Psychology, 12, 97–136. doi:10.1016/0010-0285(80)90005-5
- Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature*, 428, 748–751. doi:10.1038/nature02447
- Wheeler, M. E., & Treisman, A. (2002). Binding in short-term visual memory. *Journal of Experimental Psychology: General*, 131, 48–64. doi:10.1037/0096-3445.131.1.48
- Wolfe, J. M. (1994). Guided Search 2.0: A revised model of visual search. Psychonomic Bulletin & Review, 1, 202–238. doi:10.3758/BF03200774
- Wolfe, J. M. (2007). Guided Search 4.0: Current progress with a model of visual search. In W. Gray (Ed.), *Integrated models of cognitive systems* (pp. 99–119). New York, NY: Oxford University Press.
- Woodman, G. F., & Luck, S. J. (1999). Electrophysiological measurement of rapid shifts of attention during visual search. *Nature*, 400, 867–869. doi:10.1038/23698
- Woodman, G. F., & Luck, S. J. (2003). Serial deployment of attention during visual search. *Journal of Experimental Psychology: Human Per*ception and Performance, 29, 121–138. doi:10.1037/0096-1523.29.1 121
- Woodman, G. F., & Vogel, E. K. (2008). Selective storage and maintenance of an object's features in visual working memory. *Psychonomic Bulletin & Review*, 15, 223–229. doi:10.3758/PBR.15.1.223
- Zhang, W., & Luck, S. J. (2009). Feature-based attention modulates feedforward visual processing. *Nature Neuroscience*, 12, 24–25. doi:10.1038/nn.2223

Received December 5, 2013 Revision received May 2, 2014

Accepted June 6, 2014 ■