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Does modulation of selective attention to features reflect enhancement or suppression of neural activity?

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ABSTRACT

Numerous studies have demonstrated that selective attention to color is associated with a larger neural response under attend than ignore conditions, but have not addressed whether this difference reflects enhanced activity under attend or suppressed activity under ignore. In this study, a color-neutral condition was included, which presented stimuli physically identical to those under attend and ignore conditions, but in which color was not task relevant. Attention to color did not modulate the early sensory-evoked P1 and N1 components. Traditional ERP markers of early selection (the anterior Selection Positivity and posterior Selection Negativity) did not differ between the attend and neutral conditions, arguing against a mechanism of enhanced activity. However, there were markedly reduced responses under the ignore relative to the neutral condition, consistent with the view that early selection mechanisms reflect suppression of neural activity under the ignore condition.

1. Introduction

Although many studies have shown that selective attention to color is associated with a larger neural response under attend than ignore conditions, they have not addressed whether this difference reflects enhanced activity under attend or suppressed activity under ignore. Understanding this process is critical to determining the ways in which top-down modulation of information processing is carried out, and delineating the mechanisms that may underlie attentional impairment in clinical populations.

Selective visual attention reflects the influence of top-down control mechanisms that facilitate the processing of information most relevant to task demands (Desimone and Duncan, 1995; Lavie et al., 2004; Rutman et al., 2010; Sawaki and Katayama, 2008). As a result of these operations, selective attention is hypothesized to improve processing efficiency and conserve resources of the capacity-limited decision making system (Awh and Jonides, 2001; Gazzaley et al., 2005a; Zanto and Gazzaley, 2009). Selective attention has been investigated using event-related potential (ERP) and functional imaging techniques. The most common ERP investigations of selective attention have involved attention to location and reveal an amplification (increased gain) of early sensory-evoked components such as the P1 or N1, which results in a change in the size of the component, but not its latency, morphology, or scalp distribution (Hillyard et al., 1998b).

In contrast to attending to location, selective attention to non-spatial features such as color has most often been associated with the generation of endogenous potentials and not the modulation of sensory-evoked ERP components (Hillyard and Anllo-Vento, 1998; Hillyard and Munte, 1984). In standard investigations of attention to color, comparing attend and ignore conditions, two ERP modulations are most commonly described: a Selection Negativity (SN) over posterior scalp locations and a Selection Positivity (SP) over frontocentral regions (Czigler, 1996; Eimer, 1997; Hillyard et al., 1998a; Kopp et al., 2007; Luck and Hillyard, 1994; Martin-Loeches et al., 1999; Potts and Tucker, 2001; Van Der Stelt et al., 1998). These potentials exhibit an overlapping time course between ~150 ms and 350 ms post stimulus presentation. There is evidence that the posterior SN reflects the activity of feature-selection areas of the extrastriate cortex that may involve the enhanced sensory-perceptual processing of relevant stimulus dimensions compared to irrelevant ones (Harter and Aine, 1984; Hillyard et al., 1998a; Kopp et al., 2007). The neural underpinnings and functional significance of the anterior SP are less well established. It has been conceptualized either as a frontally mediated index of the motivational salience of a stimulus based on task relevance (Potts and Tucker, 2001; Riis et al., 2009) or as a marker of a detection process sensitive to stimulus features, such as color, orientation, or size that

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have been specified by task instructions as being significant (Luck and Hillyard, 1994).

A few recent studies have also reported modulations of early sensory-evoked potentials in response to attention to color. For example, Zhang and Luck (2009) found enhanced P1 amplitude to an attended relative to an ignored color at an unattended location, but only under conditions in which attended and ignored colors were presented simultaneously rather than sequentially. Zanto et al. (2010b) found a larger N1 amplitude to colored stimuli under an attend than ignore condition when they showed subjects a series of colored or moving dots, and compared the effects of attending to vs. ignoring the feature of color.

Most commonly, the study of selective attention has involved a comparison of the neural activity elicited by the same physical stimuli that are presented under attend vs. ignore conditions, often by using subtraction techniques (attend minus ignore). The standard subtraction method is able to demonstrate that a difference exists between attending and ignoring. However, it cannot determine whether the difference reflects increased activity under the attend condition, reduced activity under the ignore condition, or both. One rarely utilized strategy to address this challenge has been to include a condition that is attentionally neutral with respect to the feature under consideration. For example, Luck et al. (1994) tested subjects in a spatial cueing experiment that included "neutral" trials in which the cues pointed toward all possible locations, presumably leading subjects not to focus spatial attention. Comparing valid to neutral trials provided an index of attentional enhancement, whereas comparing invalid to neutral trials provided an index of attentional suppression. Interestingly, the amplitude of the sensory-evoked P1 component was smaller on invalid (ignore) than neutral trials, with no enhancement on valid (attend) trials. In contrast, the N1 component only showed enhancement on valid (attend) relative to neutral trials, but no suppression on invalid (ignore) relative to neutral trials.

A similar approach has been applied to the study of non-spatial features. Gazzaley et al. (2005a,b, 2008) and Zanto et al. (2010a) have used a neutral condition to investigate selective attention in several functional imaging and ERP experiments. For example, subjects were shown a series of faces and scenes under three conditions: (1) remember faces (and ignore scenes), (2) ignore faces (and remember scenes), and (3) passively view both faces and scenes. In one of the ERP experiments, young adults exhibited both significant enhancement (attend > passive view) and suppression (passive view > ignore) for P1 amplitude and N1 latency in response to faces (Gazzaley et al., 2008). ERP studies of selective attention to color that have used a neutral condition have been extremely rare. In the Zanto et al. study (2010b) cited earlier, subjects viewed a sequence of colored or moving dots under four experimental conditions and were instructed to attend to motion, hue, both motion and hue, or to just passively view the stimuli. Subjects demonstrated enhancement (attend > passive view) but not suppression (passive view = ignore) of the N1 amplitude in response to color. Although Selection Negativity was examined (attend–ignore difference waves), the authors did not compare activity under attend or ignore conditions with activity under the passive condition.

In the current study, attention to a specified color was investigated by comparing attend and ignore conditions to a neutral condition. Young adult subjects were shown a series of red and blue letters, of which five were designated as targets. Under the color-selective attention task, subjects were told to respond to target letters in a designated color and to ignore stimuli in the other color. Under the color-neutral attention task subjects were told to respond to target letters that appeared in either color. The color-selective attention (SA) task allowed us to examine the neural responses to stimuli in which subjects were instructed to attend (Attend condition) or to ignore (Ignore condition) based on color. The color-neutral attention (NA) task allowed us to examine the neural responses to physically identical stimuli under circumstances in which color was not task-relevant (Neutral condition). The critical difference between the SA task and the NA task is the additional requirement of color selectivity. Our working assumption was that carrying out the SA task included all of the cognitive operations involved in the NA task, plus ones that mediate the color selection process. For example, both tasks required subjects to actively attend to the experiment, focus gaze on a central location, perceptually process the physical stimuli, make decisions about whether the presented stimulus matches one of the target letters, prepare and execute the appropriate motor responses, update memory, and prepare for the next stimuli. However, under the SA task, subjects had to account for color as well as letter forms.

Selection of color and letter forms may be hierarchical (with the processing of one dimension dependent on the outcome of prior selection within the other dimension), or may take place in parallel. Theories about early selection lead to the expectation that subjects would initially filter input on the basis of the most easily identifiable physical characteristic (color) linked to target stimuli, and then process more complex features (letter forms) of stimuli in the relevant color in order to complete target identification activity (Hillyard and Munte, 1984; Looren et al., 1988). A potential challenge to this version of a hierarchical framework is the observation that in experienced readers, words are automatically (and rapidly) processed, which, for example, manifests in the Stroop effect (MacLeod, 1991). In accordance with this idea, the letter forms presented in the current study would be processed first, target letters identified, and then color attributes determined in order to complete the selection of appropriate targets. In this scenario, discrimination of color would reflect a late selection process, occurring in the service of final target identification. Against this possibility are studies indicating that the Stroop effect is attenuated or absent using a single letter format (Besner et al., 1997; Brown et al., 2002). Functional imaging studies have also found that single letters do not reliably engage the fusiform visual word form area (Turkeltaub et al., 2008). In ERP studies, the N170 component has been used as an index of the processing of word forms. The N170 sensitive to word forms is larger over left hemisphere sites (Maurer et al., 2008; Rossion et al., 2003). In the current study, if subjects treated individual letters like whole word forms and thus processed them in a rapid, automatic fashion, we would expect to find a larger N170 component over the left hemisphere.

An alternative to these hierarchical models of selection would suggest that the attributes of color and letter form are processed in parallel by independent analyzers. Theoretically, even in this model, once stimuli are identified as lacking a critical attribute, processing of that stimulus could be terminated (Hillyard and Munte, 1984). Letter forms represent a less discriminable feature than color, and likely require more time to resolve. Consistent with this framework, color selection would take place early, and play an important role in efficiently carrying out the task demands of identifying targets.

Analysis of ERPs is particularly well-suited for determining where along the information processing stream color selection takes place. We examined the posterior P1, posterior N1 (N170), SP, and SN components. Based on the extant literature, we expected that the most salient changes would be observed during the temporal intervals traditionally associated with color processing, the anterior SP and posterior SN. The ERP subtraction methodology allowed us to focus on color processing. For example, the comparison of color positive, letter form negative (C+/L−) events to color negative, letter-form negative (C−/L−) events is a way to isolate color selection by subtracting out processing activity specifically related to letter forms.