The neural correlates of feature-based selective attention when viewing spatially and temporally overlapping images

Jun Wang [a], Brett A. Clementz [a,*], Andreas Keil [b]

[a] *Departments of Psychology and Neuroscience, BioImaging Research Center, University of Georgia, Athens, GA 30602, United States*
[b] *Department of Psychology, University of Konstanz, Germany*

Abstract

We used dense-array EEG to study the neural correlates of selective attention to specific features of objects that spatially overlapped an unattended image. Participants viewed superimposed images (horizontal and vertical bars differing in color) and attended to one image to identify bar width changes in specific locations. Images were frequency tagged so attention directed to unique parts of the stimuli could be tracked. Steady-state visual evoked potentials were used to quantify attention-related neural activity. As expected, selectively attending to specific parts of the attended image enhanced brain activity related to the attended element, and left unchanged activity elicited by spatially overlapping unattended stimuli. Under specific conditions, however, we found increased activity to unattended stimuli. The specificity of the selective attention effects presented herein, however, may be limited under certain complex stimulus conditions.
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Visual attention supports the ability to focus on relevant aspects of the visual environment. In particular, selective attention is responsible for enhancing perception of specific stimulus properties such as location, size, color, etc., at specific times (Driver & Frackowiak, 2001; Kastner & Pinsk, 2004). Several authors have proposed that visual selective attention is mediated by neural amplification of cell populations encoding the to-be-attended stimulus (e.g., Hillyard & Anllo-Vento, 1998; Kastner & Pinsk, 2004). In the realm of spatial selective attention, amplitude modulation of activity in neuron populations coding for particular spatial locations is regarded as a simple and effective means for achieving optimized processing at attended locations (Driver & Frackowiak, 2001). With increasing complexity of the visual array under consideration, however, additional processes are required to resolve ambiguity and efficiently direct resources to the task-relevant stimulus. For instance, in situations where attended and unattended stimuli overlap spatially, knowledge of spatial location may be insufficient for separating targets from non-targets (e.g., when trying to detect a white-tailed deer in a thick stand of trees in late fall). In these cases, additional processes such as feature- or object-based selection are required to successfully and correctly identify the visual scene (e.g., Pei, Pettet, & Norcia, 2002; Valdes-Sosa, Bobes, Rodriguez, & Pinilla, 1998). In the laboratory, these kinds of selective attention have been examined using sequentially presented stimuli differing along one or more distinct feature dimensions (i.e. color, size, orientation, etc.). Given the close conceptual relationship between object features and objects defined by distinct features, there has been debate about how feature- versus object-based attention can be independently examined. On the level of brain processes, one common finding has been that large-scale neural activity is reliably enhanced as a function of attentional allocation to visual features (Müller & Keil, 2004), objects (Valdes-Sosa et al., 1998), or spatial locations (Morgan, Hansen, & Hillyard, 1996).

An aspect of this problem that has been rarely studied is the role of selective attention to specific features for resolving visual objects that overlap in space and in time, although this is close to the requirements during most activities of daily life. Valdes-Sosa and co-workers (Rodriguez, Valdes-Sosa, &

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* Corresponding author. Tel.: +1 706 542 4376; fax: +1 706 542 3275.
E-mail address: clementz@uga.edu (B.A. Clementz).

Freiwald, 2002; Valdes-Sosa et al., 1998) have used this method of overlapping stimuli with success for examining the neural correlates of space and object-based attentional mechanisms. Chen, Seth, Gally, and Edelman (2003) also evaluated the specificity of selective attention to an attended image that spatially overlapped an unattended image. They measured the strength of steady-state visual evoked potentials (ssVEPs) to horizontal and vertical gratings (one of which was attended, each image oscillating at its own specific frequency) in 11 participants under broad and narrow attention conditions. There was greater neural activity for the attended relative to the unattended image under the broad attention condition, but paradoxically lower activity for the attended relative to the unattended image in the narrow attention condition. Chen et al. (2003) proposed the functioning of an inhibitory mechanism under the narrow attention condition. Their design prevented them from evaluating changes in the locus of attention within the attended image as a function of broad and narrow attention. Measuring changes in neural activity to different parts of the attended image under broad and narrow attention conditions would more specifically address whether an inhibitory mechanism accounted for the Chen et al. (2003) results.

The ssVEP, a useful index of neural activity, is a response of visual cortex to flickering stimuli, where the frequency of brain response tends to equal the flicker rate of the stimuli. Four advantages of the ssVEP for present purposes are that (i) the experimenter can select the flicker rate (frequency) of the intensity-modulated stimulus, and stimulus-driven evoked power changes take place at the fundamental frequency of the flicker rate (Regan, 1989), (ii) ssVEPs are characterized by high signal-to-noise ratios (Mast & Victor, 1991), and, in contrast to VEPs where changes occur in a wide frequency range, changes in ssVEPs occur at a known, single frequency of interest, (iii) strength of the ssVEP is easily quantified using Fourier analysis, and (iv) multiple stimuli flickering at different frequencies can be presented simultaneously to the visual system, so attention to independent objects and spatial locations can be tracked (Morgan et al., 1996; Müller & Hübner, 2002; Müller, Malinowski, Gruber, & Hillyard, 2003; Regan & Regan, 2003).

Steady-state stimulus delivery has facilitated knowledge acquisition in a variety of areas. For instance, steady-state responses are sensitive to attention manipulations (Morgan et al., 1996; Müller & Hillyard, 2000; Müller & Hübner, 2002; Müller, Teder-Salejarvi, & Hillyard, 1998), the emotional content of stimuli (Keil et al., 2003; Keil, Moratti, Sabatinelli, Bradley, & Lang, 2005; Moratti & Keil, 2005; Moratti, Keil, & Miller, 2006; Moratti, Keil, & Stolarova, 2004), and tonic changes in brain state (Picton, Vajsar, Rodriguez, & Campbell, 1987; Plourde & Picton, 1990; Silberstein et al., 1990). Attention-related changes in N1 ERP amplitudes also correlate with attention-related modulations of ssVEP amplitudes, suggesting a functional link between these two measures (Müller & Hillyard, 2000).

In the present studies, superimposed visual images (Chen et al., 2003) were used to investigate the neural correlates of selective attention (specifically color selection) for an attended stimulus that spatially overlapped an unattended stimulus differing in color. The ssVEP was used to quantify the large-scale neural correlates of selective attention (Morgan et al., 1996). To take full advantage of the ssVEP for studying attentional selection, the present design allowed for measuring changes in the locus of attention within the attended image (by using multiple unique frequency tags) as a function of broad and narrow attention. By virtue of variations in stimulus conditions, we also evaluated the interaction between attentional selection and the size of the to-be-attended area. Thus, changes in attention demands within an attended visual object could be studied in addition to evaluating differences in neural activity between attended and non-attended objects.

1. Method

1.1. Participants

Three experiments comprise this study. All experiments had 12 participants (Experiment 1: 7 males, ages 18–26 years; Experiment 2: 7 males, ages 18–21 years; Experiment 3: 9 males, ages 18–22 years), all of whom participated in only one experiment. Participants had normal or corrected-to-normal vision, had no evidence of neurological impairment, were free of psychiatric or substance use disorders (by self-report), and were given class credit for their participation. The
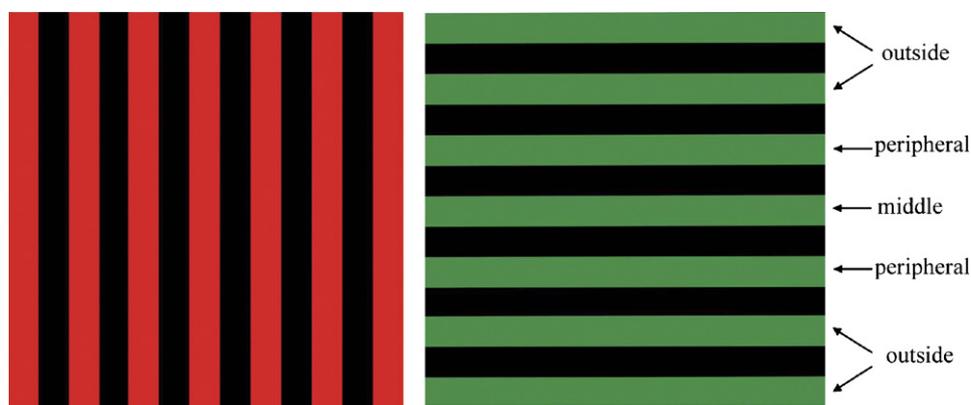

Fig. 1. The two images (horizontal and vertical bars) used in these experiments are shown as spatially distinct, but they perfectly overlapped during testing. For the 7-bar study, both images were presented as they are shown here. For the 3-bar study, only the three middle bars of each image were presented to the participants (i.e. the middle bar and the peripheral bars). For the 5-bar study, only the five middle bars of each image were presented to the participants (i.e. the middle bar, the peripheral bars, and the outside bars that were immediately adjacent to the peripheral bars).