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Research Report

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

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ABSTRACT

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.