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Feature priming and the capture of visual attention: Linking two ambiguity resolution hypotheses

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Visual search for a unique stimulus is often faster when the feature defining this target is repeated. Recent research has related this feature priming to ambiguity: priming effects appear stronger when the search target is perceptually ambiguous, as when the search array contains a salient distractor. Here we link the ambiguity that underlies feature priming to ambiguity in neural representation caused by the receptive field organization of visual cortex. We show that as the magnitude of neural activity involved in resolving perceptual ambiguity in early stages of visual cortex increases–indexed in posterior aspects of the N2pc component of the visual-event related potential–so does the behavioral feature priming effect. When ambiguity resolution mechanisms act strongly and the target repeats, target processing is facilitated. When these mechanisms act strongly, but the features that have previously defined the target come to characterize the distractor, attention is captured to the distractor location. These results suggest that ambiguity and the attentional mechanisms responsible for resolving it play central roles in feature priming.

1. Introduction

Visual search for a unique target item is quicker when the property that defines this object is repeated between trials. In one of the first studies to demonstrate this Maljkovic and Nakayama (1994) had subjects search for a uniquely colored diamond–a *color singleton*–that was presented with two distractor diamonds. Critically, the colors that defined the target and distractors could swap between trials such that the target could be red on one trial (with green distractors) but green on the next (with red distractors). Reaction times (RTs) to the target were up to 100 ms faster when the colors stayed the same from trial to trial, a pattern that has become widely known as feature priming.

One compelling explanation for feature priming is that perception of target features is facilitated when they are repeated (e.g. Maljkovic and Nakayama, 1996; Found and Müller, 1996; Müller et al., 2003). This basic premise is reflected in Maljkovic and Nakayama's (1996) "capacitor" model of priming, which suggests that increases in target activation (and decreases in distractor activation) summate over repetitions, resulting in a target representation that is more likely to draw attention efficiently. Physiological measures support this notion: neurons in monkey frontal eye fields respond more strongly to a color singleton target when the color defining that target has not changed from the previous trial (Bichot and Schall, 2002), and in humans an early stage of the exogenous visual response indexed by the lateral P1 event-

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related potential (ERP) component is speeded in repeat trials (Olivers and Hickey, 2010). However, others have argued that the facilitation caused by target repetition is rather due to priming of response-related representations (Cohen and Shoup, 1997; Cohen and Magen, 1999; Kumada, 2001). For example, Kumada (2001) found that priming occurred in a simple search task when participants were required to report the presence or absence of a color singleton target, but was absent in a compound search task where the target was always present and response was based on a small arrow contained within this object.

To account for these disparate findings, Meeter and Olivers (2006; Olivers and Meeter, 2006) have suggested that the effects of repetition priming in visual search might become apparent only under circumstances of ambiguity. The level at which priming expresses then depends on the level at which the ambiguity arises. If a visual search task is perceptually ambiguous, as when a salient distractor is present in the display and competes for resources, then priming will aid visual selection when target features repeat between trials (Meeter and Olivers, 2006). However, visual search tasks can also be ambiguous at higher levels, for example at processing stages where the stimulus is mapped onto a response. Ambiguity at this later stage may cause priming to occur as a function of response characteristics, even when visual displays do not change.

The ambiguity resolution hypothesis of feature priming is a developing account, and it can be criticized for providing only a loose definition of what is meant by "ambiguity." One goal of the current study was to develop a more objective definition of ambiguity in perceptual processing. Definitions of perceptual ambiguity have been offered in the literature in other contexts. In fact, Olivers and Meeter are not the first to develop an 'ambiguity resolution hypothesis'; Luck et al. (1997a) also used this name for a model of visual attention. According to Luck et al., ambiguity occurs when visual objects share a neural receptive field (RF). This is based on the observation that visual neurons are preferentially selective for stimuli that fall in their RFs. At low-level visual areas RFs are small and the information encoded by any given neuron is quite simple. High-level visual areas consolidate information such that the encoded information becomes more complex, and RFs associated with these higher-level neurons become correspondingly larger (Desimone and Ungerleider, 1989). This eventually creates a problem: stimuli come to share receptive fields and cellular output can no longer be attributed to discrete stimuli. Luck et al. propose that the core responsibility of visual attention is the resolution of this problem, and that this takes place through the suppression of distractor representations. This makes Luck et al.'s ambiguity resolution hypothesis similar in nature to other competition-based theories of attention like the biased competition model of Desimone and Duncan (1995) and the spatial tuning model of Tsotsos et al. (1995).

A central premise of the Luck et al. (1997b) hypothesis is that ambiguity resolution can be indexed in the N2pc component of the visual event-related potential (ERP). The N2pc is a lateralized component that is evident as an increased negativity in the ERP elicited over visual cortex contralateral to an attended item (Luck and Hillyard, 1994a,b).

Early work suggested that the N2pc reflects distractor suppression, for example showing that the component is absent when visual search displays do not contain distractor stimuli or when distractors cannot be suppressed because they contain relevant information or somehow define the target (Luck and Hillyard, 1994b). There also appears to be a close correspondence between the N2pc and electrophysiological evidence of attentional suppression in monkey visual cortex: both become evident at approximately 175 ms post-stimulus and are more pronounced for difficult discrimination tasks and when distractors are near the target rather than far away (Luck et al., 1997b).

Other results have been difficult to reconcile with the distractor suppression hypothesis. For example, the N2pc can be observed contralateral to a single lateralized stereoscopic image in the absence of conventional distractors (Shedden and Nordgaard, 2001), and contralateral to a target when it is the only stimulus presented in one visual hemifield and all distractors are presented to the contralateral hemifield (Eimer, 1996). This latter finding is important as it suggests that the N2pc is created in cortex that is responsible for representing the target, and thus does not reflect modulation of the distractor representation itself.[1] A more recent study has demonstrated that N2pc amplitude does not vary as a function of the need for distractor suppression, and that the component can be elicited under circumstances where distractor suppression would presumably be counter-productive (Mazza et al., 2009). Results like these have led to the recent proposal that the N2pc may index ambiguity resolution through the action of multiple mechanisms, some acting on brain areas responsible for representing the distractor and others acting on brain areas responsible for representing the target itself (Hickey et al., 2009).

This last perspective is the one adopted in the current study: we believe that the N2pc indexes more than one attentional mechanism, as suggested by Hickey et al. (2009), but that the core purpose of these operations is the resolution and disambiguation of visual input, as suggested by Luck et al. (1997b). In the context of feature priming, this motivates the possibility that the type of perceptual ambiguity resolved by the N2pc may be similar in nature to the type of perceptual ambiguity that Meeter and Olivers (2006; Olivers and Meeter, 2006) suggest causes feature priming. A prediction can be generated from this idea, namely that manipulations of perceptual ambiguity that increase intertrial priming–such as the inclusion of a salient distractor in a display–should create a larger target-elicited N2pc.

In order to test this hypothesis we recorded ERPs while participants completed a task based on the *additional singleton paradigm* of Theeuwes (1991). Participants searched for a shape singleton and responded based on the orientation of a line contained within this object. There were two important manipulations in the experimental design. First, display ambiguity was varied by replacing one of the non-targets in

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[1] This does not discount the possibility that the N2pc indexes a suppressive process that inhibits distractor-related input to neurons responsible for target representation. Such a mechanism could be indexed contralateral to the target, yet still reflect distractor suppression.

the search display with a task-irrelevant singleton defined by unique color. This is known to slow reaction time (RT) and increase error in this task, reflecting increased competition for selection (Theeuwes, 1991). Second, in order to measure intertial priming, the colors that defined the target and distractor in any one trial could remain the same in the next trial or could swap.

Given this design we generated three predictions. First, the amplitude of target-elicited N2pc should be larger when displays contain a salient distractor and attention is deployed to the target. Second, if the N2pc reflects the action of mechanisms responsible for the resolution of perceptual ambiguity, and there is a relationship between these mechanisms and intertrial priming, there should be a correlation between this increase in target-elicited N2pc and the corresponding increase in behavioral feature priming: those participants who show a larger N2pc should also show greater priming. Finally, as suggested by existing behavioral work (Pinto et al., 2005; Becker, 2007), attention should be misallocated to the salient distractor when the colors defining the target and distractor swap between trials, and this should be evident in a distractor-elicited N2pc (Hickey et al., 2006, 2010a). This would suggest that the activation of target features and/or suppression of distractor features involved in target resolution has a residual impact on visual processing, resulting in a net benefit for the processing of features that have characterized the target. When the colors swap between trials, and the primed color comes to characterize the distractor, this will benefit resolution of the distractor at the expense of the target.

2. Results

2.1. Behavioral results

The salient distractor slowed target response (absent RT: 820 ms, present RT: 902). Swap trials were 19 ms slower than no-swap trials in the distractor present condition (no-swap: 893 ms, swap: 912 ms) and 6 ms in the distractor absent condition (no-swap: 817 ms, swap: 823 ms). A repeated measures analysis of variance (RANOVA) with factors for distractor presence (present vs. absent) and intertrial condition (swap vs. no-swap) identified a main effect of distractor presence ($F(1,11)=21.089$, $p<0.001$), a marginally significant effect of intertrial condition ($F(1,11)=3.724$, $p=0.080$), and a marginally significant interaction between factors ($F(1,11)=3.822$, $p=0.077$). A planned contrast of the simple effect of intertrial contingency in the distractor-present condition confirmed the reliability of the intertrial effect in this condition ($t(11)=2.530$, $p=0.014$). Analysis of error revealed no significant effects (distractor present no-swap: 8.2%, swap: 8.9%; distractor absent no-swap: 8.0%, swap: 7.3%; distractor presence: $F(1,11)=1.608$, $p=0.231$, all other $Fs<1$).

2.2. Electrophysiological results

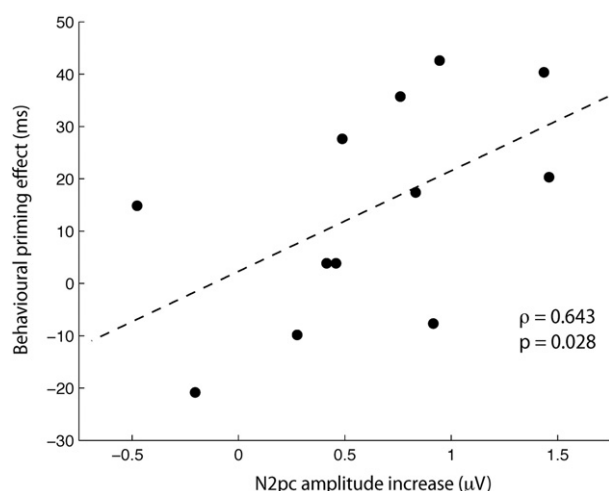Our expectation was that the N2pc would increase in magnitude when a salient distractor was included in the visual search display and attention was deployed to the target. The results
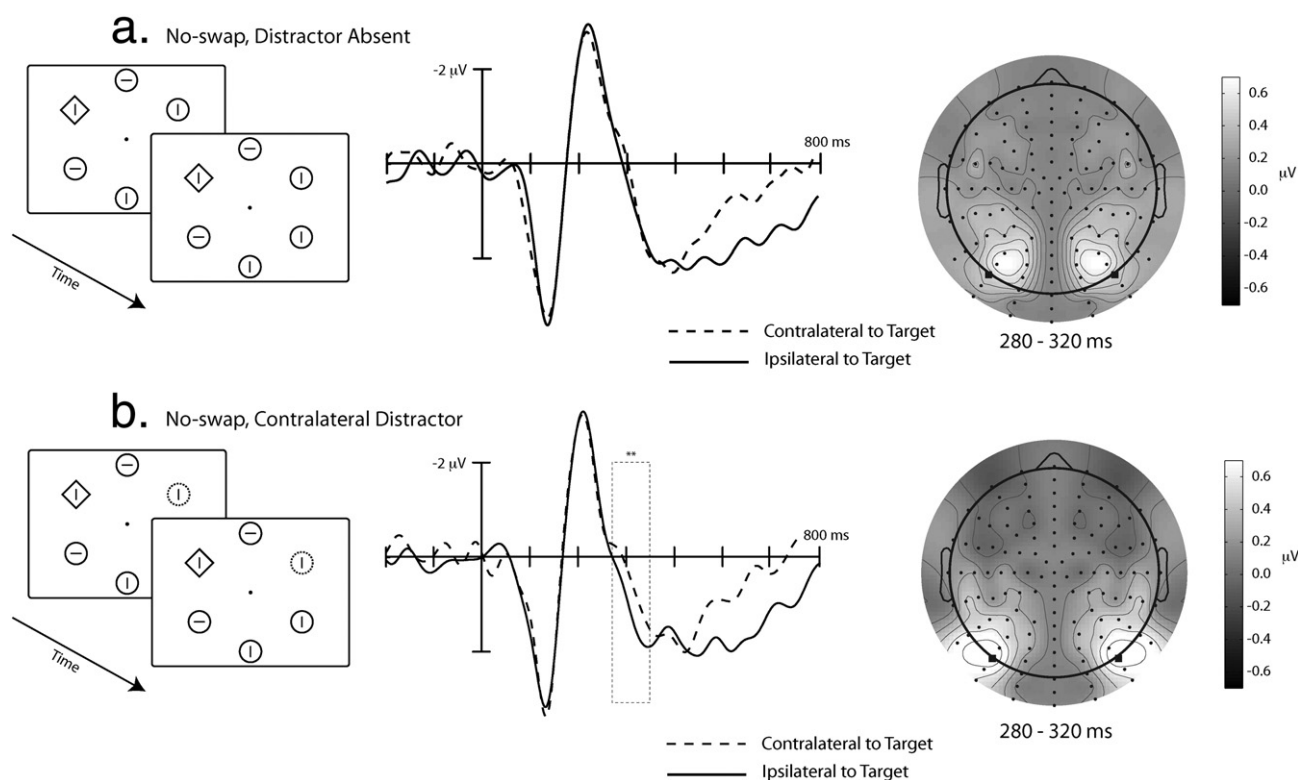
Fig. 1 – ERPs and topography from conditions in which the colors have not swapped between trials, and (a) the distractor is absent from the display, and (b) the distractor is presented to one of the contralateral display positions.

show that the presence of the salient distractor in fact had two effects on the N2pc, causing an increase in amplitude and a general broadening and shift of the topography towards more posterior and lateral visual cortex (cf. topographic maps in Fig. 1a and b). There is little in the way of an N2pc apparent at posterior electrode locations in the no-swap, distractor absent condition (Fig. 1a), but the component is clear in the divergence of ipsilateral and contralateral waveforms between 280 and 360 ms in the no-swap, distractor present condition (Fig. 1b). To test the reliability of this increase in the posterior aspect of the N2pc we conducted a three-way repeated measures analysis of variance (RANOVA). This analysis was based on mean amplitude in the no-swap conditions measured from 280 to 360 ms with factors for electrode location (ipsilateral vs. contralateral), target location (left hemifield vs right hemifield), and distractor presence (distractor-present vs. distractor-absent). The interaction between distractor presence and electrode location was significant ($F(1,11)=6.789$, $p=0.025$), reflecting a reliable increase in target-elicited N2pc amplitude from Fig. 1a to b. No other effects were reliable (electrode location: $F(1,11)=4.327$, $p=0.062$; target location: $F(1,11)=2.686$, $p=0.130$; all other $Fs<1$). A corresponding analysis based on peak amplitude garnered much the same pattern (electrode location: $F(1,11)=12.167$, $p=0.004$; distractor presence × electrode location: $F(1,11)=5.267$, $p=0.042$; all other $Fs<1$). Note that here and in subsequent analyses of peak amplitude computations are based on the amplitude of the ipsilateral and contralateral waveforms as observed at the maximum ipsilateral/contralateral difference in the 200 to 400 ms post-stimulus interval.

To test whether this posterior amplitude increase/topographic shift was related to behavior, we correlated the change in target-elicited N2pc observed in trials where the colors repeated to the behavioral priming effect. We calculated an absolute measure of the increase in behavioral feature priming caused by the salient distractor priming for each subject in two steps. We first subtracted the no-swap RT from the swap RT for both distractor present and distractor absent conditions, and then further subtracted the value thus calculated for the distractor absent condition from that for the distractor present condition. We measured the per-subject increase in N2pc amplitude from the no-swap, distractor-absent condition (Fig. 1a) to the no-swap, contralateral distractor condition (Fig. 1b) by subtracting the contralateral waveform from the ipsilateral waveform for each condition and subsequently subtracting the value thus calculated for the no-swap, distractor-absent condition from the value calculated for the no-swap, contralateral-distractor condition. As illustrated in Fig. 2, the early aspect of this increase in N2pc (as measured from 270 to 330 ms) correlated with the measure of increase in behavioral feature priming (Spearman's $\rho=0.643$; permutation test $p=0.028$).[2]

Because the target-elicited N2pc is not evident in the ERP illustrated in Fig. 1a, which was elicited in the no-swap, distractor absent condition at posterior electrode sites roughly equivalent to PO7 and PO8 of the 10/10 electrode placement system, Fig. 3a presents the ERP elicited in the same condition as recorded at slightly more anterior electrode locations.[3] The magnitude, latency, and topography of this N2pc (Fig. 3a) are quite similar to the same measures observed when the colors swapped between conditions (Fig. 3b). In statistical analysis of these components, a 3-way RANOVA with factors for electrode location, target location, and intertrial condition (based on mean amplitude from 255 to 300 ms) revealed a significant main effect of electrode location ($F(1,11)=5.197$, $p=0.043$) but no other effects (electrode location × target location × intertrial condition: $F(1,11)=2.502$, $p=0.138$; all other $Fs<1$). Analysis of peak amplitude garnered similar results (intertrial condition × electrode location: $F(1,11)=3.874$, $p=0.071$; electrode location: $F(1,11)=6.117$, $p=0.031$; all other $Fs<1$).

Fig. 2 – The relationship between the behavioral priming effect, on the Y-axis, and the increase of N2pc amplitude from the ERP illustrated in Fig. 1a to the ERP illustrated in Fig. 1b on the X-axis.

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[2] The correlation described here is based on N2pc amplitude as observed in repeat trials, rather than in both repeat and swap trials, and this deserves some explanation. The presence of the salient distractor in the repeat condition caused a quantitative difference in target-elicited N2pc amplitude: the N2pc became larger. Results in the swap condition were quite different: the presence of the salient distractor resulted in the capture of attention, as reflected in a distractor-elicited N2pc (see Fig. 4c). This makes comparison of the N2pc components elicited as a function of distractor presence in the swap condition problematic. Distractor-elicited N2pc components, when present at all, are often smaller, shorter, and less reliable than the target-elicited sort (e.g. Hickey et al., 2006; Eimer and Kiss, 2008). A distractor-elicited N2pc is thus likely to be smaller than a target-elicited N2pc, irrespective of visual ambiguity. Moreover, the distractor-elicited N2pc and target-elicited N2pc may not vary as a function of perceptual ambiguity in the same way; a salient distractor might increase target-elicited N2pc, because the target representation is more ambiguous and target resolution is more difficult, but decrease distractor-elicited N2pc, because the distractor representation is less ambiguous and distractor resolution is easier. By limiting correlational analysis to the repeat condition we circumvent these potential problems.

[3] The ERPs presented in Figs. 1, 3, and 4 were recorded at posterior electrodes labeled A10 and B7 in the Biosemi nomenclature. These positions are identified by black squares in the topographic maps presented in Figs. 3 and 4. The ERPs presented in Fig. 2 were recorded at slightly more anterior electrodes labeled A8 and B5 in Biosemi nomenclature, and these positions are identified in the topographic maps in Fig. 2.
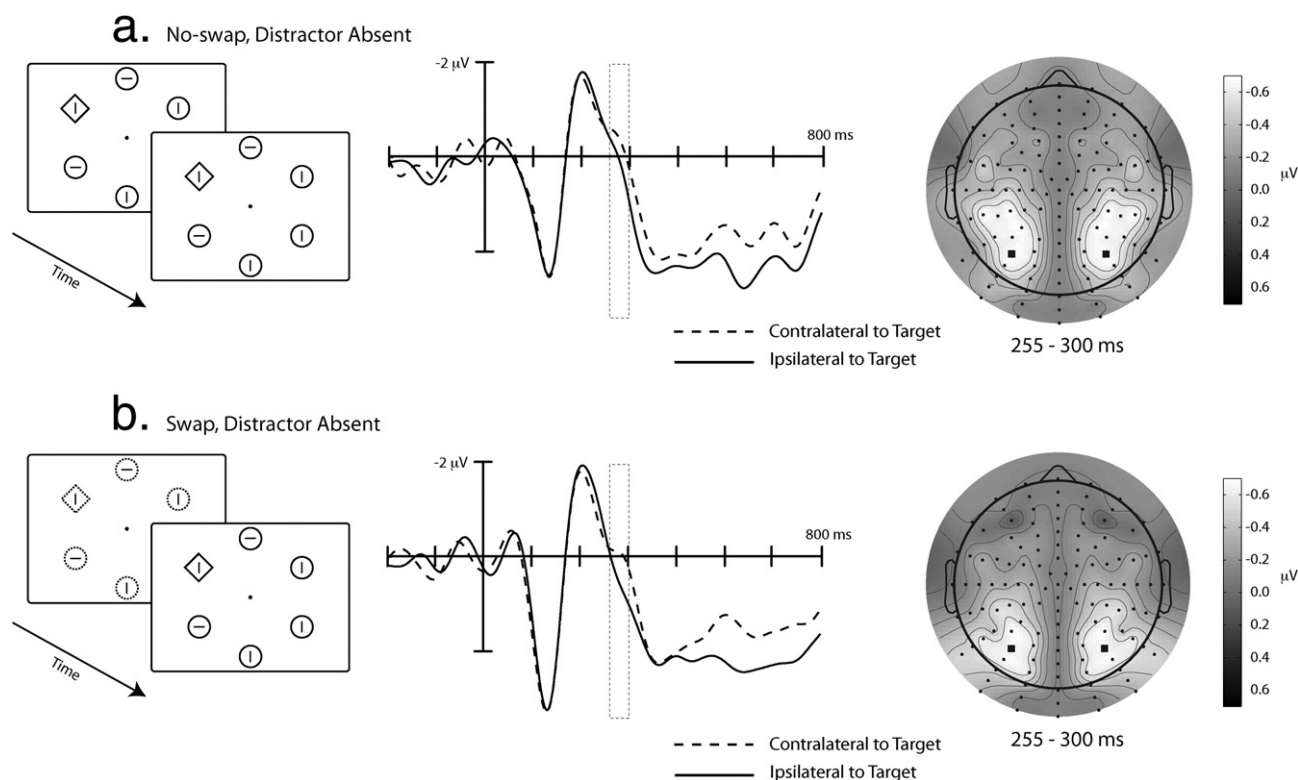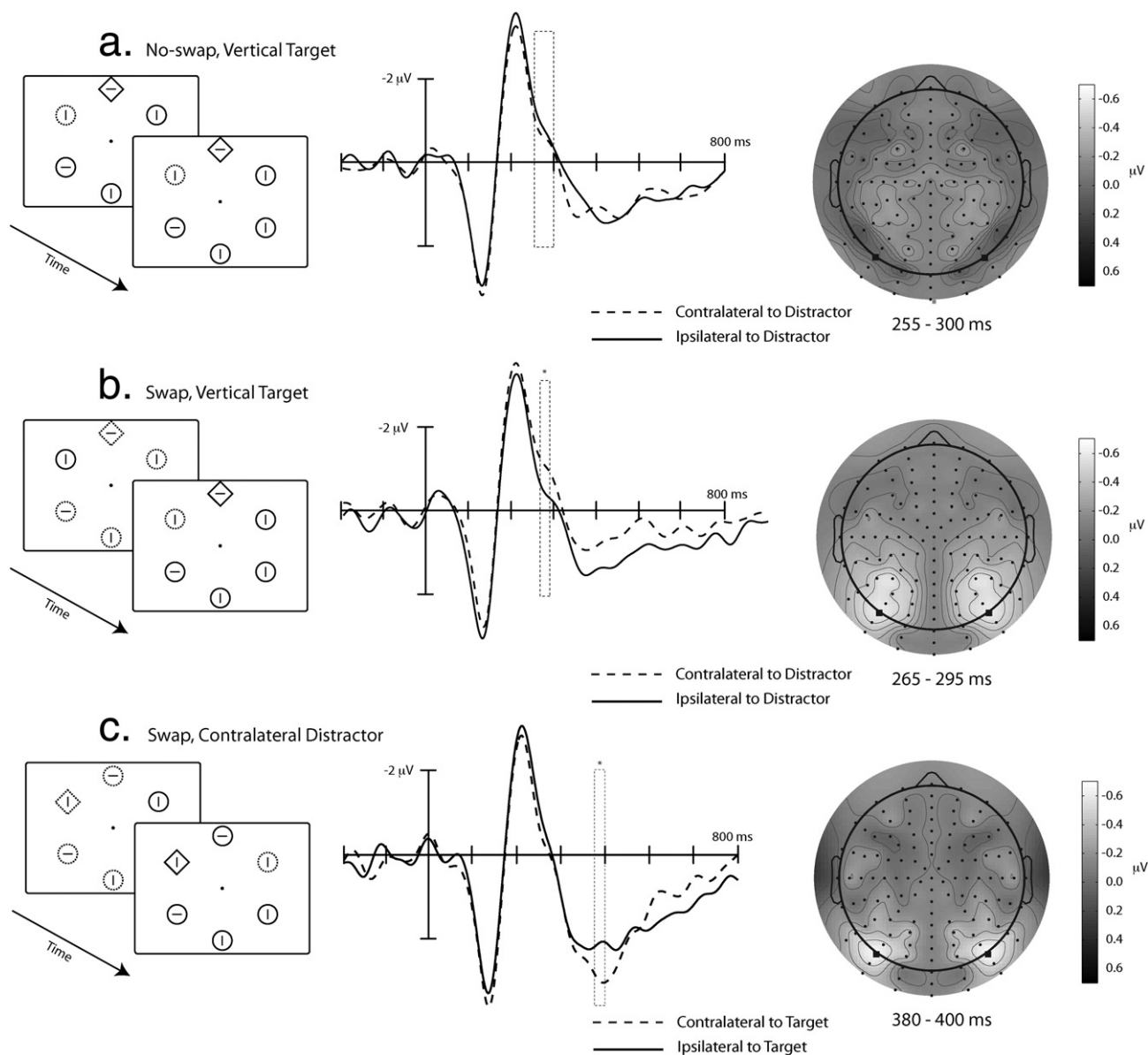
Fig. 3 – ERPs and topography from conditions in which no salient distractor was present in the display and (a) the colors defining the target have not changed from the immediately preceding trial to the current trial, and (b) the colors defining the target and distractors have swapped between trials.

Our final prediction was that attention would be deployed to the distractor in swap trials, resulting in a distractor-elicited N2pc. With this in mind we examined the ERP created when the target was presented on the vertical meridian of the visual search array and the salient distractor was presented to a lateral position. Under these circumstances the target is equally represented in both of the visual cortices and deployment of attention to its location does not create lateralized activity in visual cortex (Woodman and Luck, 2003; Hickey et al., 2006, 2009, 2010a). This means that any lateralized activity identified in the ERP elicited by this stimulus configuration can be unambiguously associated to processing of the distractor. In the no-swap condition there is little evidence of any difference between ipsilateral and contralateral waveforms (Fig. 4a), but in the swap ERP a distractor-elicited N2pc is evident (Fig. 4b). This pattern was statistically assessed in a 3-way RANOVA with factors for electrode location, target location, and intertrial condition based on mean amplitude from 265 to 290 ms. A significant interaction between electrode location and intertrial condition was revealed, reflecting a reliable increase of distractor-elicited N2pc amplitude in the swap condition ($F(1,11)=4.996$, $p=0.047$). No other effects were significant (electrode location: $F(1,11)=1.227$, $p=0.288$; target location: $F(1,11)=1.786$, $p=0.204$; electrode location×target location: $F(1,11)=1.087$, $p=0.316$; all other $Fs<1$). Analysis based on amplitude observed at the latency of the N2pc peak in the swap condition garnered similar results (electrode location×intertrial condition:

$F(1,11)=5.725$, $p=0.036$; electrode location: $F(1,11)=2.661$, $p=0.131$; all other $Fs<1$).

Consistent with the idea that attention was deployed to the distractor in swap trials, there is little evidence of a target-elicited N2pc in the ERP elicited when the colors swapped and the target and distractor were presented contralateral to one another (Fig. 4c). In contrast, a late distractor-elicited N2pc is apparent. Beginning at approximately 380 ms the waveform elicited contralateral to the *distractor* (and thus ipsilateral to the target) is more negative than the waveform elicited ipsilateral to the distractor (and thus contralateral to the target). To demonstrate that the target-elicited N2pc elicited in the no-swap condition (Fig. 1b) was reliably different from the ERP elicited through the same time period in the swap condition (Fig. 4c) we conducted a 3-way RANOVA with factors for electrode location, target location, and target. This analysis was based on mean ERP amplitude measured from 280 to 360 ms post-stimulus and revealed a significant interaction between the electrode location and color-repetition factors, demonstrating a reliable increase in target-elicited N2pc amplitude in Fig. 1b ($F(1,11)=5.385$, $p=0.041$). In addition a main effect of target position was identified ($F(1,11)=10.317$, $p=0.008$), reflecting a larger N2 component over the right visual cortex; this effect is unimportant for the purposes of the present study. No other effects were significant (electrode location: $F(1,11)=1.729$, $p=0.215$; color repetition: $F(1,11)=2.295$, $p=0.158$; all other $Fs<1$). Analysis based on peak amplitude observed at the peak of the N2pc illustrated in Fig. 1b garnered

Fig. 4 – ERPS and topography from conditions in which (a) the target was presented to a position on the vertical meridian of the display, the distractor was presented to a lateral position, and the colors did not swap, (b) the target was presented to a position on the vertical meridian, the distractor was presented to a lateral position, and the colors did swap, and (c) the target was presented to a lateral position, the distractor was presented at one of the positions located contralateral to the target, and the colors did swap.

similar results (electrode location × intertrial condition: $F(1,11)=$ 6.339, $p=0.029$; target position: $F(1,11)=12.887$, $p=0.004$; color repetition: $F(1,11)=1.468$, $p=0.251$; all other $Fs<1$).

A second 3-way RANOVA was conducted to demonstrate that the distractor-elicited N2pc observed in the swap condition (Fig. 4c) was reliably different from the ERP elicited through the same period in the no-swap condition (Fig. 1b). This analysis was based on mean ERP amplitude measured from 380 to 400 ms. An interaction between electrode location and color repetition factors was revealed, reflecting a reliable increase in late distractor-elicited N2pc amplitude in Fig. 3c ($F(1,11)=5.697$, $p=0.036$). A main effect of target position was

also identified ($F(1,11)=10.217$, $p=0.009$), as was a main effect of color repetition ($F(1,11)=5.080$, $p=0.046$). The latter reflects an average increase in positivity through the tested latency period in the swap condition possibly caused by an increase in early aspects of the P3a in swap trials. No other effects were significant (electrode location: $F(1,11)=3.665$, $p=0.082$; all other $Fs<1$). Analysis based on amplitude observed at the peak of the late, distractor-elicited N2pc illustrated in Fig. 4c garnered similar results (electrode location × intertrial condition: $F(1,11)=8.116$, $p=0.016$; target position: $F(1,11)=9.668$, $p=0.010$; color repetition: $F(1,11)=4.236$, $p=0.064$; all other $Fs<1$).

3. Discussion

This study was motivated by the idea that the type of perceptual ambiguity suggested by Olivers and Meeter (2006; Meeter and Olivers, 2006) as underlying feature priming might be the same type of ambiguity that Luck et al. (1997b) propose is resolved by the attentional mechanisms reflected in the N2pc. Consistent with this hypothesis, our results show that including a salient distractor in a compound search task–a manipulation used by Olivers and Meeter (2006) to increase perceptual ambiguity– results in both an increase in intertrial priming and an increase in target-elicited N2pc amplitude at posterior electrode sites (see Fig. 1). Moreover, these measures correlate strongly; subjects who show the greatest increase in intertrial priming effects are also those who show the greatest increase in posterior N2pc (see Fig. 2).

The relationship between posterior N2pc amplitude and behavioral feature priming suggests that priming may be created by the attentional mechanisms indexed in the N2pc. These mechanisms are thought to be responsible for sheltering the target representation from contamination by non-target information (Luck et al., 1997b), and this is known to involve modulation of activity both in cortex responsible for the representation of the target and in cortex responsible for representation of the distractor (Hickey et al., 2009). We believe that the action of these mechanisms has a residual effect on perception and attention, and that this carry-over effect is more pronounced when these mechanisms act with greater strength. In the context of the current study, this means that when a visual search display contained a salient distractor, selection of the target facilitated subsequent processing of the color that characterized the target (and suppressed subsequent processing of the color that characterized the distractor). This benefited target selection when the target continued to be characterized by the facilitated color in the next trial, but increased the chance that attention would be captured when the primed color came to characterize the distractor.

Two caveats need to be attached to this proposal. First, our results do not make it clear whether the putative increase in posterior N2pc caused by the presence of a distractor reflects an actual amplitude effect, an underlying shift in N2pc topography, or some combination of these effects. A comparison of the topographic maps in Fig. 1a and b suggests that inclusion of a salient distractor in the display caused the N2pc to generally become broader, with a more distributed topography, and that the component shifted laterally and towards the back of the head. As noted above, an increase in amplitude and distribution of the N2pc is consistent with the idea that the distractor causes an increase in perceptual ambiguity, and thus triggers the need for increased action of the attentional mechanisms responsible for resolving this ambiguity. Interpretation of a possible posterior shift in N2pc topography must be more tentative, in large part because it is difficult to determine if this shift is reliable. Statistical testing of subtle topographic changes is problematic; change in amplitude and change in topography are confounded, making standard statistical tests based on electrode location inappropriate. More suitable tests of topographic shift, like that proposed by Lehmann and Skrandies (1980), do not have the statistical

power to detect small changes in distribution such as those evident in the current data. However, if inclusion of a salient distractor in the search display were to create a reliable shift of topography, one interpretation is that under the more difficult, ambiguous circumstances created by the presence of the salient distractor attention comes to act more at lower-level stages of cortical processing. This would be consistent with recent fMRI (e.g. Ress et al., 2000; Munneke et al., 2010) and animal research (e.g. Chen et al., 2008).

Second, the relationship between N2pc and intertrial priming we identify is probably limited to feature priming. *Dimension priming* can be observed in experiments where there are multiple manners in which the target can be defined (for example, when red items of any shape are targets and so are diamonds of any color). Under these circumstances there is a performance benefit when the target is defined in the same dimension in sequential trials (e.g. Found and Müller, 1996; Müller et al., 2004). Dimension priming is apparent even when a target is presented by itself (Goolsby and Suzuki, 2001; Mortier et al., 2005), a situation where the N2pc is not elicited (Luck and Hillyard, 1994b). This dissociates dimension priming from the attentional mechanisms that underlie the N2pc, and the implication is that feature priming might reflect different underlying processes than those involved in dimension priming. However, the idea that dimension priming may fundamentally differ from feature priming is not far-fetched. The two types of priming are known to have very different characteristics: dimension priming has a substantially larger and more reliable impact on search (Found and Müller, 1996; Müller et al., 1995; Becker, 2008), and whereas dimension priming appears to be cognitively penetrable (Müller et al., 2003) feature priming seems rather automatic (Maljkovic and Nakayama, 1994). Moreover, the two types of priming appear additive: the magnitude of feature priming does not vary as a function of whether dimensional context changes (Olivers and Meeter, 2007).

The current paper focuses on the impact of perceptual ambiguity on feature priming, with the N2pc acting as an indirect index of ambiguity. This is subtly distinct from the investigation of priming on the mechanisms indexed in the N2pc, which has been the focus of other recent studies. Eimer et al. (2010) have demonstrated that the N2pc occurs more quickly when target and distractor colors repeat between trials, suggesting a speeding of target selection, and that this occurs even under conditions of relatively low perceptual ambiguity. We did not find the same pattern in the distractor-absent condition of the current study (i.e. the N2pc did not vary much as a function of intertrial contingency; see Fig. 3), but this likely reflects a fundamental difference in experimental designs: in Eimer et al. (2010) the target was defined by color, whereas in the current study the target was defined by shape and color was effectively irrelevant, likely rendering color priming less effective. Similar to Eimer et al. (2010), but in the context of dimension priming, Töllner et al. (2009) found that the N2pc elicited by a target presented in the absence of salient distractors was larger and earlier when defined in a repeated dimension. The authors interpreted this pattern as evidence that pre-selective perceptual processing of the target was facilitated in repeat trials, in line with the dimension weighting account of Müller and colleagues (e.g. Found and

Müller, 1996). Support for a perceptual locus in priming has also come from Olivers and Hickey (2010), which have shown that the lateral P1 component of the visual ERP–reflecting early perceptual processing contralateral to a color-singleton target–is speeded in color-repeat trials.

In addition to adding to this developing literature, the current study confirms the idea that attentional capture can be driven by feature priming. Existing behavioral work has suggested that the costs associated with a salient distractor stem primarily from swap trials, where the features that characterize a salient distractor have recently characterized the target, and that this is caused by increased likelihood of capture in these trials (e.g. Pinto et al., 2005; Becker, 2007, but see Lamy and Yashar, 2008). Consistent with this, when the target was presented on the vertical meridian of the search display in the current study, and thus could not have a lateralized impact on the ERP, the distractor elicited a clear N2pc in swap trials that was absent in no-swap trials (cf. Fig. 4a and b). These results suggest that target processing causes a reinforcement of target features and devaluation of distractor features, resulting in a bias of attention towards objects with features that have characterized the target in earlier experience. When these features came to characterize a distractor in swap trials, this drives the misallocation of attention to the distractor location (see also Hickey et al., 2010b).

Support for this notion is further provided by results from the lateral-distractor, contralateral-target condition (cf Figs. 1b and 4c). A clear target-elicited N2pc is apparent in the no-swap condition (Fig. 1b) but is absent in the swap condition (Fig. 4c), where a late distractor-elicited N2pc becomes evident. The reduction or elimination of the target-elicited effect is consistent with the idea that the deployment of attention to the target is disrupted by the swap in stimuli color, and the distractor-elicited N2pc suggests the deployment of attention to the distractor location. This distractor-elicited N2pc is, however, substantially delayed relative to both the target-elicited N2pc (Fig. 1b) and the distractor-elicited N2pc observed in the vertical-target, lateral-distractor condition (Fig. 4b). This is an unexpected and frankly puzzling result. One possibility is that the early portion of this component has been lost in the signal averaging process. According to this idea, attention may have often been captured to the distractor in this swap condition, but in a subset of trials it was deployed directly to the target. A target-elicited N2pc was created in these no-capture swap trials, and when these no-capture trials were averaged together with capture trials, early aspects of the target-elicited and distractor-elicited N2pc components canceled one another out. The late aspect of the distractor-elicited N2pc evident in Fig. 3b was not affected by this problem of signal averaging because this aspect of the N2pc is specific to the distractor-related component. This possibility is provided some support in comparison of the distractor-elicited N2pc illustrated in Fig. 4b and the target-elicited N2pc illustrated in Fig. 1b; there is clear laterality in the 350–450 ms latency range in the distractor-elicited component but no corresponding activity in the target-elicited component. The late distractor-elicited N2pc might thus reflect residual activity not cancelled out by opposite-polarity, target-elicited N2pc.

In summary, the present results demonstrate a relationship between the resolution of perceptual ambiguity–as indexed by the N2pc–and feature priming. We propose that as perceptual ambiguity increases, so does the need for attentional mechanisms responsible for ambiguity resolution. The action of these mechanisms has a residual effect such that subsequent trials are affected. When these mechanisms act strongly and the target repeats, perceptual processing of the target is facilitated. In contrast, when target and distractor colors swap it is perceptual processing of the distractor that is facilitated, and this can result in the misallocation of attention to the distractor location. Ambiguity–and the attentional mechanisms responsible for resolving it–appears to play an important role in feature priming.

4. Experimental procedures

4.1. Participants

Fourteen healthy university students gave informed consent before beginning the experiment. All subjects reported normal or corrected-to-normal vision and were paid for their participation. Data from two participants were discarded due to excessive eye movement artifacts in the electroencephalogram (EEG; >33% of trials tainted by eye movement artifacts). All of the remaining 12 participants (4 women; mean age 20.7 years±2.5 SD) were right handed.

4.2. Stimuli and procedure

The experimental stimulus was a visual search array containing 6 shape stimuli, each equidistant (9.1°) from a central fixation point and each other (see figures for examples). Individual objects could be red or green outlines (0.3° line thickness) of diamonds (4.2°×4.2°) or circles (3.4° diameter), and each contained a gray line (0.3°×1.5°) randomly oriented vertically or horizontally. All stimuli were presented on a dark gray background.

In each trial one of the objects was different in shape than the other five. This could mean that one object was a diamond with the other five objects circles or vice versa, with the identity of the shape singleton randomly determined for each trial. Participant response was based on the orientation of the line contained inside this shape singleton. In 75% of trials one of the five identically shaped items was a color singleton, either red with all other objects green or vice versa. Color-singleton presence and color were determined per trial, such that each trial had a 75% chance of including a color singleton, and, in singleton present trials, there was a 50% likelihood that the color singleton would be red and a 50% likelihood it would be green. The visual search array was configured such that two of the six possible stimulus positions were located on the vertical meridian of the display. In each trial the target and salient distractor positions were randomly selected with the sole confine that these stimuli be presented to different positions.

The search displays were presented on a CRT monitor located 60 cm. away from the participant's eyes. Each trial began with presentation of fixation point for a random duration of 400 to 1400 ms. This was followed by presentation of the search array, which remained on the screen until 100 ms after response was made (when the next trial began). Participants

completed 60 blocks of 30 trials, for a total of 1800 trials. They were instructed to respond as quickly as possible while maintaining an average accuracy of 90% or better, and feedback regarding accuracy and reaction time was provided at the end of each block. They were also instructed to maintain eye fixation throughout the experiment and told that eye movements were being monitored. Prior to beginning the experiment, each participant completed at least one practice block.

4.3.   Recording and analysis

EEG and electrooculogram (EOG) were recorded from 134 sintered-AG/AgCl electrodes using the Biosemi ActiveTwo system (Biosemi, Amsterdam, the Netherlands). Horizontal EOG was recorded from electrodes located 1 cm. lateral to the external canthi and vertical EOG was recorded from two electrodes located 2 cm. above and below the right eye socket. Electrophysiological signals were digitized at 1024 Hz and resampled offline to 250 Hz. The data were high-pass filtered by convolving each channel with a Hamming-windowed finite impulse response (FIR) function with half-amplitude attenuation at ~0.49 Hz and a 6 dB transition bandwidth of ~0.1 Hz, and low-pass filtered with a similar function that resulted in half-amplitude attenuation at 40 Hz and a 6 dB transition bandwidth of 8 Hz. ERP analysis was conducted using a combination of custom scripts for Matlab (Mathworks, Natick, MA) and the EEGLAB toolbox (Delorme and Makeig, 2004). Analysis began with the computation of independent components using the logistic infomax independent component analysis (ICA) algorithm (Bell and Sejnowski, 1995). The primary component associated with eye movements was identified and used to reject epochs in which participants moved their eyes, which resulted in the average rejection of 8.5% of total trials per subject (±3.6% SD). Following this all components associated with blinks, line noise, and other sources of artifact were removed from the data. All ERPs were computed with respect to a 150 ms baseline period beginning 100 ms prior to stimulus onset and were referenced to the average of all 128 encephalic electrodes.

ERPs were computed for conditions as defined by two factors, namely the location of the target and salient distractor and whether the colors that defined the target and distractor had been the same in the immediately previous trial or had swapped. Except where explicitly noted all ERPs correspond to trials where the target was presented at one of the four lateral locations in the search array (i.e. trials where the target was presented on the vertical meridian are excluded). Waveforms elicited ipsilateral and contralateral to the target are presented in the figures. The contralateral waveform reflects the average of the signal recorded over the left visual cortex when the relevant stimulus was presented to the right visual hemifield and the signal recorded over the right visual cortex when the target was presented to the left visual hemifield. The ipsilateral waveform was similarly calculated. In the "contralateral distractor" condition the target was presented to one of two lateral locations in one hemisphere and the distractor was presented to one of two lateral locations in the contralateral hemifield. The "vertical target" condition is the exception to the rule above; here the target is presented at one of the two locations on the vertical meridian, the distractor is

presented to one of the four lateral array locations, and the "contralateral" and "ipsilateral" labels are in reference to the distractor location. In swap trials, the distractor was characterized by the color that had been associated with the target in the immediately preceding trial and the target was characterized with the color that had been associated with the distractor.

The topographical maps presented in the figures were created from contralateral-minus-ipsilateral difference waves. The difference wave data was mirrored across the electrode midline and the values on midline electrodes were artificially set to zero. This procedure creates a symmetric whole-head topographical map of the N2pc.

Acknowledgments

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