THE CATHOLIC UNIVERSITY OF AMERICA

Electrophysiological Correlates of Object-Based Selective Attention

A DISSERTATION

Submitted to the Faculty of the

Department of Psychology

School of Arts and Sciences

Of The Catholic University of America

In Partial Fulfillment of the Requirements

For the Degree

Doctor of Philosophy

©

By

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Washington, D.C.

2010

Electrophysiological Correlates of Object-Based Selective Attention

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A visual stimulus may be selectively attended on the basis of its location in space, a specific feature, or as a whole object. While a relatively large amount of research has examined the neural basis of location-based and feature-based attentional selection, few studies have examined the neural correlates of the spread of attention from one feature of an object to another, reflecting the selection of an object as an "integrated feature ensemble" (Schoenfeld et al., 2003; O'Craven, Downing, & Kanwisher, 1999). The research in this dissertation examined the electrophysiological correlates of the spread of selective attention to a task-irrelevant color feature of an object using the event-related potential (ERP) brain imaging technique. The temporal dynamics of this spread of attention were examined for two classes of objects, grouped-arrays of lines (Study 1) and geometric shapes (Study 2). In each study, overlapping objects were presented and the participants' task was to sustain attention to one object versus another to judge a change in the thickness of one of the lines of the grid (Study 1) or a change in object shape (Study 2). On some trials, either the attended object or the unattended object was colored, and color was irrelevant to the task. Difference ERPs indicated that color was first encoded in the visual cortex by 100 ms. However, the effect of attention on the task-irrelevant color feature was evident in later ERP modulations. A bilateral parietal/occipital positivity beginning at 200 ms (Study 2) and a midline occipital negativity beginning at 280 ms (Studies 1 & 2) were associated with the selection of the

irrelevant color of the attended object. Source localization analyses suggested that the neural

generators of the attention-related facilitation of the irrelevant color feature were situated in

ventral occipital cortical regions near color-selective cortical areas. These data provide

further evidence for the "integrated competition" model (Duncan, 1996; 1997), which posits

that the neural basis for the perceptual integration of an attended object consists of enhanced

activity in the network of specialized modules that encode its individual features, including

those that are not relevant to the immediate task.

This dissertation by Marla Raye Zinni fulfills the dissertation requirement for the doctoral degree in Applied Experimental Psychology approved by Raja Parasuraman, Ph.D., as Director, and by Steven A. Hillyard, Ph.D., Pamela M. Greenwood, Ph.D., and James H. Howard, Jr., Ph.D. as Readers.

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It's a funny thing about comin' home.
Looks the same, smells the same, feels the same.
You'll realize what's changed is you.

--Benjamin Button
The Curious Case of Benjamin Button (2008)

ACKNOWLEDGMENTS

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CHAPTER 1: INTRODUCTION

Attention is the cognitive process that allows us to select relevant information from the multitude of signals that the sense organs send to the brain. Because information processing capacity is limited, attention serves as a filter to protect the limited higher processing resources from overload (Desimone & Duncan, 1995). In some cases, selection is based upon the location in space where an event is expected, such as knowing that a friend will be approaching from the right side of the street. At other times, a particular feature of interest, such as color when meeting a person who will be wearing a blue colored shirt, may drive selection. In many cases, attention may select an entire object such as a ball flying through the air. There is little debate that attention may operate in a space-based, feature-based, or object-based manner depending on task demands (Hopf, Heinze, Schoenfeld, & Hillyard, 2009; Hopf, Schoenfeld, & Heinze, 2005). While a substantial amount of research has been conducted to examine the neural mechanisms of space-based attention and a growing amount on feature-based attention, little research has focused on the neural mechanisms of object-based attentional selection. Given the importance of object processing to our everyday perceptual experience, understanding the neural basis of object-based attention is of fundamental importance. This will be the focus of this dissertation.

It has been argued that objects, perceptual groups or units (Vecera & Behrmann, 2001) should be a natural basis for selection, because we perceive the world around us as being structured into objects. It is this structure, either based upon grouping by Gestalt principles of visual organization (Wertheimer, 1923; 1958) or based upon object familiarity

that may serve as the basis for this attentional selection (Vecera & Farah, 1997). Attention then operates on these structured objects, selecting one object over others, while respecting the boundaries of the object selected (e.g. Egly, Driver, & Rafal, 1994). Under some conditions, object-based attention may operate under a grouped-array representation (or spatiotopic representation (Kramer, Weber, & Watson, 1997). However, object-based attention may also select objects in a spatially-invariant manner (Vecera & Farah, 1994). In these latter studies, objects cannot be selected solely based on their spatial location, for example, when objects are overlapping in space (Duncan, 1984). Both grouped-array and spatially-invariant accounts of object-based attention provide essential evidence of the role of objects in the selective processing of information. The review in this chapter as well as the studies included in this dissertation will be restricted to the visual modality. However, object-based attention may also act upon multi-modal objects, selecting both modalities (e.g. visual and auditory) of one object over another object (Molholm, Martinez, Shpaner, & Foxe, 2007; Busse, Roberts, Crist, Weissman, & Woldorff, 2005).

While there is no general theory of object-based attention, there are several predictions of object-based models. The first is that once a part of an object is selected, attention then spreads through the entire object selecting it over other objects in the environment (reviewed by Scholl, 2001). In addition, the selection of one object over another can be accomplished without the use of space-based or feature-based attention. Perhaps, the most important prediction of object-based attention models is that once one feature of an object is selected (such as shape), attention spreads to select other features of that object (such as its color) (O'Craven, Downing, & Kanwisher, 1999). The studies

included in this dissertation will focus on this last prediction, in particular, the timing and

neural mechanisms of the selection of a task-irrelevant object feature as measured by event-

related brain potentials (ERPs), which offer a sensitive method for assessing the temporal

course of neural processing.

Behavioral studies of object-based attention will be reviewed below, followed by

evidence for object-based attentional selection in neuropsychological patients. Additionally,

the time course of attentional selection in the brain using ERPs with human subjects will also

be discussed with a focus on the timing of object-based selection. Because the selection of

all of the features of an object implies that these features are bound into a single object

representation, theories and evidence for feature binding will then be addressed. This will be

followed by a review of biased competition theory and the integrated competition hypothesis

that predicts that selection of all of an object's features with attention. Finally, the current

evidence for integrated competition will be presented, followed by the rationale and design of

the current studies.

Behavioral Evidence for Object-based Attentional Selection

Divided-attention

The earliest evidence for object-based attentional selection came from studies such as

Duncan's (1984) in which it was demonstrated that divided attention is less efficient across

objects than within an object. In Duncan's task, two objects were overlapped, appearing as a

box with a line struck through it. Participants were asked to report two aspects of the display

such as box size (small or large), position of the gap on the box (right or left), the tilt of line

(clockwise or counterclockwise), or the texture of the line (dotted or dashed). Various keys indicated the judgment responses, for example, one key for clockwise tilt of the line or another key for counterclockwise tilt of the line. Duncan found that two judgments concerning the same object (such as line tilt and texture) can be made simultaneously without loss of accuracy, whereas two judgments that concern different objects cannot. In other words, attention cannot be divided efficiently across objects. The results were interpreted within an object-based attentional framework in which scenes are segmented pre-attentively into objects, followed by a focal attention process that selects one object at a time.

Using the same stimuli as Duncan (1984), Vecera & Farah (1994) examined whether these findings could be replicated when the box and line were separated in space versus grouped together. If location played no role in the object-based effects seen, then there should be no additive cost of separated locations with the cost of dividing attention across objects. When the two objects were separated in space, the cost of attending to two dimensions from different objects did not increase in magnitude, suggesting that attention was operating directly on spatially invariant object representations in Duncan's task.

Lavie & Driver (1996) also used a divided attention task, however their stimuli included two intersecting dashed lines having a wide spatial extent. Subjects compared the lengths of two target elements (a dot or a dash in the line). When the targets appeared on the same line, participants were faster than when they appeared on different lines, demonstrating a same-object advantage. In particular, subjects were faster at the comparison when the targets were far apart on a common line than when located closer together on different lines,

providing evidence that the structure of the line objects influenced performance more than the spacing between the targets to be compared.

Spatial cueing

Evidence for object-based selection has come not only from divided attention experiments but also from studies of spatial cueing. Egly, Driver, & Rafal (1994) utilized cueing effects to examine the interaction between space-based and object-based selection. The stimuli consisted of a fixation cross and two rectangles that could be oriented to the left and right of fixation or above and below fixation. A cue then appeared by brightening one of the four ends of the two rectangles. A target gray square then appeared superimposed on top of one of the four ends of the two rectangles so that the square filled in one end of a rectangle. Reaction time was faster when the target was validly cued as opposed to invalidly cued demonstrating location-based selection. However, when the cue was invalid, reaction time was faster for targets presented on the cued object than for targets occurring on the un-cued object, even though both of the targets occurred the same distance away from the cued location. These findings suggest that selection can be based on location per se but it can also be mediated by object-based attention.

Neuropsychological Evidence for Object-based Attention

Striking accounts of object-based attention come from reports of patients with Balint syndrome and in particular a component of the syndrome termed simultanagnosia, the inability to see more than one object at a time (reviewed by Rafal, 1997). The syndrome generally occurs as a result of bilateral parietal cortex lesions. These patients demonstrate symptoms that are more than pure neglect of one or another hemifield. Persons with this

syndrome have difficulty in comparing objects, such as the determination of whether two parallel lines are of equal lengths (Holmes & Horax, 1919). They are also unable to see two separate discs simultaneously unless a line connects them in order to form a dumbbell (Humphreys & Riddoch, 1993; Luria, 1959). In addition, if two triangles are overlapped to form a 'Star of David', perception of the star is typical unless the two triangles are differently colored. In that case, only one triangle at a time is perceived (Luria, 1959). Findings from these patient studies suggest that attention can occur in an object-based frame of reference and indicate an essential role of the posterior parietal lobes in the ability to perceive two objects simultaneously.

A recent case of simultanagnosia was reported in which the patient not only had an inability to see more than one object at a time, but also had difficulties in reporting more than one feature of the same object, thus demonstrating problems with the binding of object features (Coslett & Lie, 2008). For example, when asked to judge a shape with stripes (indicate if stripes are present then the shape of the stimulus and vice versa), he could correctly indicate the feature that was asked first but then indicated that he did not see the second feature of the object. In addition to damage to both posterior parietal lobes, other areas of damage in this patient included the left middle temporal gyrus and the left middle frontal gyrus (an area that has also been associated with the switching of attention in object-based paradigms (Serences, et al., 2004). Perhaps the damage in these other areas may have accounted for the difficulties in reporting more than one feature of an object, which had not been previously reported as symptoms of simultanagnosia.

As reviewed above, accuracy and response time measures have provided evidence that when attending to an object, other features or locations on that object are processed preferentially as compared to equidistant locations on a different object. These findings suggest that objects are selected as wholes and that attention spreads through an attended object to its unattended locations. In addition, neuropsychological studies have suggested that areas of bilateral parietal cortex may serve a role in the perception of more than one object at a time as indicated by the inability to process two objects simultaneously when these areas of cortex are lesioned. Thus, both behavioral and neuropsychological studies have provided evidence for object-based attention and in particular, processing limitations when attending to two objects versus one when the role of spatial attention is controlled. However, the underlying neural mechanisms of object-based attention, in particular its time course, have not been extensively studied. Because the ERP method is sensitive to differences in timing between attended and unattended stimuli, this method was used in this dissertation. As such, a brief review of the literature on studies of attention (space, feature, and object-based) using the ERP method will be described below.

Event-related potential studies of attention

The ERP is a transient series of voltage oscillations in the brain that can be recorded from the scalp in response to environmental events. These signals are generated by summated postsynaptic potentials in the cerebral cortex, conducted through the brain, skull, and scalp (Luck, 2005). Because ERPs are small voltage fluctuations at the microvolt level, they are extracted from the large voltage fluctuations (tens of microvolts) of the ongoing electroencephalogram (EEG) by averaging time-locked responses to stimulus events. It is

assumed that the ongoing EEG activity that is not associated with the process being measured will not be time-locked to the presented stimulus event, such that over an average of many trials, the background EEG response will average to zero leaving only the response associated with the process of interest. ERPs are viewed as a sequence of separate but sometimes temporally overlapping components that are influenced by some combination of the physical parameters of the eliciting stimuli and psychological processes such as memory, attention, or response preparation. ERP components are traditionally defined in terms of their latency range relative to a discrete stimulus or response, distribution of voltages across the scalp, polarity, sequence, and sensitivity to experimental manipulations and instructions (Donchin, Ritter, & McCallum, 1978; Luck, 2005). Visual ERP waveforms following the onset of a stimulus have a characteristic set of early sensory evoked *exogenous* components (e.g. C1, P1, N1). In addition, *endogenous* components associated with particular stages of perceptual and cognitive processing may also be isolated by subtracting the ERPs elicited by different stimulus conditions (e.g. P300, N400, N2pc, SN). The millisecond resolution of ERP recordings makes them particularly well suited for answering questions related to the timing of attentional selection. While the timing resolution of the method is considered its strength, the spatial localization capabilities of ERPs are less precise. However, source analysis techniques may be performed to provide a general estimate of the cortical source of a particular ERP component. Another benefit of using the ERP method is that it provides a means of measuring responses to unattended stimuli without requiring a behavioral response, thus allowing the differential processing of attended and unattended stimuli to be measured while allowing an unattended stimulus to remain unattended.

Research into the neural basis for spatial attention using the ERP method has been particularly extensive (Hopfinger, Luck, & Hillyard, 2004; Luck & Hillyard, 2000). In addition, a significant amount of research has also been conducted examining feature-based attention (Maunsell & Treue, 2006; Hillyard & Anllo-Vento, 1998). Information about the neural mechanisms of object-based attention however is particularly lacking (review of all three types: Anllo-Vento, Schoenfeld, & Hillyard, 2004, Hopf et al., 2009). ERP evidence for the mechanisms of each of these three types of attention will be discussed below.

ERP studies of spatial attention

Psychophysical studies have indicated that when attention is allocated to a region of space, the perception of the stimuli at that location is faster and more accurate than to stimuli presented at other locations (Posner, 1978; Posner et al., 1980; Eriksen & St. James, 1986). ERP studies have investigated the cortical source of this advantage by comparing waveforms elicited by the same stimulus when attended versus unattended. Cueing tasks in which advance knowledge is given about where a target may appear, have provided evidence that the benefits for attended stimuli are associated with selection at an early level of visual processing as manifested by an increase in amplitude of the P1 (80-100 ms) and/or N1 (130-200 ms) components with little change in their timing or scalp distribution (Di Russo, Martinez, & Hillyard, 2003 and Hillyard & Anllo-Vento, 1998 for reviews; Fu, Greenwood, & Parasuraman, 2005). These findings suggest that attention acts as a gain control that amplifies the neural response to stimuli at the attended location (Hillyard, Vogel, & Luck, 1998). Whether or not attention effects occur earlier than the P1 component, e.g., the earlier C1 component, and thus suggest modulation of the initial volley of activation through striate

cortex is controversial (Clark & Hillyard, 1996; Clark, Fan, & Hillyard, 1995; Fu, et al., 2009; Kelly, Gomez-Ramirez, & Foxe, 2008; Martinez, et al., 1999;Wu, Chen, & Han, 2005). However, in general, the results from spatial attention ERP experiments provide evidence that when a stimulus is flashed at an attended location, it is selected early (prior to 100 ms) in visual processing.

These early selection effects occur when a spatial cue is provided that allows the participant to shift attention voluntarily or reflexively to the location in which the target will appear. Localization of a target in space may not occur this early when a predefined target stimulus must be found within an array of distractors. When this is the case, selection is not manifested in the ERP response until the time range of the N2 component (180-350 ms). This attention-related component is known as the N2pc, which is elicited over the posterior cortex contralateral to the search target. This component is associated with a shifting and focusing of attention on the target item (Luck & Hillyard, 1994; Luck et al., 1997; Woodman & Luck, 1999; Woodman & Luck, 2003).

ERP studies of feature-based attention

In contrast with the modulation of P1 and N1 component amplitude seen with spatial attention, the selection of stimuli based upon a specific attended feature generally elicit components having a different profile. The paradigm typically used to study the electrophysiological mechanisms of feature-based attention consists of the sequential presentation of stimuli of differing values of some feature (e.g. red flashes mixed with green flashes). Participants are required to attend to one feature value (e.g. red) and ignore the other value (e.g. green). The ERP elicited by a stimulus with the unattended feature value

(e.g. a green stimulus when red is attended) is subtracted from the ERP elicited by the same stimulus when it has the relevant value of the attended feature (e.g. a green stimulus when green is attended). The early effects of this comparison may differ based upon the type of feature attended. For example, paying attention to stimulus color is associated with an early positivity (PD130) with an onset latency of 100 ms and an occipitoparietal scalp distribution (Anllo-Vento, Luck, & Hillyard, 1998), whereas when spatial frequency is the attended feature, the earliest modulation is also at 100 ms but differs in polarity and hemispheric predominance depending on whether the attended spatial frequency is high or low (Kenemans, Lijffijt, Comfferman, & Verbaten, 2002; Martinez, Di Russo, Anllo-Vento, & Hillyard, 2001). These components are followed by the more commonly observed broad negative component, the selection negativity (SN), that is present regardless of the type of feature attended, that typically onsets at 140-180 ms with its maximal amplitude over occipital areas of scalp, and may extend for several hundreds of milliseconds (Harter & Aine, 1984). In some studies investigating the selection negativity, participants may be asked to attend to *conjunctions of features* (e.g. blue vertical lines) in a set of stimuli composed of two values of each of the two features (e.g. blue or red and horizontal or vertical). When attended conjunctions are compared to stimuli that do not share either of the features of the relevant conjunction, selection negativities are also seen with an onset that varies between 145-284 ms (Karayanidis & Michie, 1997; Smid, Jakob, & Heinze, 1999), depending on the stimulus and difficulty of the task performed.

A few notable exceptions to the selection negativity findings have been recently noted. When a selection is made between feature dimensions, such as comparing the same

stimulus when attending to motion versus attending to color, selection is much earlier, 90-120 ms after stimulus onset, suggesting an early role of selection in feature-based attention (Schoenfeld, et al., 2007). Another hallmark of feature-based attention is when attending to a particular feature, stimuli containing that feature are also influenced at other locations in the visual field, known as "global feature based attention" (Saenz, Buracas, & Boynton, 2002; Treue & Martinez-Trujillo (1999). The presence of "global feature based attention" was tested with ERPs in a study by Zhang & Luck (2009) in which participants were to attend to intermixed red and green dots on one side of fixation while probe dots of the attended or unattended color were presented in the opposite visual field. An enhanced P1 component was observed for dot probes of the attended color versus the unattended color at the electrode sites contralateral to the probe. Thus, feature selection can occur within 100 ms of stimulus onset, similar to the effects of spatial attention.

ERP studies of object-based attention

A few ERP studies have investigated the timing of object-based attentional selection. When objects are separated in space and selection is based upon grouped-array representations, early effects on the exogenous ERP components are found. For instance, using stimuli similar to the Egly et al. (1994) paradigm described above, when participants are cued to sustain attention to a corner of one of the rectangles in the two rectangle display, probes presented at the other end of that rectangle elicit a larger N1 component than probes located at an equidistant location on the other rectangle (Martinez et al., 2006). These findings suggest that, in accordance with the previously reported behavioral data, attention spreads through the locations on the attended object resulting in a shallower gradient of

spatial attention than for locations that are equidistant but on a different object. These results have also been demonstrated in similar paradigms using exogenous cues in which the location of the cue changes on each trial (He, Fan, Zhou, & Chen, 2004; He, Humphreys, Fan, Chen, & Han, 2008) as well as with stimuli formed by perceptual completion such as Kaniza rectangles in which the results cannot be due to line tracing (Martinez, Teder-Salejarvi, & Hillyard, 2007; Martinez et al., 2007).

In addition to the results investigating the interaction between spatial and object-based attention, evidence for object-based attention in paradigms in which spatial selection is not possible have also been demonstrated. One seminal study by Valdes-Sosa and colleagues utilized random-dot stereograms in order to give the perception of two intermingled dot surfaces (Valdes-Sosa, Bobes, Rodriguez, & Pinilla, 1998). The surfaces were formed by presenting dots of two different colors in which dots of each color moved coherently in opposite, counter-rotating directions. Participants were asked to attend to one dot surface or another to detect a translation of a subset of the dots in a specific direction. Translations occurred on the attended and unattended dot surfaces. Evidence for suppression of the P1 and N1 components was seen for translations of the unattended surface. Early object-attention related results were also seen in another paradigm in which dot surfaces were utilized however attention was directed to one surface or another using an exogenous cue of dot displacement that was followed by another displacement on the same attended surface or on the unattended surface. Posterior C1 and N1 components to the second translation were larger when on the cued attended surface versus the unattended surface (Khoe, Mitchell, Reynolds, & Hillyard, 2005). These findings provide evidence of that object-based attention

occurs rather rapidly in information processing (generally in the time frame of the N1 component 130-200 ms) even when spatial selection cannot play a role.

Objects are not only defined by their extent in space but also by their constituent features such as color, shape, spatial frequency, and orientation. Any description of object-based attention must account not only for the selection of one object over another, but must also be able to describe the selection of a unified objects in which attention spreads to encompass all of the features of an object. The integration of an object's features is also referred to as feature binding. Theories and evidence for feature binding will be described below.

Feature binding

Evidence for a binding problem in vision

Physiological evidence from single and multiple neuron recordings in animals suggests that there are specialized visual processing modules along the dorsal & ventral brain pathways (Ungerleider & Mishkin, 1982). Generally speaking, motion and space are processed in brain areas in the dorsal pathway and other features such as color and shape are processed in areas of the ventral pathway. In humans, focal brain damage in one of these areas can lead to loss of function in that module without affecting other modules. For example, damage to the inferior occipitotemporal region, area V4, may lead to cerebral achromatopsia, an inability to perceive color, without any impairment in shape or motion perception (Meadows, 1974; Damasio et al. 1980) and damage to the middle temporal gyrus in areas identified as the human equivalent to area MT may lead to akinetopsia, the inability to perceive motion (Zihl et al., 1983; Zeki, 1991). Also, in normal healthy subjects, during

PET and fMRI recording, focal brain activity shifts from one area to another when subjects are asked to respond to different aspects (shape, color, or motion) of the same displays (Corbetta et al. 1991; Sereno et al. 1995; Schoenfeld et al., 2007), suggesting specialized processing modules in the visual cortex.

Based on these data, it has been hypothesized that the visual system analyzes input based on these different feature dimensions, and that the binding problem concerns how these basic features are "recombined" into coherent objects. Thus, it becomes a problem for the visual system to determine which object to assign the correct color, shape, or direction of motion since activity is present in all of these areas. Even though the mechanisms of the binding process have not been resolved experimentally, the visual system typically solves this binding problem easily. In the experimental setting, however, miscombinations of object features may be observed even in healthy participants. In studies of "illusory conjunctions", subjects are briefly presented with displays of several objects, such as shapes and letters (Treisman & Schmidt, 1982). In divided attention tasks of this sort, participants are asked to report the two digits on the peripheral ends of the display while different shapes of various colors encompass the center of the display. After the display is removed, participants must report as many features as possible of the object that appeared in that specific location. During about 18% of the trials, conjunction errors are produced in which the color and shape of the objects are erroneously recombined.

These binding conjunction errors have also been reported for patients with damage to their parietal lobes, such as patient R.M. (Friedman-Hill et al., 1995; Robertson et al., 1997). Importantly, these errors did not occur when objects were presented successively. Not only

did R.M. report illusory conjunctions even when only two objects were present in a display and were presented for up to 10 seconds, but he also exhibited symptoms of simultanagnosia. Both the findings of illusory conjunctions as well as the findings from patient R.M. suggest that focused spatial attention may be necessary for the binding of object features.

Feature integration theory

Treisman & Gelade (1980) proposed a special role for spatial attention in the binding problem. Their feature integration theory proposed that features are separately coded, that focused attention is required to solve the binding problem, and that attention is not required for the simple detection of unique features. They tested their theory using visual search tasks in which a target is defined by a unique feature or by a conjunction of features that are similar to the distractors. For example, feature search may entail a search for a vertical line in a display of horizontal lines whereas a conjunction search may require the detection of a vertical red line in a display of horizontal red and vertical green lines. Targets may be detected rapidly during a feature search with relatively no interference when the display size is increased. In contrast, during a conjunction search, the time required to detect the target increases as the display size is increased. These findings were interpreted to suggest that features are coded pre-attentively and that the binding of features requires focused attention to each object in turn. While spatial attention may be used in some cases to resolve the binding problem by isolating one object from another, in many cases, objects overlap one another in space. Biased competition theory, discussed below, provides a different explanation for how feature binding may occur.

Biased competition theory

        Biased competition theory predicts that attentional selection does not arise from a "unified attentional system", but instead, that object selection occurs as a result of distributed brain activity (Duncan, 1996). This theory provides several predictions that are important for object-based attention and feature binding. Importantly, this theory does not rely on spatial attention to resolve the binding problem between objects. The three main tenets of this theory are that objects compete for selection, that competition between objects is controlled by top-down (goal-directed) or bottom-up (stimulus salience) biases, and that competition is integrated across brain systems. Each of these tenets will be briefly discussed in turn.

        Evidence for competition between objects has accumulated using behavioral, and brain measures, and in particular single-cell recordings from animals (see Beck & Kastner, 2009 for review). Biased competition serves a particularly important role in solving the binding problem. The receptive field size of neurons increases as one moves through the ventral visual stream that is thought to underlie object recognition (Underleider & Mishkin, 1982). The neurons in the primary visual cortex, V1, have receptive field sizes of less than one degree of visual angle. This receptive field size increases to tens of degrees of visual angle when neurons are recorded in inferior temporal (IT) cortex. Object recognition is thought to occur in the higher visual areas, such as IT. These large receptive fields are thought to facilitate object recognition by allowing for invariance over factors such as the orientation and size of the object because the object in its entirety is processed within the same receptive field. However, the cost is that often two different objects can fall within the same large receptive field and cannot be resolved. Findings from single-cell recordings in

the macaque have provided evidence that when two objects are presented within the receptive field of the same cell, the neural response to the pair of stimuli is less than the sum of the response when each object is presented individually within the receptive field, suggesting that the pair of stimuli act in a mutually suppressive manner (Reynolds, et al., 1999). This result has been found in several visual areas of the monkey brain, V2, V4, MT, MST, and IT (Miller et al., 1993; Recanzone et al., 1997; Reynolds et al., 1999; Snowden et al., 1991) as well as in the human brain using fMRI (Beck & Kastner, 2005, 2007; Kastner, De Weerd, Desimone, & Ungerleider, 1998; Kastner et al., 2001).

Selective attention is thought to play a role in solving the binding problem by resolving this competition between objects for representation. When one of the two stimuli within the receptive field of the same neuron is attended, the response elicited by that pair of stimuli is driven by the attended stimulus. The effect that is observed is described as attention causing the receptive field to shrink around the attended object resulting in that stimulus driving the response of the cell while excluding the unattended stimulus from the receptive field (Moran & Desimone, 1985).

This competition between objects is *biased* in favor of one object over the others by the cognitive demands of the task (such as direction to one or another stimulus based on its location) or by the increased salience of one of the objects over the others. For example, when a monkey is asked to attend to one of two stimuli presented within its receptive field, attention can counteract the suppression of the other stimuli such that the response to a pair of stimuli in the same receptive field will be comparable to the presentation of the attended stimulus alone (Luck et al., 1997; Reynolds et al., 1999). In addition, if two stimuli are

presented in the same receptive field but one of the stimuli is more salient than the other, the response of the cell will be driven by the more salient stimulus (Reynolds & Desimone, 2003).

The last tenet, that the competition between systems is *integrated,* is perhaps the most relevant for object-based attention. Integrated competition predicts that when an object becomes dominant in one brain system, its representation will then gain dominance in other brain systems thus selecting all of the properties of that object such as its color, shape, as well as action related properties of the object. Thus, theories of object-based attention predict that in addition to the selection of all of the locations on an object, that all of the constituent features of that object will also be selected. Integrated competition is an important mechanism for object-based attention because it allows for the selection of all of the features of an object without the need for spatial selection as indicated in feature-integration theory (Treisman & Gelade, 1980; Treisman, 1993; Treisman, 1998). Few studies have investigated the integrated competition hypothesis of biased competition theory, the spread of attention to all of the features of an object. These studies will be discussed below.

Evidence for integrated competition in object-based attention

While prior studies have shown behavioral and neural evidence for the selection of one object over another, only a few studies have provided evidence for one of the fundamental hypotheses of object-based attention, the selection of an object as an integrated ensemble of features. Several psychophysical studies have investigated the spread of attention from one object feature to another, using moving dot stimuli. In one such study,

participants attended to one of two surfaces of dots segregated by their color and motion. During some trials, while detecting a luminance increment on the attended surface, a sub-threshold motion prime was presented on either the attended or unattended surface. This prime affected subsequent motion direction discrimination performance only if the prime occurred for dots of the attended color (Melcher & Vidnyánszky, 2006). This finding suggests that by selecting one feature of an object such as its color, unperceived features such as motion are also selected and can later influence performance. This object-based spread of attention from an attended color feature to the motion feature of the object has been demonstrated in other studies using moving dot surfaces (see Sohn, Papathomas, Blaser, & Vidnyánszky, 2004; Melcher, Papathomas, & Vidnyánszky, 2005). The spread of attention to a task-irrelevant feature was measured in a priming paradigm in which the spatial frequency, color, and orientation of Gabor line patches were manipulated (Kristjánsson, 2006). Faster performance occurred when the task-relevant feature of the line patch was repeated, irrespective of feature type. However, when the task-irrelevant feature of the line patch was repeated, only the task-irrelevant color feature (not orientation or spatial frequency) resulted in priming effects. Together, these findings indicate that while attention may spread to task-irrelevant features of objects, this may not always be the case.

Few brain imaging studies have tested the spread of attention to other features of an object. O'Craven and colleagues, using functional magnetic resonance imaging, fMRI, cleverly showed such selection by taking advantage of the knowledge that specific areas of the brain are differentially activated when face, house, and moving stimuli are attended (O'Craven, Downing, & Kanwisher, 1999). The display consisted of superimposed face and

house stimuli, one moving and one stationary.   Participants were asked to monitor the

display for consecutive repetitions of face or house stimuli, or the direction of motion across

trials. The cue word (face, house, or motion) appeared before each block to indicate which

object was to be attended. A higher signal change in areas coding for the attended object but

not for the other superimposed object would provide evidence for object-based attention. A

higher signal change was observed in the area for the preferred attribute; fusiform face area

(FFA) for faces, parahippocampal place area (PPA) for houses, and MT/MST for motion. In

each region the change in signal was greater when subjects attended to the preferred attribute

for that cortical region than when they attended to a different attribute of the same display.

Importantly, task irrelevant attributes of an attended object were also selected with the task

relevant attribute. When participants attended to motion; a higher signal change was

observed in the FFA when the faces moved than when the houses moved. These results

cannot be explained by space- or feature-based attributes alone. These findings suggest that

selection may be object-based under circumstances in which selection by location is not

possible and in addition, that object-based attention spreads to cortical areas that process

other attributes of the attended object.

        While the O'Craven and colleagues (1999) study provided initial evidence for a

spread of attention across cortical features of an object, the fMRI method does not provide

the time resolution to determine whether selection of the task-irrelevant feature occurred

within enough time to participate in the binding and perceptual integration of the object (e.g.

before response selection). Schoenfeld et al. (2003) investigated the timing of the spread of

object-based attention to a task-irrelevant color feature by measuring ERPs, event-related

magnetic fields (ERFs), and the fMRI BOLD response while participants attended to overlapping multi-feature objects formed by moving-dot arrays. Participants attended to dots of one of two directions of motion and responded if the velocity of the dots was faster than the standard dot velocity. On some trials, dots of one of the surfaces would change color after the motion began. Trials during which a color change occurred on the unattended surface were compared to ones during which there was no color change to determine the sensory effect of the color change. This sensory effect was compared to effect of attention on the sensory effect. Attended surface color changes were compared to unattended surface color changes to determine the effect of attention. Their study determined that the neural processing associated with the task-irrelevant color feature was enhanced when it belonged to the attended surface within 40-60 ms after the initial sensory color registration, demonstrating a rapid binding of features across a multi-feature object. In addition, the source activity of the sensory color and attention effects both occurred in the ventral occipital region of the fusiform gyrus. These findings together provided strong evidence for the integrated competition hypothesis (Duncan, 1996; Duncan, Humphreys, & Ward, 1997).

Interestingly, these findings did not indicate an early selection of the task-irrelevant color feature (i.e. in the time frame of the P1/N1 components of the ERP), rather attentional selection occurred during the later time frame of the SN difference component as seen during studies investigating the processing of conjunctions of features. Also, these findings did not indicate any specific role for the parietal cortex in the selection of the task-irrelevant feature as seen in the patient studies described above.

Specific aims of the studies in this dissertation

While the Schoenfeld et al. (2003) study provided initial and fundamental spatial and temporal insights into the brain processes involved in the selection of multi-feature objects, it is unclear whether the results were specific to the particular set of stimuli/objects used. While motion is a powerful cue for object segregation, many of the objects that are processed by the visual system on a daily basis are static in nature. As discussed before, much of the fundamental evidence for the occurrence of object-based attention, including the pioneering study by Duncan (1984), used objects in which no motion was involved. Therefore, the studies in this dissertation sought to determine whether the Schoenfeld et al. (2003) object-based attention findings can be generalized to different types of static objects, more specifically, grouped arrays defined by orientation (Chapter II) and objects defined by geometric shape (Chapter III). Since orientation and shape are common defining features of objects in the real world, they were selected to provide ecological validity to the investigated object types. In addition, the timing of the attentional selection of the task-irrelevant color feature was of particular interest. If the timing and distribution of an object-based attentional effect is the same as in the Schoenfeld and colleagues (2003) study, this would suggest a general mechanism for the selection of a task-irrelevant color feature, independent of the object defining feature, such as the general feature-based attention finding of the selection negativity (SN) difference component.

Design of studies in this dissertation

The studies in this dissertation followed the general design of the Schoenfeld et al. (2003) study in several ways.

First, by placing two objects in the visual field such that their spatial extents overlapped, any interpretation of the results based on spatial attention mechanisms could be ruled out.

Second, the use of color versus its absence as the task-irrelevant feature was maintained as a factor, so that the timing of the initial color registration as well as the attentional selection of the task-irrelevant color could be determined. The difference between these two times provided an estimated binding time for the spread of attention to the task-irrelevant color feature. In addition, the use of color as the task-irrelevant feature allowed for a more direct comparison between the studies in this dissertation and the Schoenfeld and colleagues (2003) study.

Third, the task-irrelevant color feature was maintained as task-irrelevant (having no associated behavioral response) throughout the experiment so that it would be selected as a result of its belonging to the same object as the task-relevant feature, rather than as a result of being associated with a response from another condition in the experiment. Because the color feature was not associated with a behavioral response, its selection was revealed solely by measuring ERPs elicited by the stimulus display.

Lastly, the main comparisons between the Schoenfeld et al. (2003) study and the studies in this dissertation remained the same. Two main comparisons of interest were derived from the ERP data:

I) the sensory effect of the presence of color in the display, and

II) the effect of attention to orientation or shape on the processing of the task-irrelevant color.

        In particular, it was investigated whether differential processing of the task-irrelevant feature would occur when the object was attended versus unattended. If such a difference were found, it would provide evidence for object-based selection. If no reliable difference was found when the colored object was attended versus unattended, it would be concluded that object-based selection did not occur. In addition, the onset of the "sensory effect" and the onset of the "attention effect" were compared to estimate a binding time for the task-irrelevant color feature to the attended object.

Hypotheses

Based on the Schoenfeld and colleagues (2003) study, it was hypothesized that

I)   There would be a spread of object-based attention throughout all of the features of the object, resulting in differential processing of the task-irrelevant feature when it belonged to the attended versus the unattended object.

II)   The spread of attention to the task-irrelevant feature should be reflected in an ERP component having the same scalp distribution (and hence neural source) as an earlier component reflecting the sensory effect of color.

III)   If the attention effects observed by Schoenfeld et al. (2003) are indicators of a general mechanism independent of the specific stimuli used (e.g., the type of object and its defining features) and task requirements, then the timing of the binding of color to the attended object and the scalp distribution of the associated ERP should be the same as previously reported.

IV)   If the timing of binding of a task-irrelevant color feature and the ERP scalp distribution is affected by the defining object feature and task requirement, then it would be concluded that different mechanisms of object-based attention are involved for different object types.

CHAPTER 2: SPREAD OF ATTENTION TO A TASK-IRRELEVANT COLOR FEATURE WHEN ATTENDING TO ORIENTATION

INTRODUCTION AND RATIONALE

The study of Schoenfeld et al. (2003) contributed important insights into the mechanisms of object-based attention. A critical question is whether the reported effects would generalize to the processing of different types of objects, particularly those that do not involve motion, or rather are specific to the conditions of that study. As such, the present study was designed to determine whether attention spreads to task-irrelevant features of a multi-feature object in a paradigm in which the objects were defined by a common orientation instead of direction of motion. Here, a grouped array of vertical and horizontal lines served as objects and the effect of attention to one orientation or another on a task-irrelevant color was investigated. It has been previously demonstrated that participants are able to selectively attend to superimposed lines of one orientation or another (Liu, Larsson, & Carrasco, 2007). Thus, the current study was designed to investigate whether attention to the orientation feature of the grouped array/object would result in selection of all of the features of the object, both task-relevant and irrelevant. Processing of the task-irrelevant color feature was assessed by calculating difference ERPs in the same manner as Schoenfeld et al. (2003) (see Chapter 1). Two effects were compared: 1) the sensory effect of the presence of color in the display and 2) the effect of attention to one orientation or another on the processing of the task-irrelevant color.

Based on the results from Schoenfeld and colleagues (2003), it was predicted that in this study, attention would also spread to the task-irrelevant color feature of the object, thus providing evidence that object-based attention includes the binding of task-irrelevant features. However, the timing and scalp topography of the ERPs associated with selection of the irrelevant feature may vary according to the intrinsic features of different types of objects, and hence may differ between the present study and the Schoenfeld et al. study. The results from this study do in fact provide evidence for the spread of object-based attention using grouped line arrays, thus, extending the findings of Schoenfeld and colleagues to a different type of object.

METHODS

Participants

Fifteen healthy human adult participants (6 male) between the ages of 18 and 25 years of age (M=19.73 years) served as paid volunteers in this experiment. All participants were right-handed, had normal to corrected-to-normal vision, and no reported color-blindness or neurological illnesses. Informed consent was obtained from all participants.

Stimuli and Task

Grids composed of superimposed vertical and horizontal line segments presented centrally served as stimuli (6.06 x 6.06° total size) (Figure 2.1). The line width was 0.20° and the spacing between lines was 0.47°. Stimuli were presented on a CRT monitor at 85 cm viewing distance in a darkened, sound-attenuated and electrically shielded room. Each grid

was presented for 161 ms and the inter-stimulus interval varied randomly between 800 and 1000 ms. A small black fixation dot was presented in the center of the display throughout each trial. One of three stimulus types was presented on each trial: i) "gray vertical & gray horizontal lines", ii) "red vertical & gray horizontal lines", and iii) "gray vertical & red horizontal lines") on a dark gray background.   Target stimuli only differed from standard stimuli by a thickening of the segments of one of the lines in the grid (Figure 2.1). In order to encourage a wide distribution of attention across all of the lines, targets never occurred in the two middle lines adjacent to the fixation dot in the center of the display.
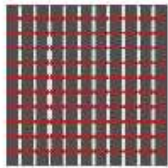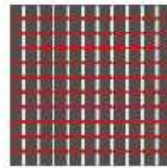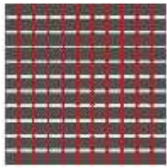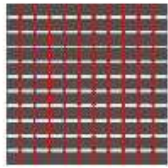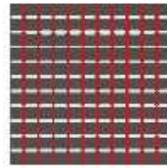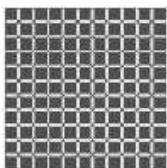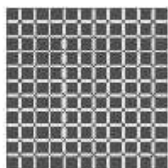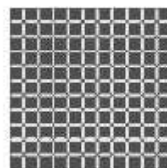
	Non-targets	Vertical Target	Horizontal Target
Red Horizontal Lines Gray Vertical Lines	26.67%	3.33%	3.33%
Red Vertical Lines Gray Horizontal Lines	26.67%	3.33%	3.33%
Gray Vertical Lines Gray Horizontal Lines	26.67%	3.33%	3.33%

Figure 2.1. Exemplars of the stimuli presented. Percentages are the frequency each type of stimulus was presented.

The RGB values for the red stimuli were (R = 226, G = 15, B = 15) and subjective brightness of the red and gray colors was equated by minimizing heterochromatic flicker in tests carried out on three color-normal experimenters (Anllo-Vento, Luck, & Hillyard, 1998). This resulted in a light gray color (R = 229, G = 229, B = 229) that was isoluminant to the red color.

Prior to task instructions, participants completed a short (5 minute long) "passive viewing" session in which only the non-target stimuli were shown. The three stimulus types

("gray vertical & gray horizontal lines", "red vertical & gray horizontal lines", and "gray vertical & red horizontal lines") were shown an equal number of times and in random order, with the same stimulus timing parameters as in the main experiment. The effect of color on the ERPs during "passive viewing" was intended to serve as a comparative control for the "sensory effect" to be investigated during the attention experiment.

At the beginning of each block of trials, participants were instructed to attend to either horizontal or vertical lines while ignoring lines of the other orientation, and to respond by pressing a button on the keyboard when a line of the attended orientation was thicker than usual. Participants were told to keep their eyes on the dot in the center of the screen throughout each block but to distribute their attention evenly over the display in order to perceptually group the lines of the indicated orientation. They were explicitly told that the color of the target did not matter and to refrain from moving their eyes to search for targets. Response accuracy and speed were emphasized equally.

Stimuli of all types were presented in random order with the percentages shown in Figure 1, and 20% of trials contained a target. Targets appeared with equal probability on the attended and unattended lines, however, a response was only required to targets of the attended orientation (10% of the trials). An initial practice session was given to familiarize participants with the task and to minimize their production of movement related artifacts. The hand used for response was counterbalanced by having each participant respond with either their right or left hand during the first half of the experiment and their other hand during the second half. A response occurring 150-1000 ms after target presentation was

scored as correct. Responses recorded during non-target trials were scored as false alarms.

Each participant was presented a total of eight blocks (four attend horizontal, four attend

vertical) resulting in a total of 1,920 trials. The presentation of blocks was randomized.

Each block lasted six minutes. A small break of five seconds was given every forty seconds

during each block. The length of the break between blocks was controlled by the participant

with the exception of a mandatory break given after the fourth block.

Electrophysiological recording and data analysis

The electroencephalogram (EEG) was recorded from 64 scalp electrode sites using a

modified 10-20 system montage (Di Russo, Martinez, & Hillyard, 2003). Standard 10-20

sites were FP1, FP2, FZ, F3, F4, F7, F8, CZ, C3, C4, PZ, P3, P4, O1, and O2. Additional

electrodes were FPZ, AFZ, AF3, AF4, FCZ, FC1, FC2, FC3, FC4, FC5, FC6, T7, T8, C1,

C2, C5, C6, CPZ, CP1, CP2, CP3, CP4, CP5, CP6, P1, P2, TP7, TP8, POZ, PO3, PO4, P5,

P6, P7, P8, PO7, PO8, OZ, IZ, I3, I4, I5, I6, SIZ, SI3, SI4, M1 and M2.   Eye blinks and

movements were monitored by placing electrodes at the right and left external canthi and

below the left eye to record horizontal and vertical electro-oculograms (EOGs). Electrodes

were referenced to the right mastoid electrode (M1) during recording and were later re-

referenced to average of the M1 and M2 electrodes for analysis. Electrode impedances were

lowered to 5 kΩ prior to recording. The EEG was digitized at 250 Hz with a gain of 10, 000

and was filtered with a bandpass of 0.1-80 Hz. Prior to signal averaging, automated artifact

rejection was performed to reject trials containing eye movements, blinks, or amplifier

blocking. The ERP analysis was restricted to non-target trials in order to exclude cortical

activity related to detection of a target stimulus as well as motor related activity resulting from a button press. Two criteria were used to avoid contamination by motor potentials. These were to discard non-target trials where either 1) the subject produced a false alarm (i.e. subjects pressed the button during a non-target trial) or 2) when there was a button-press response in the previous trial. For each subject and condition, ERP averages were time-locked to the onset of the grid stimulus. Prior to data analysis, the averages were digitally low-pass filtered with a Gaussian finite impulse function to remove high frequency noise and were baseline corrected using the mean amplitude of a 100 ms pre-stimulus baseline. For all analyses, ERPs to non-target stimuli of each type were pooled to create grand-average waveforms. The six experimental conditions are illustrated in Figure 2.2.

The two variables of interest were I) attention to orientation (attend horizontal lines versus vertical lines) and II) stimulus configuration (red horizontal, red vertical, and both gray). The six experimental conditions were combined into: i) "attended red", ii) "unattended red", and iii) "both gray", collapsing over conditions of attention to horizontal and vertical lines. Because this analysis was aimed at investigating whether the task-irrelevant color feature was selected in general, regardless of whether the attended orientation was vertical or horizontal, ERPs were averaged over the attention to orientation variable in this analysis. ERPs recorded under the various conditions were combined and subtracted to create specific comparisons of interest.
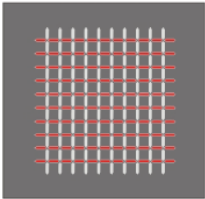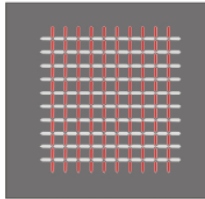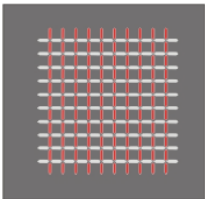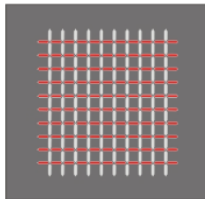
Figure 2.2. The six experimental conditions defined by a combination of the stimulus configuration and the attended orientation.

To assess the "sensory effect" of the presence of color, difference waves were calculated by subtracting ERPs elicited by stimuli in which the lines of both orientations were gray from ERPs elicited by "unattended red" stimuli (Figure 2.3A). This comparison provided a measure of the processing of color in the display. The "orientation effect" was examined by subtracting ERPs elicited when the subject attended to horizontal lines from ERPs when vertical lines were attended, both lines being gray (Figure 2.3B).

Experimental Comparisons
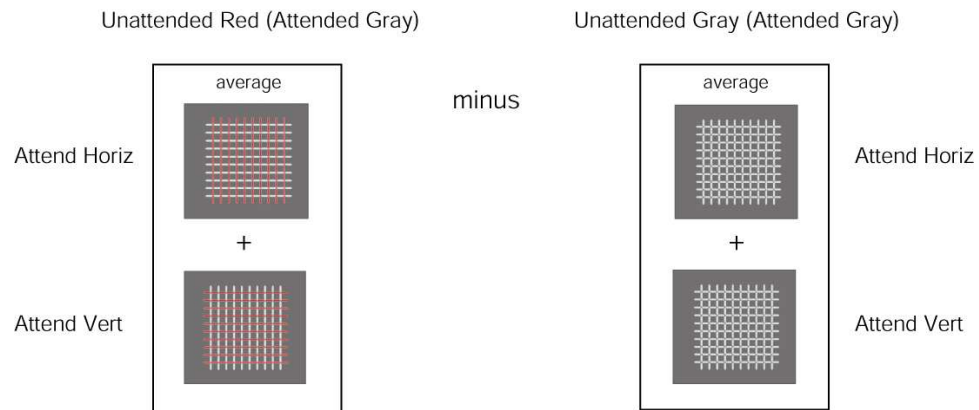
A   Sensory Effect of Color: Difference Wave

Unattended Red (Attended Gray)   Unattended Gray (Attended Gray)

minus

Attend Horiz   Attend Horiz

Attend Vert   Attend Vert

B   Attention to Orientation Effect: Difference Wave

Attended Vertical Lines   Attended Horizontal Lines

minus

C   Effect of Attention on Task-Irrelevant Color: Difference Wave

Attended Red (Unattended Gray)   Unattended Red (Attended Gray)

minus

Attend Vert   Attend Horiz

Attend Horiz   Attend Vert
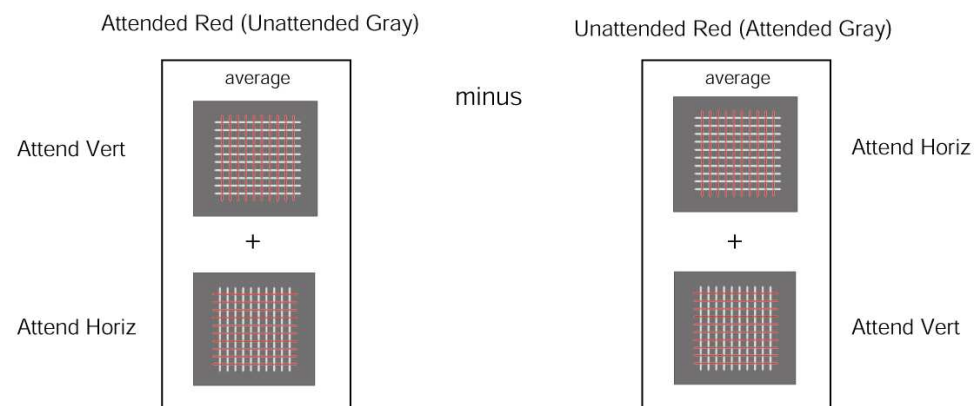
Figure 2.3. Graphical depiction of the comparisons calculated.

To examine the main effect of interest, the effect of attention on task-irrelevant color processing, a difference wave was created by subtracting ERPs to "unattended red" stimuli from "attended red" stimuli (Figure 2.3C). Differential processing of the color feature when the colored object is attended versus unattended would provide evidence for the spread of object-based attention to the irrelevant feature. Because the analysis was aimed at investigating whether the task-irrelevant color feature was selected in general, regardless of whether the attended lines were vertical or horizontal, this analysis was averaged over the attention to orientation variable. The resulting difference wave reflected selection of the task-irrelevant color feature independently of whether there was an orientation effect. Importantly, the same stimulus was compared under the different attention conditions (attend horizontal or attend vertical), as such stimulus differences could not account for any attention effects observed.

For all analyses, difference wave components were quantified as mean amplitudes within specific latency windows around the peak of each identified component. Each effect was measured as the mean voltage over a specific cluster of electrodes at which the difference component amplitude was maximal. The time window and specific clusters used are listed in the significance tables given for each experimental ERP effect. All analyses were performed using repeated measures ANOVA and Tukey HSD post-hoc testing unless otherwise indicated. Differences in scalp distribution between the "sensory" and "attention" effects were calculated after normalizing their amplitudes, prior to ANOVA, according to the method described by McCarthy and Wood (1985). Comparisons were made over 38

electrodes spanning frontal, central, parietal and occipital sites. Differences in scalp

distribution were reflected in significant "experiment by electrode" interactions. The

Greenhouse-Geisser correction was applied to analyses that had more than two degrees of

freedom (i.e., electrode site).

<u>Modeling of ERP sources</u>

To estimate the cortical generators of the sensory and attention effects, source

localization analyses were performed on the grand-averaged difference waves within the

same intervals used for statistical testing. Current density distributions were estimated using

a local autoregressive average (LAURA) algorithm (Grave de Peralta Menendez, Gonzalez

Andino, Lantz, Michel, & Landis, 2001). LAURA uses a realistic head model with a

solution space of 4024 nodes evenly distributed within the gray matter of the Montreal

Neurological Institute (MNI) average template brain. It makes no a priori assumptions

regarding the number of sources or their locations and can deal with multiple simultaneously

active sources (Michel, Thut, Morand, Khateb, Pegna, Grave de Peralta, Gonzalez, Seeck, &

Landis, 2001). LAURA analyses were implemented using the Cartool software

(http://brainmapping.unige.ch/Cartool.php). The Talairach coordinates of the current source

maxima given by the LAURA algorithm were entered into the Talairach Client (Lancaster,

Woldorff, Parsons, Liotti, Freitas, Rainey, Kochunov, Nickerson, Mikiten, & Fox, 2000) to

determine the brain region of the estimated maximal sources. Maps illustrating both the

sensory and attention effects and their overlap were created using the AFNI software (Cox,

1996) and were projected onto a structural brain image supplied by MRIcro (Rorden & Brett, 2000).

RESULTS

Behavioral Results

A 2 x 3 ANOVA was calculated with the factors of attended orientation (horizontal or vertical) and stimulus configuration ("attended red, "unattended red", and "both gray"). The mean hit rates, false alarm rates, and response times for target detection during the experimental session are provided in Table 2.1. Interestingly, detection of target lines was faster and more accurate for vertically oriented than horizontally oriented lines (Vertical: $M = 607.20$ ms, 83.33%; Horizontal: $M = 629.05$ ms, 67.01%) ($F(1,14) = 20.18$, $p < 0.001$, response time; $F(1,14) = 28.30$, $p < 0.001$, hit rate). The color configuration of the stimuli also significantly affected response time ($F(2,28) = 9.22$, $p < 0.001$). However, importantly, post-hoc analysis indicated that the response time to targets when color was present in the display was not significantly different from target response time when all of the lines were gray ("attended red" vs. "grays", $p = 0.45$; "unattended red vs. grays", $p > 0.18$). There was no significant attention x configuration interaction for the response time data ($F(2,28) = 1.34$, $p = 0.28$). Response time during the "all gray" line stimulus condition served as a baseline, thus allowing this approach to the post-hoc analysis. As such, while there was a significant effect of stimulus configuration in the omnibus analysis, post-hoc examination indicated that the presence of red in the display did not change response times significantly more or less from the baseline comparison of interest.

For hit rate, there was a significant attention x configuration interaction ($F(2,28) =$ 4.83, $p < 0.05$). Nevertheless, again when this effect is further investigated with post-hoc analysis considering separately the "attend vertical" and "attend horizontal" line conditions, no difference in hit rate performance existed for color configuration in the attend vertical condition ($F(2,28) = 0.76$, $p = 0.48$). When attending to horizontal lines, there was no significant difference in target hit rate when color was present in the display versus when all of the lines were gray ("attended red" vs. "grays", $p = 0.26$; "unattended red vs. grays", $p = 0.09$). Thus, once more, while there was a significant effect of stimulus configuration for the "attend horizontal" line condition, post-hoc analysis indicated that the presence of red in the display did not change hit rate significantly more or less than during the "both gray" condition, our baseline comparison of interest.

There were no significant differences in the false alarm rate data for any of the conditions. Thus, the presence of red in the display did not significantly affect performance any differently than when all of the lines in the display were gray.

Attended Orientation	Stimulus Configuration	Hit Rate (%)	*SEM* hit rate (%)	FA rate (%)	*SEM* FA rate (%)	Mean RT (ms)	*SEM* RT (ms)
Attend Horizontal Lines	Att Red/Unatt Gray	75.42	4.90	0.69	0.34	616.05	11.53
	Att Gray/Unatt Red	57.71	5.54	1.44	0.44	650.89	15.10
	Att Gray/Unatt Gray	67.92	3.07	2.08	1.24	620.20	8.50
Attend Vertical Lines	Att Red/Unatt Gray	83.54	3.92	0.69	0.22	587.79	10.58
	Att Gray/Unatt Red	81.04	4.89	1.71	0.70	622.40	12.73
	Att Gray/Unatt Gray	85.42	3.08	1.64	0.68	611.42	11.40

Table 2.1. Mean behavioral performance for the detection of target lines of the attended orientation during the main experimental session. (*SEM*: standard error of the mean, FA: false alarm, RT: response time, Att: attended, Unatt: unattended)

ERP results

The ERP waveforms elicited by the grouped line arrays were consistent with typically observed waveforms in other visual experiments (Hopfinger, Luck, & Hillyard, 2004). The first prominent component was a central, occipitally distributed negativity (C1; from 60-150 ms, peak 100 ms). The next component was a laterally distributed occipito-parietal positivity (P1; from 70–150 ms, peak 110 ms). These were followed by an occipito-parietal negativity (N1; from 150–190 ms, peak 180 ms, a subsequent positivity (P2; 200–280 ms, peak 220 ms, and a large amplitude negativity (N2; from 250–380 ms, peak 290 ms).

Sensory effect of color

Sensory Effect - Passive viewing session

In order to assess sensory effects of color in the absence of a task-specific attention requirement, participants were run in a five-minute passive viewing session prior to the active attention session. Non-target stimuli were presented with the same timing parameters as in the main experimental session. This sensory effect of color was measured by comparing the grand-averaged ERPs elicited by the line stimuli when red was present in the display versus when both line orientations were gray (Table 2.2; Figures 2.4, 2.5). This sensory effect was observed as a positive component (80-95 ms) at midline occipital sites. This component was followed by a negative component (96–223 ms) that was accompanied by a broad frontal/central positivity during the same time frame. The sensory effect during this passive condition became significantly different from the baseline at 80-89 ms ($t(14) =$ 3.51, $p < .01$).

Time window	Electrodes Clustered	ANOVA of the Passive Sensory Effect			Sensory Effect	
		Red lines present µV (*SEM*)	vs.	All lines gray µV (*SEM*)	*F* (1,14)	*p* <
80 – 95 ms	OZ, IZ	-3.59 (1.08)	vs.	-4.61 (1.09)	13.16	0.01
96 – 223 ms	OZ, IZ	-0.63 (0.98)	vs.	1.29 (0.62)	11.63	0.01
96 – 223 ms	CZ, CPZ	-0.43 (0.71)	vs.	-1.91 (0.74)	7.29	0.05

Table 2.2. The sensory effect of color during the passive viewing session. Mean voltage amplitude given in µV. (*SEM*: standard error of the mean, vs.: versus)
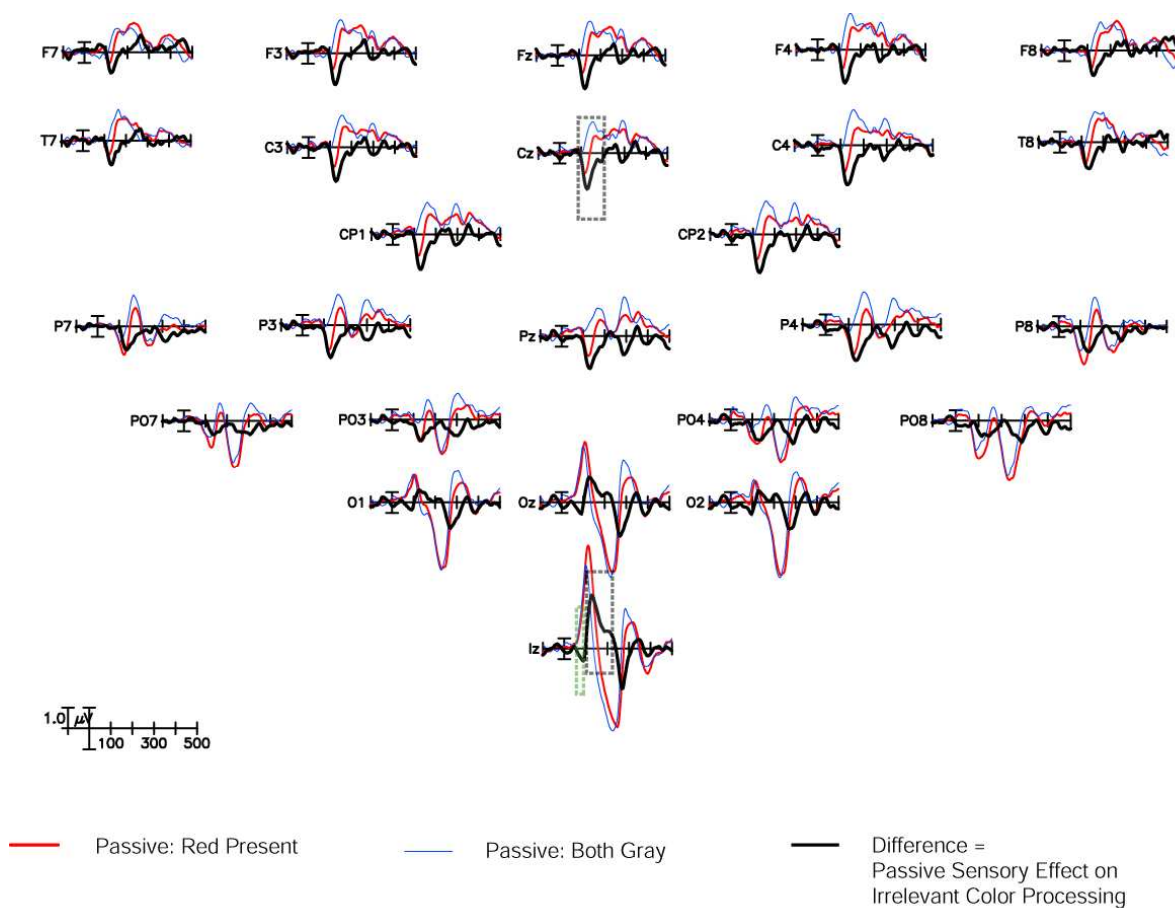
Figure 2.4. Grand-average ERPs associated with the sensory effect of color during the passive viewing session. Negative voltage is plotted upward. Dotted line boxes indicate the time windows used for statistical testing.

A) Red Present   B) Both Shapes Gray   C) Difference Waves
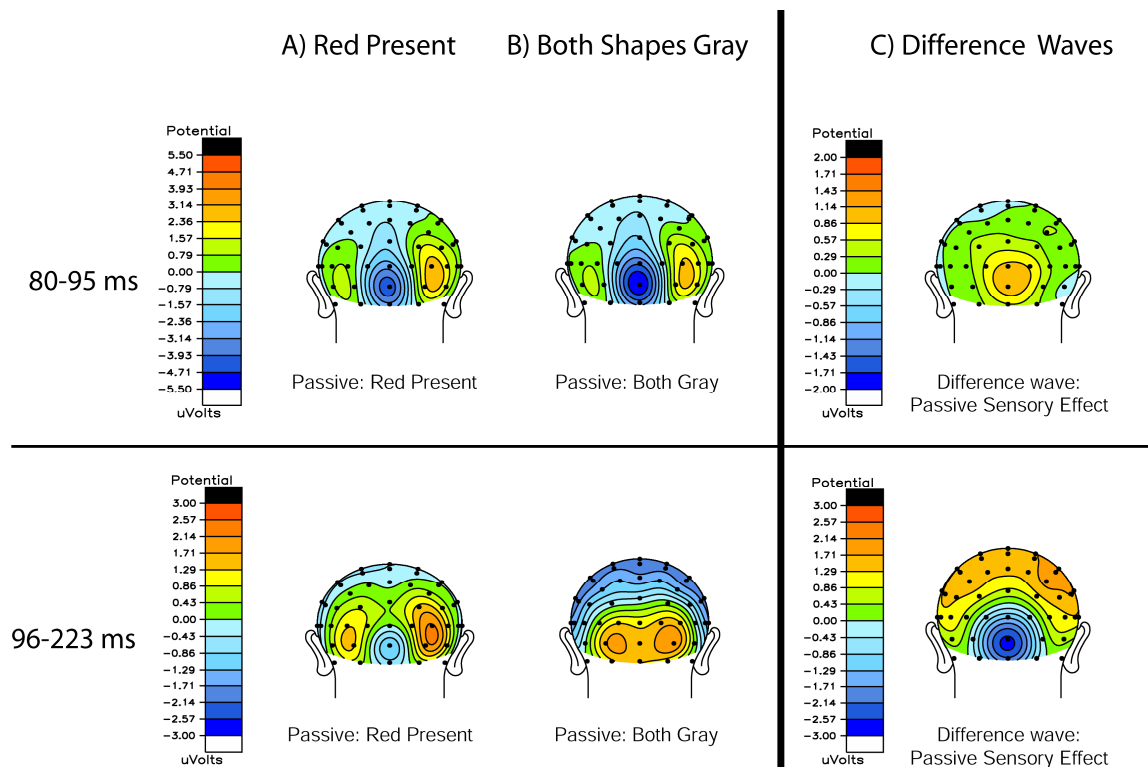
Figure 2.5. Topographical maps of ERP amplitudes indexing the sensory effect of color during the passive viewing condition. A) The distribution for trials in which red occurred in the display. B) The distribution for trials in which both line orientations were gray. C) The red minus gray difference wave distribution. The scale on the left is associated with columns A and B.

Sensory Effect - Attention experiment

The sensory effect of color was measured by comparing the grand-averaged ERPs elicited by the line stimuli to the "unattended red" and "both gray" configurations (Figure 2.3A; Table 2.3; Figures 2.6, 2.7). This sensory effect was observed as a greater negativity (96–223 ms) at midline occipital sites when the color red occurred on the unattended surface as compared to displays in which lines of both orientations were gray. In addition, a second sensory difference wave component (304–335 ms) represented by a medial occipital negativity accompanied by a broad frontal positivity was observed. The sensory color effect

became significantly different from the baseline at 100–109 ms ($t(14) = -2.45$, $p < .05$). For both, "attend to the horizontal" and "attend to the vertical" line conditions, the sensory effect of color was significantly different from the baseline, for horizontal lines at 100-109 ms ($t(14) = -3.27$, p < 0.05) and for vertical lines at 110-119 ms ($t(14) = -3.55$, $p < 0.01$). In order to further investigate potential differences associated with specific orientation, the difference waves from attending to vertical and attending to horizontal lines were compared. There were no significant differences in mean amplitude when attending to vertical versus horizontal lines for any of the sensory effects (96-223 ms/occipital, $p = 0.39$; 96-223 ms/ central, $p = 0.63$; 304-335 ms/occipital, $p = 0.33$; 304-335 ms/central, $p = 0.28$).

The sensory effect difference ERP component observed during the passive viewing session began earlier than the sensory effect during the active attention session. In addition, the amplitude of the effect was significantly larger during the active attention session at the occipital electrode sites ($M = -2.74$ µV($SE = 0.36$)) than during the passive viewing session ($M = -1.84$ µV ($SE = 0.55$), ($F(1, 14) = 6.43$, $p = 0.02$). However, the difference between the two sessions was not significantly different at central electrode sites ($F(1, 14) = 0.92$, $p = 0.35$). The difference in amplitude at the occipital electrodes and the onset of the sensory effect between the two sessions could be due to several differences, such as the need to perform a task and the inclusion of targets during the active attention session. However, importantly, the effect occurring between 96-223 ms that is present in both sessions is visually very similar in the timing and distribution of the effect, suggesting that the

comparison of "unattended red" stimuli versus "gray" stimuli is a valid measure of the

sensory effect for the presence of color in the display.

		ANOVA of the Sensory Effect			Sensory Effect	
Time window	Electrodes Clustered	Unatt-Red / Att-Gray µV (*SEM*)	vs.	Att-Gray / Unatt-Gray µV (*SEM*)	F (1,14)	$p <$
96 – 223 ms	OZ, IZ	-2.56 (1.24)	vs.	0.27 (0.96)	60.16	0.0001
96 – 223 ms	CZ, CPZ	0.10 (0.72)	vs.	-1.92 (0.62)	113.80	0.0001
304 – 335 ms	OZ, IZ	-4.56 (0.99)	vs.	-3.46 (0.82)	6.43	0.05
304 – 335 ms	CZ, CPZ	0.06 (0.80)	vs.	-1.94 (0.91)	46.10	0.0001

Table 2.3. The sensory effect of color. Mean voltage amplitude given in µV. (Att: attended, Unatt: unattended, *SEM*: standard error of the mean, vs.: versus)
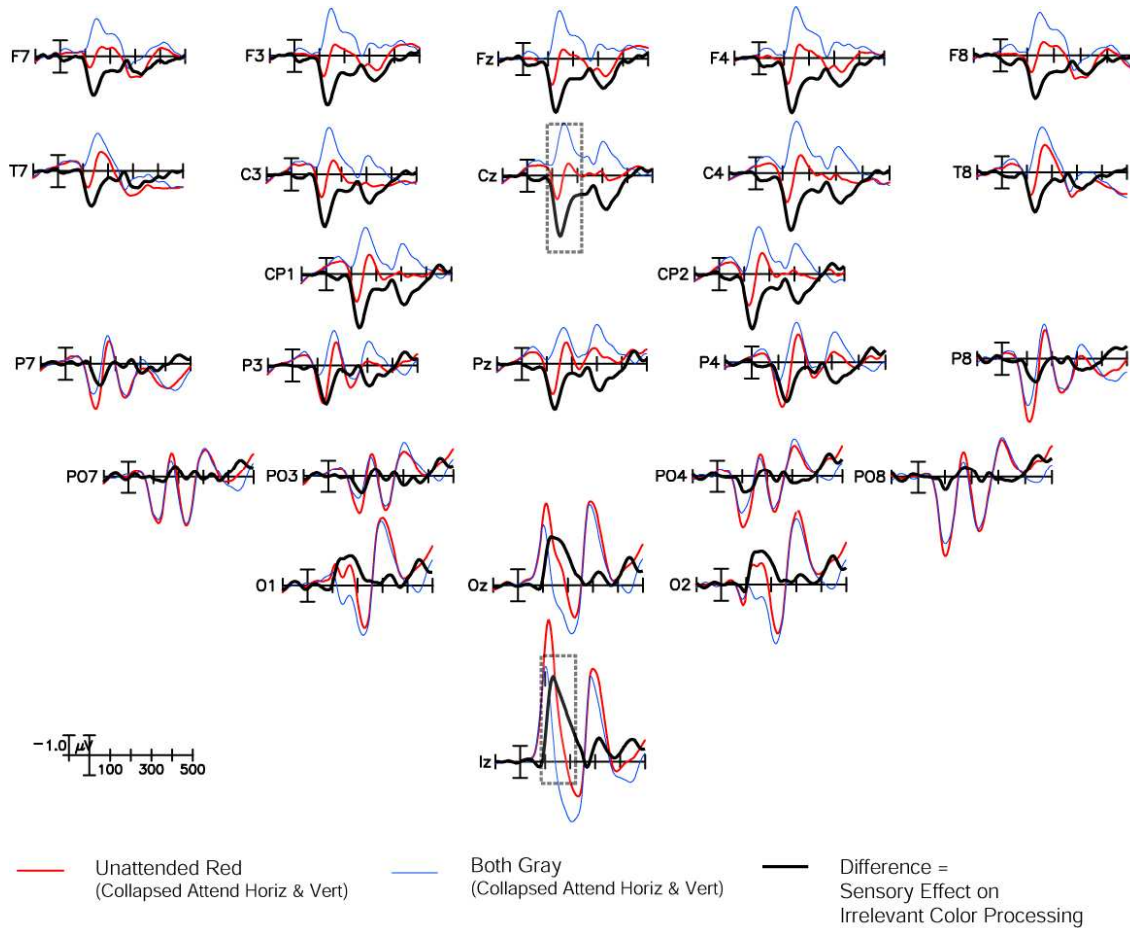
Figure 2.6. Grand-average ERPs (non-target trials) associated with the sensory effect of color, collapsed over attend horizontal and attend vertical conditions. Negative voltage is plotted upward. Dotted line boxes indicate the time windows used for statistical testing.
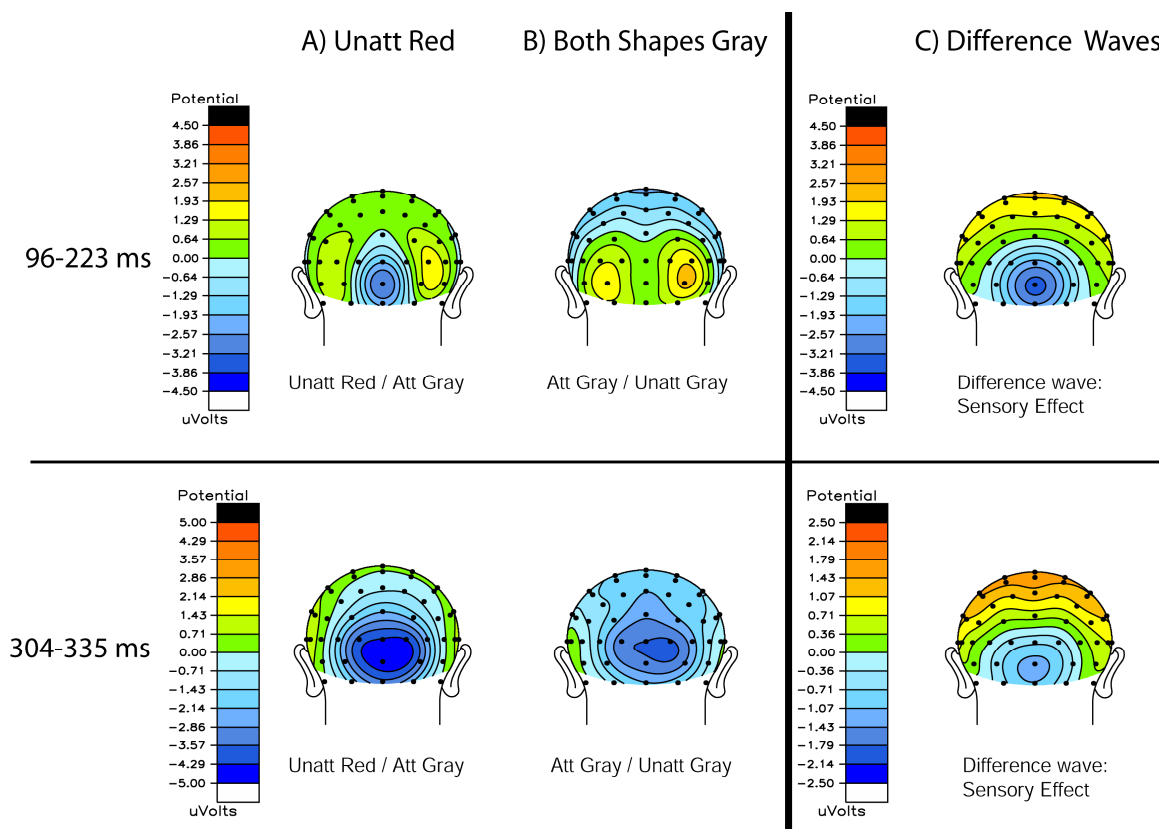
Figure 2.7. Topographical maps of ERP amplitudes indexing the sensory effect of color collapsed over attend vertical and attend horizontal conditions. A) The distribution for trials in which red occurred on the unattended orientation. B) The distribution for trials when both line orientations were gray. C) The red minus gray difference wave distribution. The scale on the left is associated with columns A and B. (Att: attended, Unatt: unattended)

No orientation effect was observed

In order to determine if there were specific effects associated purely with attention to one orientation or another, in the absence of color in the display, an orientation effect difference wave was computed. The effect of attended orientation was examined by subtracting the response of attending to horizontal lines from that of attending to vertical lines for stimuli in which both vertical and horizontal lines were gray (Figure 2.3B). However, none of the components visible in the difference wave were significantly different from the baseline amplitude ($p > 0.05$).

Effect of attention on task-irrelevant color processing

In order to maintain consistency between the sensory analysis and the attention effect, Schoenfeld and colleagues (2003) analyzed the effect of attention by collapsing ERP difference waves over the two attended surfaces. Here, because there was no ERP difference in attending to one orientation versus another, the same analytical approach was followed by collapsing over the two orientations. Thus, the effect of attention on task-irrelevant color processing was isolated by subtracting ERP waveforms on trials in which the red lines were unattended from trials in which the red lines were attended (Figure 2.3C). One significant component was observed in the collapsed difference waveform, a negativity peaking at about 300 ms at medial occipital electrodes (Table 2.4; Figures 2.8, 2.9). This difference was due to a greater negative voltage when the red lines were attended versus unattended. This effect became significantly different from the baseline between 280 – 289 ms ($t(14) = -2.78$,

$p < .05$). While the medial occipital distribution of this difference wave component appears similar to the sensory effect, the distribution of the "sensory effect" and of this "attention effect" were significantly different from one another (Effect x Electrode interaction: $F(37, 518) = 4.95, p < 0.001$).

		ANOVA of the Attention Effect			Attention Effect	
Time window	Electrodes Clustered	Att-Red / Unatt-Gray µV (*SEM*)	vs.	Unatt-Red / Att-Gray µV (*SEM*)	*F* (1,14)	*p* <
272 – 327 ms	OZ, IZ	-5.86 (1.24)	vs.	-5.14 (1.18)	10.82	0.01

Table 2.4. Effect of attention on color processing: collapsed over attended orientation. Mean voltage amplitude given in µV. (Att: attended, Unatt: unattended, *SEM*: standard error of the mean, vs.: versus)
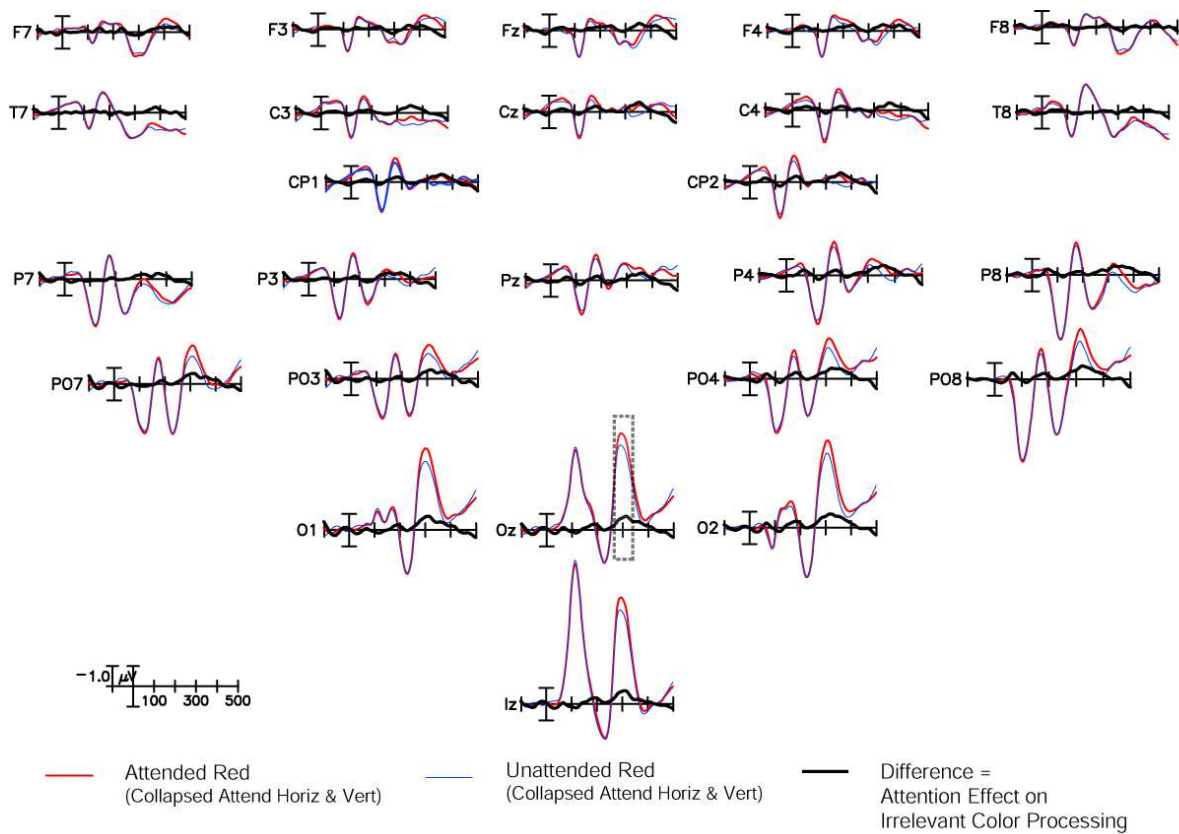
Figure 2.8. Grand-average ERPs (non-target trials) associated with the effect of attention on the task-irrelevant color, collapsed over "attend horizontal" and "attend vertical" conditions. Negative voltage is plotted upward. Dotted line boxes indicate the time windows used for statistical testing.
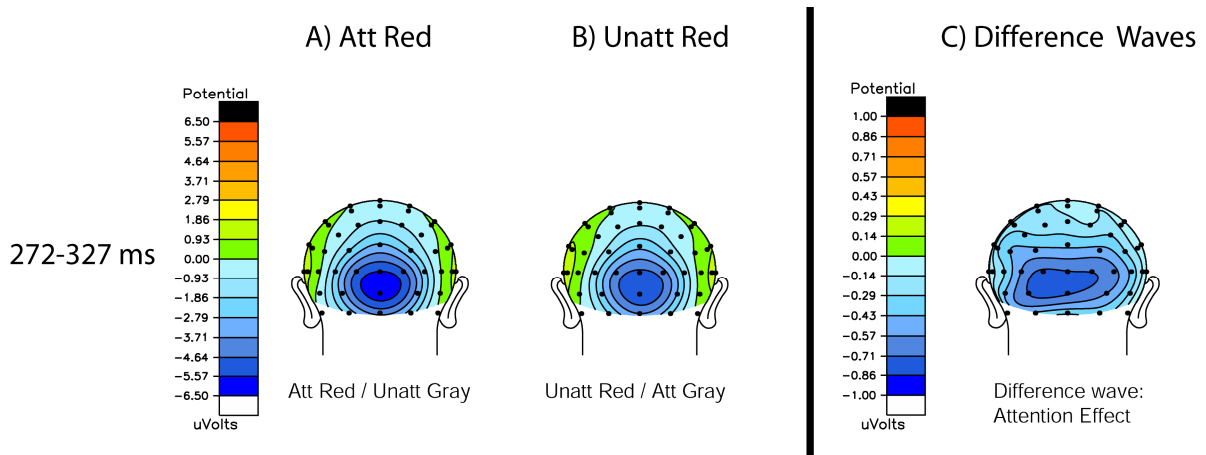
Figure 2.9. Topographical maps of ERP amplitudes indexing the effect of attention on the task-irrelevant color, collapsed over "attend horizontal" and "attend vertical" conditions. A) The distribution for the "attended red" wave. B) The distribution for the "unattended red" wave. C) The "attended red" minus "unattended red" difference wave distribution. The scale on the left is associated with columns A and B. (Att: attended, Unatt: unattended)

Orientation specific (vertical or horizontal) attention effects on task-irrelevant color processing

To determine if the processing of a task-irrelevant color feature differed depending on the orientation attended, separate difference waves were calculated for each of the attended orientations (e.g. attend horizontal difference wave = attended red horizontal lines *minus* unattended red horizontal lines). For both the "attend vertical" lines condition and the "attend horizontal" lines conditions, a medial occipital negative difference component peaking at about 300 ms was present as in the grand averaged attention effect. (Table 2.5; Figure 2.10).

Time window	Electrodes Clustered	ANOVA of the Attention Effect			Attention Effect	
		Att-Red / Unatt-Gray µV (*SEM*)	vs.	Unatt-Red / Att-Gray µV (*SEM*)	*F* (1,14)	*p* <
Attend vertical lines condition						
272-319 ms	OZ, IZ	-6.03 (1.30)	vs.	-5.32 (1.24)	5.01	0.04
Attend horizontal lines condition						
304-327 ms	OZ, IZ	-5.63 (1.11)	vs.	-4.52 (1.09)	8.04	0.01

Table 2.5. The effect of attention on color processing for the "attend vertical lines" and "attend horizontal lines" conditions separately. Mean voltage amplitude given in µV. (Att: attended, Unatt: unattended, *SEM*: standard error of the mean, vs.: versus)
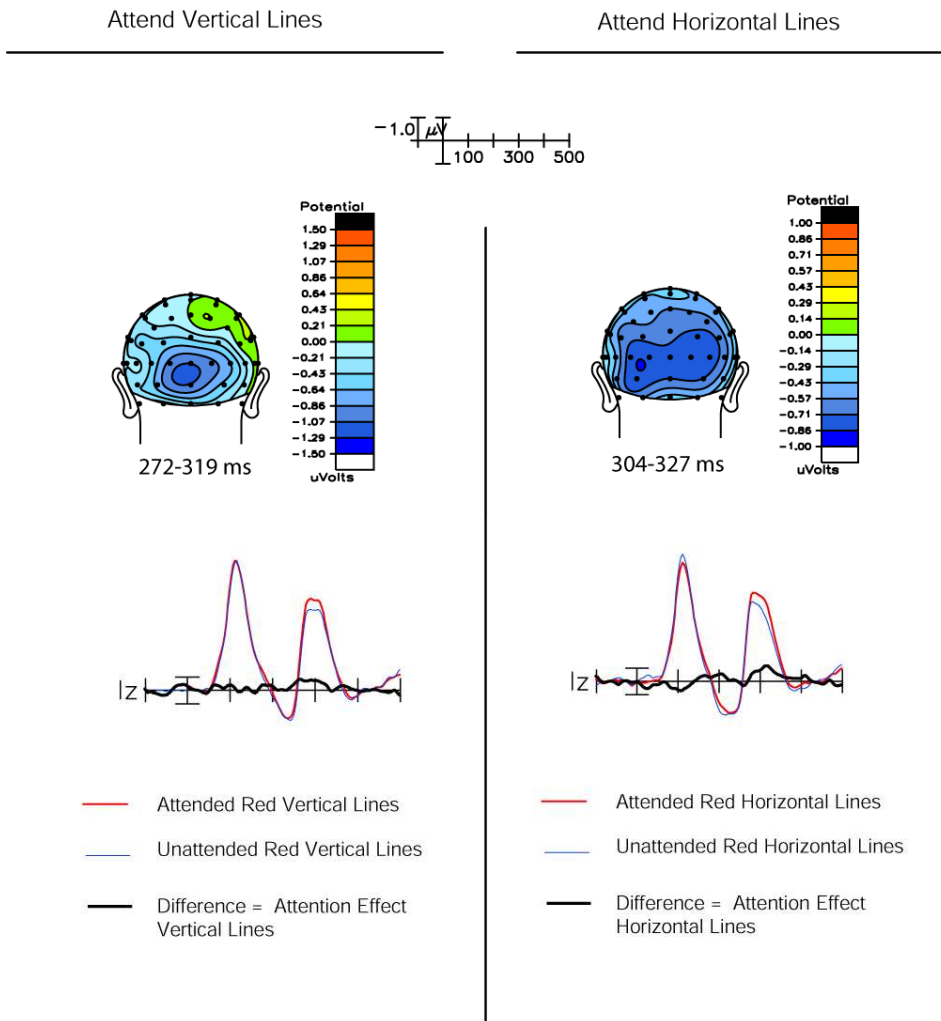
Figure 2.10. Topographical maps and grand-average ERPs (non-target trials) associated with the effect of attention on the task-irrelevant color, shown separately for the "attend vertical" and "attend horizontal" conditions. Negative voltage is plotted upward.

ERPs to target stimuli

Target stimuli elicited a P300 wave indicating that these stimuli were processed in a manner that is consistent with previously reported results gathered from other paradigms in which infrequent, task-related stimuli were presented (Polich, 2007). Both vertical and horizontal targets elicited this widely distributed component that peaked between 500 and 600 ms with a maximum voltage at central-parietal electrode sites (Figure 2.11). The P300s were considerably larger for attended than unattended targets in both trials where a vertical target was present as well as trials where horizontal targets were present (vertical targets, $F(1, 14) = 23.38$, $p < 0.001$; horizontal targets, $F(1, 14) = 48.67$, $p < 0.0001$). There was no significant difference in mean amplitude between the vertical target and horizontal target P300 difference wave components ($F (1, 14) = 2.73$, $p = 0.12$; vertical target difference, $M = 3.21$ μV ($SE = 0.68$); horizontal target difference, M = 2.17 μV (SE = 0.34)).

Attended and Unattended Target Trials
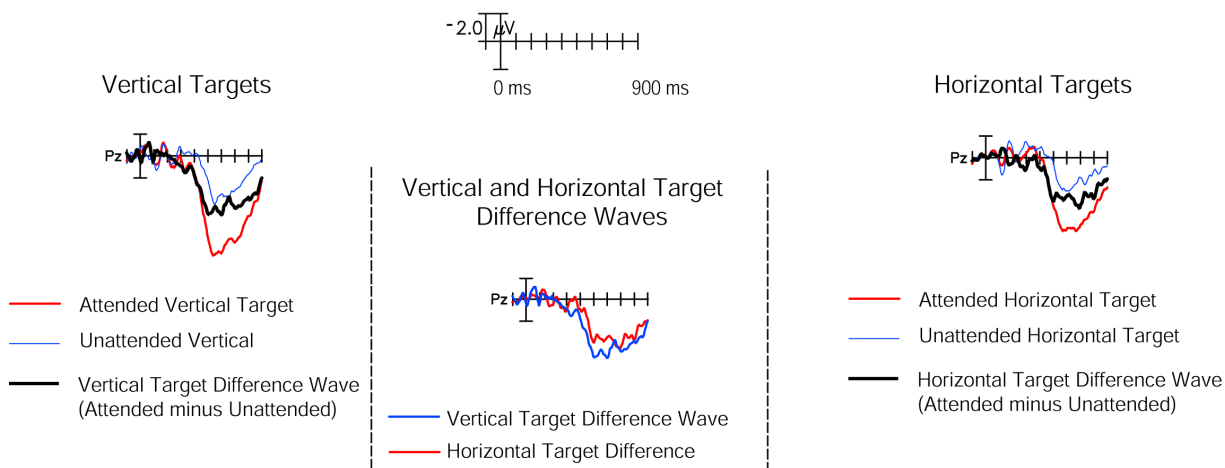
Figure 2.11. Grand-average ERPs for vertical and horizontal target trials. Waveforms for attended and unattended vertical target waveforms and their difference waveform are presented in the left column. Attended and unattended horizontal target waveforms and their difference waveform are presented in the right column. Vertical and horizontal target difference waves are plotted in the center column. Negative voltage is plotted upward.

LAURA Source Analysis

LAURA source analyses were performed on the grand-averaged "sensory effect" waveforms, as well as on the "attention effect". Estimated sources are shown in Figure 2.12 and the current source maxima for each condition are given in Table 2.6. The sensory effect of color included bilateral source estimates in fusiform gyrus. The effect of attention also included estimated sources in the fusiform gyrus. These findings point to common sources in lateral occipital cortex associated with the processing of the sensory and attention effects which can be seen in Figure 2.12C. The spread of the attention effect also included additional lateral sources in extrastriate visual cortex.

ERP component	x (mm)	y (mm)	z (mm)	Brain region
Sensory Dif (96-223 ms)	±18	-87	-13	Fusiform gyrus (BA 18)
Attention Collapse Dif (272-327 ms)	±29	-80	-12	Fusiform gyrus (BA 19)
	±47	-57	-11	Fusiform gyrus (BA 37)

Table 2.6. Talairach coordinates and corresponding brain regions of the current source maxima as modeled by LAURA for the components in the sensory and attention difference waveforms. (Dif: difference wave, BA: Broadmann's area)

A Sensory Effect of Color (96-223 ms)
  Collapsed Across Attend Vertical and Attend Horizontal Line Conditions

y = -87   0.01 µA/mm³

L
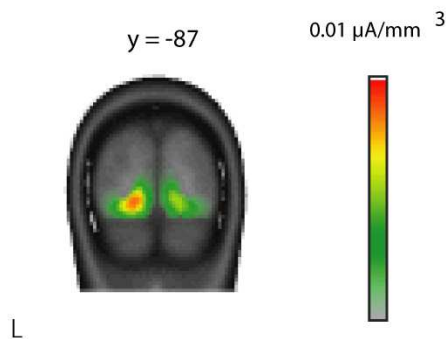
B Effect of Attention on the Task-Irrelevant Color (272 - 327 ms)
   Collapsed Across Attend Vertical and Attend Horizontal Line Conditions

0.001 µA/mm³

y = -80   y = -57

L   L
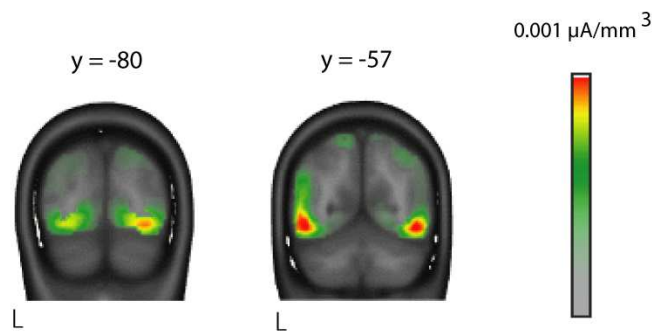
C Comparison of Sensory and Attention Effects
   Collapsed Across Attend Vertical and Attend Horizontal Line Conditions

y = -80

Sensory Effect

Attention Effect

Both Sensory and Attention Effects

L
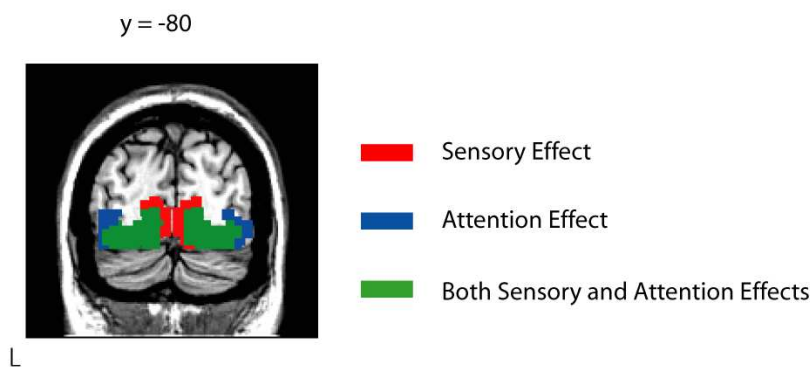
Figure 2.12. Estimated sources for the major components in the (A) sensory effect difference waveform and (B) the effect of attention on the sensory effect difference waveform. (C) A comparison of the sensory and attention effects. Both effects localize to similar areas; however, the attention effect has an additional, more lateral fusiform gyrus source. LAURA inverse solutions are represented in units of current source density. (L: left hemisphere)

DISCUSSION

The present study was designed to investigate whether all of the features of a perceptual grouping or "object" are selected when that object is attended even if those features are not relevant to task performance. In particular, the differential processing of a task-irrelevant color when attending to line orientation was examined using the event-related potential (ERP) method. Two main effects of interest were compared to determine the timing of the binding of orientation and color: 1) the sensory effect of color and 2) the effect of attention to orientation on the processing of the task-irrelevant color. Based on the findings of Schoenfeld and colleagues (2003), it was predicted that an effect of attention on irrelevant color processing would be observed, thus providing evidence for object-based attentional selection. Evidence for the spread of object-based attention to the irrelevant color feature was indeed found in the current study. However, the timing and distribution of the "attention" and "sensory" effects differed markedly from those reported by Schoenfeld et al. (2003) as discussed below.

The effect of attention on task-irrelevant color processing

The effect of attention on task-irrelevant color processing was marked by a negative component that was greater when the red lines were attended versus unattended. This effect was centered over medial occipital electrode sites, became significantly different from the baseline at 280 ms, and source analyses using LAURA indicated that it originated in the posterior fusiform gyrus. This "attention effect" provides evidence that the task-irrelevant

color feature was selected, thereby contributing a novel finding that the spread of attention throughout an object extends to objects defined by orientation.

The estimated sources for the "attention effect" reported above occurred in ventral, posterior occipital areas and are consistent with those estimated for the "sensory effect". This suggests that binding of the task-irrelevant feature results from differential activity in the same areas that process the initial selection of color information. As such, these findings support the integrated-competition hypothesis (Desimone & Duncan, 1985; Duncan, Humphreys, & Ward, 1997), which predicts that selection of an object in a visual scene composed of several objects occurs as a result of enhanced activity in all of the feature modules coding the properties of the selected object, both task-relevant and irrelevant. While the sensory and attention effects both included source estimates within the fusiform gyrus, the source for the attention effect includes a more lateral estimate in the extrastriate cortex. Thus, the binding process itself may be associated with the recruitment of additional lateral occipital color processing areas. The difference in scalp topography between the sensory and the attention effect, indicating that the cortical sources of these components are similar but not entirely identical, also supports this hypothesis.

The behavioral results indicate a difficulty difference in judging horizontal versus vertical lines that is independent of color processing. This difference may have resulted from perceptual differences in attending to lines of different orientations. Previous studies have yielded interesting insights into differential effects of orientation on performance. For example, multiple studies have reported an oblique effect, where details about stimuli are

better resolved if the stimuli are at vertical or horizontal angles than oblique angles (Appelle, 1972; Li, Peterson, Freeman, 2003). The exact neural mechanisms underlying this effect are still a subject of controversial discussion. Another line of investigation has revealed a different orientation related effect, the so called "vertical-horizontal line illusion". This occurs when vertical and horizontal lines are oriented perpendicularly to one another and a judgment of the length of the lines typically results in an overestimation of the extent of the vertical line (Robinson, 1972). Lastly, another related phenomenon reported in previous studies of the influence of orientation is "the crowding effect", in which visual discrimination of a target is more difficult if the target is surrounded by distractors. This difficulty is greater if the flanking distractors are arranged horizontally rather than vertically (Feng, Jiang, & He, 2007).

While none of these reports used exactly the same stimulus or paradigm presented in the current study, they do suggest that orientation effects, and interactions between orientations, may be common phenomena. However, this was not the focus of the current study. Most importantly for the purpose of this study, our results show an object-based attention effect indicating a spread of attention through all of the features of an object defined by orientation. Although there were behavioral differences when attending to horizontal versus vertical lines, this ERP effect of object-based attention was observed for both the "attend horizontal" and "attend vertical" line conditions. Thus, this attention effect extends the Schoenfeld et al. findings to objects defined by vertical and horizontal orientations.

The timing of feature binding

As it was inferred in the Schoenfeld et al. study, it was considered here that the binding of the orientation and color occurred at some point in time between the onset of the processing of color in the visual system (the sensory effects), and the onset of the attention effects. Thus, the time required for the binding of orientation and shape was estimated by subtracting the time for onset of the "sensory effect" from the time of the onset of the "attention effect". In our study, this subtraction provides an average estimate of 180 ms for the binding of orientation and color. As in the Schoenfeld and colleagues study, the effect of attention on the task-irrelevant color did not emerge at the same time as the initial processing of color in the display. However, the current estimate of binding time is much longer than the time given in the Schoenfeld et al. study (approximately 50 ms).

The difference between the two studies may be due to factors such as stimulus/object composition and task design. While Schoenfeld and colleagues used objects defined by dot motion coherence, the objects in the current study were defined by the orientation of perceptually grouped line arrays. In addition, the task in the Schoenfeld et al. study was defined by a change in the velocity of a subset of the moving dots. In the current study, targets were defined by a change in line thickness. These major differences in the object stimuli could have resulted in the difference in the binding time of the task-irrelevant color feature. For example, the need to perceptually group the lines in the current study might have taken longer than the object-grouping based on coherent motion, thereby leading to the increase in the time required for binding the task-irrelevant feature.

Independently of the noted differences between the Schoenfeld et al. study and the current study, in both cases a paradigm to test the potential spread of object-based attention to irrelevant features (color) was used, and in both cases, the spread of attention to a task-irrelevant feature was found. Thus, the current findings not only support but also expand the previous results by adding the novel finding that this phenomenon occurs for at least two different types of objects. It is of paramount importance to test to what extent this binding effect can be generalized, which led us to the experiments described in the next chapter.

CONCLUSIONS

In conclusion, these findings indicate that the attentional selection of competing stimuli in the visual environment can occur in an object-based manner. In particular, the attentional selection of a task-irrelevant color feature can be generalized to at least two types of objects, those defined by motion and those defined by orientation. When attending to the orientation of a grouped line array, the binding of a task-irrelevant color feature takes approximately 180 ms to occur after the sensory registration of color in the display. In comparison with the Schoenfeld et al., 2003 study, this suggests that the exact timing of feature binding of the task-irrelevant feature may vary depending on the nature of the object and the task design. Specifically, perhaps the need to perceptually group the lines in the current study might have taken longer than the object-grouping based on coherent motion, thereby leading to the increase in the time required for binding the task-irrelevant feature. In addition, the cortical region where selection of task-irrelevant features of an object seems to occur is the same region responsible for processing that feature. These findings will be

further explored in the following study in which object-based attention effects on the binding

of geometric shape and color will be examined.

CHAPTER 3: SPREAD OF ATTENTION TO A TASK-IRRELEVANT COLOR FEATURE WHEN ATTENDING TO SHAPE

INTRODUCTION AND RATIONALE

In order to further explore the neural basis for object-based attention, the current study was conducted to examine the hypothesis that attention spreads through all of the features of an object. In particular, this second study was designed to assess if this phenomenon can be generalized to different types of objects. Here, shape was used to define the objects and color served as the task-irrelevant feature. As it was important to test whether the attention effects seen in the previous study (Chapter 2) would generalize to stimuli that included more structure such as edges and corners, we chose stimuli that consisted of overlapping outlines of ovals and rectangles, in which one or the other of the shapes was sometimes colored. This set of stimuli was chosen because shape is a defining feature of most objects, thus providing ecological validity to the analysis. Stimulus presentation was structured in the same way as in the previous study (i.e. subjects were required to attend to one object or another in a blocked manner, and color occurred at random on one or another of the shapes). Because processing of the task-irrelevant color feature did not require a response, selection of the color feature was assessed via recordings of event-related brain potentials (ERPs) to the stimuli. Specifically, difference ERPs were calculated in the same manner as in Chapter 2.

Three experiments were conducted with several variations of the stimulus shapes in order to determine the robustness of the effect. In the first experiment, stimuli were

composed of overlapping oval and rectangle outlines, large and small and in combination. The second experiment, used the same stimuli, but with the presentation of ovals or rectangles in the foreground counterbalanced. A further question was whether the results from the first two experiments were affected by differences in stimulus discrimination difficulty. Accordingly, the third experiment was conducted in order to equalize the difficulty of shape discrimination when attending to rectangles versus ovals.

The main comparisons of interest were the same as in the previous study. A sensory effect of color was determined by comparing ERPs on trials in which color was in the display versus trials in which all of the stimuli were gray. An attention effect on color processing was also assessed in ERP difference waves to determine whether attention to one shape or another would result in differential processing of the colored stimulus. If differential processing of the colored stimulus occurred with the attention manipulation, it would be concluded that object-based attention occurred. This is in fact what was found in the current study.

METHODS

Participants

In all three experiments, participants were right-handed human adults with normal to corrected-to-normal vision and no reported color-blindness or neurological illnesses. Informed consent was obtained from all participants. In experiment one, thirteen healthy participants (7 male) between the ages of 19 and 34 years of age ($M = 26$ years) served as paid volunteers. In experiment two, ten participants (8 male) between the ages of 18 and 34

years of age ($M = 23$ years) participated. In experiment three, eighteen participants (8 male)

between the ages of 18 and 35 years of age ($M = 24$ years) were included.

Stimuli and Task

Overlapping outlines of rectangles and ovals (Figure 3.1, 3.2, 3.3) (4 x 4 ° total size)

were centrally presented (for 161 ms durations) on a CRT monitor at an 80 cm viewing

distance in a darkened, sound-attenuated and electrically shielded room. A central fixation

cross was present throughout each block of stimulus presentations, in which the different

overlapping shape stimuli were presented in randomized order. Inter-stimulus intervals were

randomly jittered (between 400 and 600 ms for Experiments 1 and 2 and between 600 and

800 ms during Experiment 3). Due to the increased difficulty in discriminating the stimuli,

the inter-stimulus interval for the third experiment was changed to decrease the pace of the

task.

The stimuli were designed such that subjects would have to attend to the overall

shape of the objects and could not distinguish a target on the basis of local features such as

intersections between the shapes or the sizes of the shapes.   Target stimuli consisted of a

circle (when ovals were attended) and squares (when rectangles were attended).Circle and

square targets were never presented together in the same stimulus. During experiment one,

ovals and circles were presented in the foreground. During one third of the trials, rectangle

stimuli were red, one-third of trials contained red oval stimuli, and another third included

stimuli in which both shapes were gray. The RGB values of the red stimuli were the same as

in the experiment reported in Chapter 2 (R = 226, G = 15, B = 15). Subjective brightness of

the red and gray stimuli was equated by minimizing heterochromatic flicker in tests carried

out on individual subjects (Anllo-Vento, Luck, & Hillyard, 1998; Schoenfeld et al., 2003).

This resulted in a light gray color that was subjectively isoluminant to the red color. All

stimuli were presented on a dark gray background.
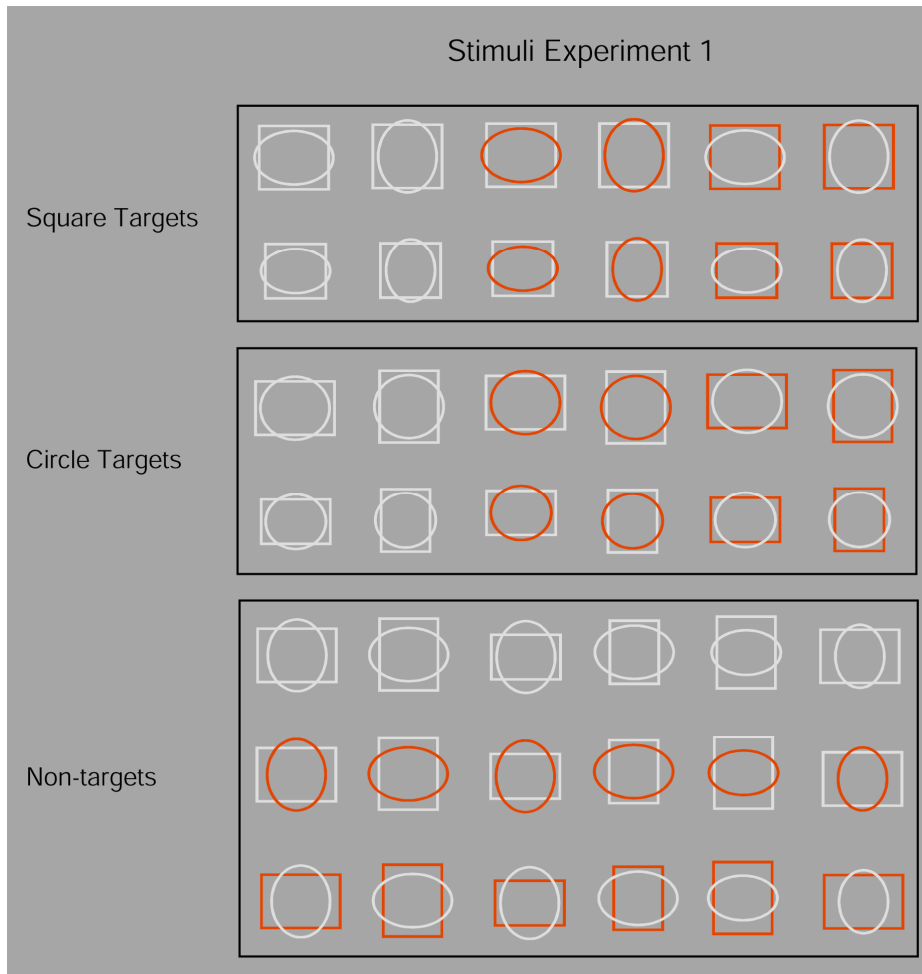
Figure 3.1. All stimulus exemplars presented during Experiment 1. Ovals and circles were presented in the foreground.
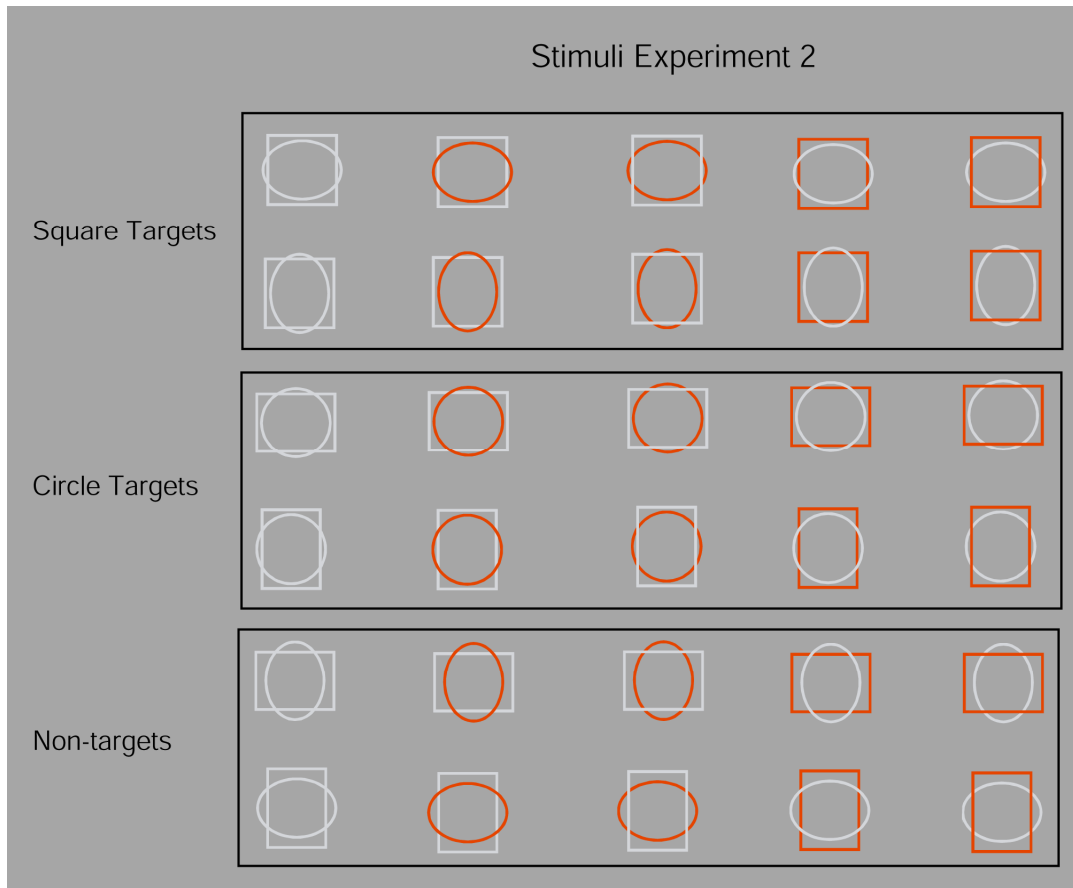
Figure 3.2. Stimuli presented during Experiment 2. These stimuli are a subset of the stimuli presented in Experiment 1 (only the larger squares and rectangles, circles and ovals). The presentation of ovals and rectangles on the foreground or background was counterbalanced.
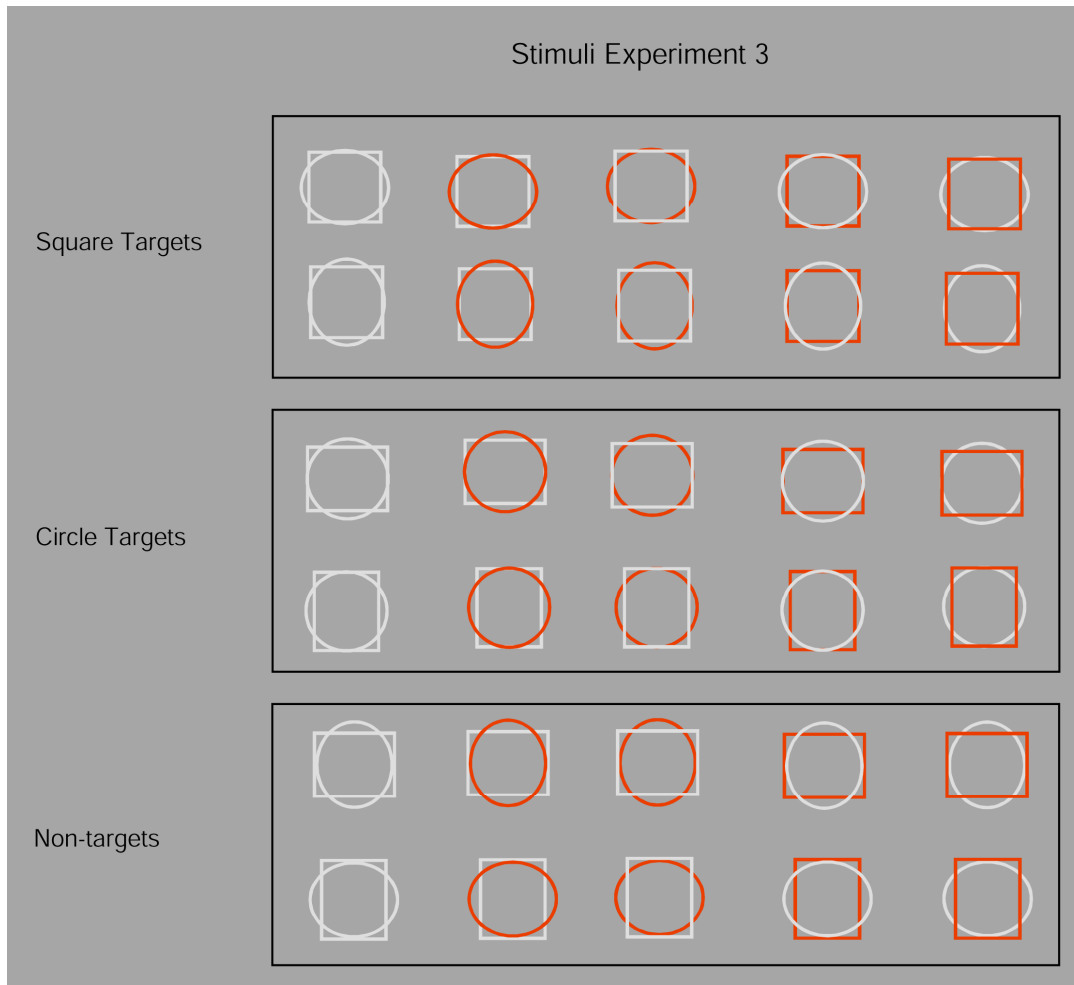
Figure 3.3. Stimuli presented during Experiment 3. As in Experiment 2, foreground and background presentation was counterbalanced but the dimensions of the rectangles and circles were adjusted to balance difficulty of shape discrimination between the two "attention to shape" conditions. This resulted in an overall task difficulty increase, for both conditions.

Prior to task instructions for experiment three, participants completed a short (approximately 5 minute long) "passive viewing" session in which only non-target stimuli were shown. Each of the stimuli was shown an equal number of times in random order, with the same stimulus timing parameters as in the main experiment. The effect of color on the ERPs during "passive viewing" was intended to serve as a comparative control for the "sensory effect" found during attention manipulation tasks.

At the beginning of each block of stimuli, participants were instructed to attend to either ovals or rectangles while ignoring the other shape. They were to respond with a button press when the attended shape (oval or rectangle) was a target (circle or square). They were explicitly told that the color of the stimuli did not matter and to attend to the entire outline of the attended shape in order to detect the designated target shape. Response accuracy and speed were emphasized equally. The different stimulus combinations shown in Figures 3.1, 3.2, & 3.3 were presented in random order with approximately 20% of trials containing a target. Circle and square targets appeared with equal probability, but a response was only required to targets of the attended shape (10% of the trials). The percentage of the time each stimulus combination was presented is shown in Table 3.1.

		Non-targets	Oval Target (circle)	Rectangle Target (square)
Red Ovals Gray Rectangles	Exp.1	26.67%	3.33%	3.33%
	Exp.2	26.67%	3.33%	3.33%
	Exp.3	26.67%	3.33%	3.33%
Red Rectangles Gray Ovals	Exp.1	26.67%	3.33%	3.33%
	Exp.2	26.67%	3.33%	3.33%
	Exp.3	26.67%	3.33%	3.33%
Gray Ovals Gray Rectangles	Exp.1	26.67%	3.33%	3.33%
	Exp.2	26.67%	3.33%	3.33%
	Exp.3	26.67%	3.33%	3.33%

Table 3.1. The frequency with which each stimulus combination was presented is given in percentages.

An initial practice session was given to familiarize participants with the task and to minimize their production of movement related artifacts. This was followed by the experimental session. A response occurring 150-1000 ms after target presentation was scored as correct. Responses following non-target stimuli were scored as false alarms. Each subject was

presented with a total of twenty blocks (10 attend oval/circle, 10 attend rectangle/square)

resulting in 2,280 trials in Experiment 1 and 2,400 trials in Experiments 2 and 3. (The trial

number difference is due to the difference in exemplar numbers between stimulus sets.) The

presentation of blocks with different attention conditions was randomized. The length of the

break between blocks was controlled by the participant with the exception of a mandatory

break given after ten blocks.

Electrophysiological recording and data analysis

The electroencephalogram (EEG) recording and data preparation procedures were

identical to the ones used in the attention to orientation study. For all analyses, ERPs to non-

target stimuli were pooled to create grand-average waveforms. The six experimental

conditions that were analyzed are illustrated in Figure 3.4. These six experimental

conditions were combined into: i) "attend red", ii) "unattended red", and iii) "both gray",

collapsing over conditions of attention to ovals and rectangles. ERPs recorded under the

various conditions were combined and subtracted to create specific comparisons of interest

(Figure 3.5).
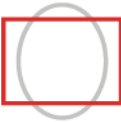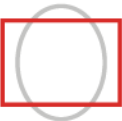
Blocks	Stimulus Configurations		
	Attended Red	Unattended Red	Both Gray
Attend Ovals/ Circles			
Attend Rectangles/ Squares			

Figure 3.4. The six experimental conditions defined by the combination of the stimulus configuration (non-targets only) and the shape attended.

To assess the "sensory effect" of the presence of color, difference waves were calculated by subtracting ERPs elicited by stimuli in which both shapes were gray from ERPs elicited when the unattended shape was colored red (Figure 3.5A).

To assess the "shape effect" (Figure 3.5B), a difference wave was computed by subtracting the ERP response when rectangles were attended from the response when ovals were attended when all of the stimuli were gray.

To examine the main effect of interest, "the effect of attention on task-irrelevant color processing", a difference wave was created by subtracting ERPs to "unattended red" stimuli from "attend red" stimuli (Figure 3.5C). Importantly, this comparison was calculated using

exactly the same stimuli under different attention conditions. As such, any differences

between the two conditions could only be related to the effects of attention and not to

physical stimulus differences. Because the analysis was aimed at investigating whether the

task-irrelevant color feature was selected in general, regardless of whether the attended shape

is an oval or rectangle, ERPs were averaged over the attention to shape variable in this

analysis. The resulting difference wave reflected selection of the task irrelevant color feature

independently of whether there was any shape-specific effect.

Experimental Comparisons
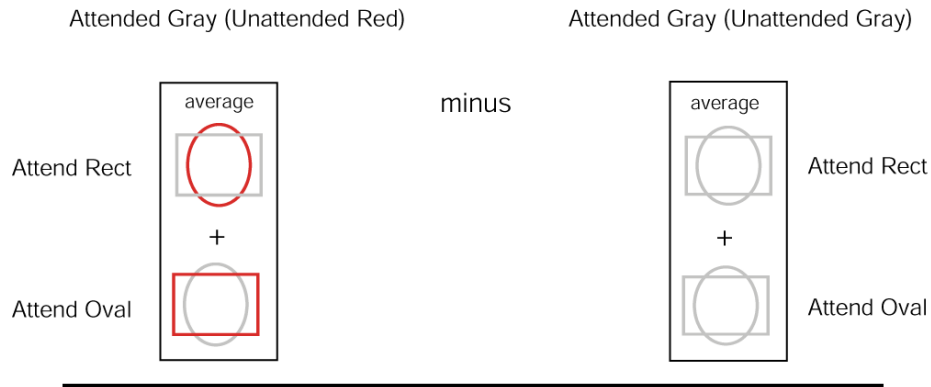
A   Sensory Effect of Color: Difference Wave

Attended Gray (Unattended Red)   Attended Gray (Unattended Gray)

minus

Attend Rect   Attend Rect

\+   \+

Attend Oval   Attend Oval

B   Attention to Shape Effect: Difference Wave

Attended Oval   Attended Rectangle

minus

C   Effect of Attention on Task-Irrelevant Color: Difference Wave

Attended Red (Unattended Gray)   Attended Gray (Unattended Red)

minus

Attend Rect   Attend Oval

\+   \+

Attend Oval   Attend Rect
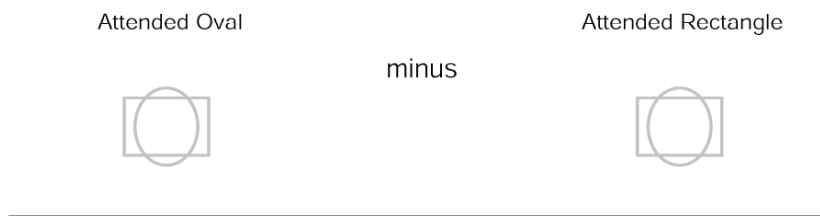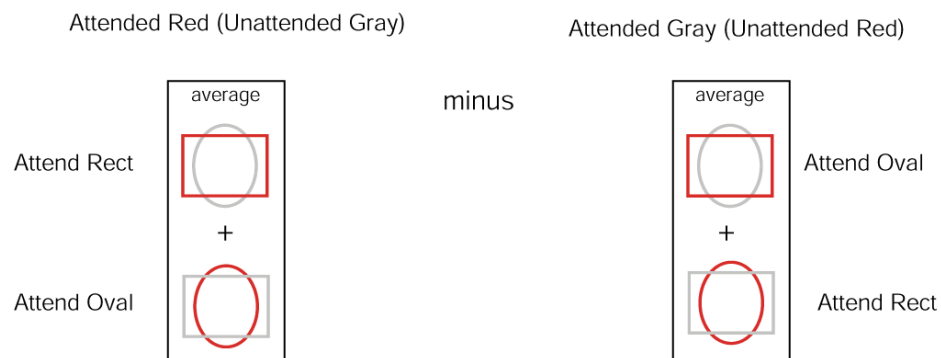
Figure 3.5. Graphical depiction of the stimuli for the ERP difference waves calculated for all three experiments. The stimuli shown are exemplars of stimuli from that category selected for illustrative purposes.

For all analyses, difference wave components were quantified as mean amplitudes within specific latency windows around the peak of each identified component. These effects were baseline corrected prior to analysis using the mean voltage of a 100 ms pre-stimulus baseline. Each effect was measured as the mean voltage over a specific cluster of electrodes at which the component amplitude was maximal. The time window and specific clusters used are listed in the tables given for each experimental ERP effect. All analyses were performed using repeated measures ANOVA and Tukey HSD post-hoc testing unless otherwise indicated. Differences in scalp distributions across experiments were calculated for the sensory and attention effects after normalizing their amplitudes, prior to ANOVA, according to the method described by McCarthy and Wood (1985). Topographical comparisons were made over 38 electrodes spanning frontal, central, parietal and occipital sites. Differences in scalp distribution were reflected in significant "condition by electrode" interactions. The Greenhouse-Geisser correction was applied to analyses that had more than two degrees of freedom (i.e., electrode site).

Modeling of ERP sources

As in the attention to orientation study (Chapter 2), to estimate the cortical generators of the sensory and attention effects, source localization analyses were performed on the grand-averaged difference waves within the same intervals used for statistical testing. Current density distributions were estimated using a local autoregressive average (LAURA) algorithm (Grave de Peralta Menendez, Gonzalez Andino, Lantz, Michel, & Landis, 2001). LAURA analyses were implemented using the Cartool software (http://brainmapping.unige.ch/Cartool.php). The Talairach coordinates of the current source

maxima given by the LAURA algorithm were entered into the Talairach Client (Lancaster, et al., 2000) to determine the brain region of the estimated maximal sources. Maps illustrating both the sensory and attention effects and their overlap were created using the AFNI software (Cox, 1996) and were projected onto a structural brain image supplied by MRIcro (Rorden & Brett, 2000).

RESULTS

Behavioral Results

A 2 x 3 ANOVA was calculated with the factors of attended shape (oval or rectangle) and stimulus configuration ("attended red", "unattended red", and "both gray").

Experiment 1: Full Stimulus Set

The mean values for all conditions and dependent measures are given in Table 3.2. Participants were more accurate when discriminating changes in the shape of the ovals than the rectangles ($M = 84.55\%$ ovals, $M = 64.94\%$ rectangles) ($F(1, 12) = 25.06$, $p < 0.001$). Also, participants were faster when detecting oval targets (circles) than rectangle targets (squares) ($M = 580.23$ ovals, $M = 612.73$ rectangles) ($F(1, 12)=6.26$, $p < 0.05$).

The configuration of the stimuli (red attended, red unattended, both gray) did not have significant effects on accuracy or response time (accuracy, $F(2, 24) = 2.14$, $p = 0.14$; response time, $F(2, 24) = 0.60$, $p = 0.55$); however, significance was reached for the false alarm data ($F(2, 24) = 3.75$, $p < 0.05$), but post-hoc analysis of the configuration of the stimuli did not reach significance (red attended vs. red unattended, $p = 0.38$; red attended vs. grays, $p = 0.17$; red unattended vs. grays, $p = 0.86$).   The interaction between attended shape and configuration of the stimuli was not significant for any of the dependent measures

(accuracy, $F(2, 24) = 3.07$, $p = 0.07$; response time, $F(2, 24) = 1.55$, $p = 0.23$; false alarm

rate, $F(2, 24) = 0.71$, $p = 0.50$).

Attention condition	Stimulus Configuration	Hit rate (%)	*SEM* hit rate (%)	FA Rate (%)	*SEM* FA Rate (%)	Mean RT (ms)	*SEM* RT (ms)
Attend Ovals	Att Red/Unatt Gray	82.69	3.62	7.79	3.17	583.11	23.52
	Att Gray/Unatt Red	86.92	2.76	5.79	3.14	575.58	23.12
	Att Gray/Unatt Gray	84.04	3.06	5.68	3.05	582.01	21.68
Attend Rectangles	Att Red/Unatt Gray	58.27	6.93	5.70	1.51	601.75	17.89
	Att Gray/Unatt Red	65.96	3.99	4.75	0.89	616.09	17.68
	Att Gray/Unatt Gray	70.58	3.35	3.73	0.79	620.35	21.25

Table 3.2. Mean behavioral performance for the detection of targets of the attended shape
for Experiment 1. (*SEM*: standard error of the mean, FA: false alarm, RT: response time,
Att: attended, Unatt: unattended)

Experiment 2: Foreground/Background Counterbalanced

Mean values for all conditions and dependent measures are given in Table 3.3.

While, there was no significant difference between discriminating oval targets (circles)

versus rectangle targets (squares), there was a trend for more accurate performance when

discriminating ovals ($M = 83.75\%$ ovals, $M = 72.58\%$ rectangles) ($F(1, 9) = 4.61$, $p = 0.06$).

Participants were again faster when detecting oval targets than rectangle targets ($M = 568.94$

ovals, $M = 604.29$ rectangles) ($F(1, 9) = 12.00$, $p < 0.01$). There was no significant

difference in false alarm rate when attending ovals versus rectangles ($F(1, 9) = 3.12$, $p =

0.11$). The configuration of the stimuli (attended red, unattended red, grays) did not have

significant effects on accuracy, false alarm rate, or response time (accuracy, $F(2, 18) = 0.16$,

$p = 0.85$; false alarm rate, $F(2, 18) = 2.01$, $p = 0.16$; response time, $F(2, 18) = 1.11$, $p = 0.35$).

The interaction between attended shape and configuration of the stimuli was not significant

for any of the dependent measures (accuracy, $F(2, 18) = 0.20$, $p = 0.82$; false alarm rate, $F(2, 18) = 2.91$, $p = 0.08$; response time, $F(2, 18) = 0.21$, $p = 0.81$).

Attention condition	Stimulus Configuration	Hit rate (%)	*SEM* hit rate (%)	FA Rate (%)	*SEM* FA Rate (%)	Mean RT (ms)	*SEM* RT (ms)
Attend Ovals	Att Red/Unatt Gray	83.25	4.66	5.82	2.55	567.62	19.40
	Att Gray/Unatt Red	83.00	5.25	5.78	2.24	573.45	20.03
	Att Gray/Unatt Gray	85.00	4.08	3.74	1.95	565.77	21.84
Attend Rectangles	Att Red/Unatt Gray	74.00	2.39	1.50	0.55	607.88	19.42
	Att Gray/Unatt Red	71.75	5.73	1.92	0.57	608.65	13.13
	Att Gray/Unatt Gray	72.00	4.42	2.11	0.58	596.35	19.18

Table 3.3. Mean behavioral performance for the detection of targets of the attended shape for Experiment 2. (*SEM*: standard error of the mean, FA: false alarm, RT: response time, Att: attended, Unatt: unattended)

Experiment 3: Equating Shape Difficulty

Mean values for all conditions and dependent measures are given in Table 3.4. There was no significant difference between discriminating oval targets versus rectangle targets, ($M = 65.30\%$ ovals, $M = 64.61\%$ rectangles) ($F(1, 17) = 0.03$, $p = 0.86$). Performance on the task overall was lower than during previous versions of the experiment. Participants were again faster when detecting oval targets than rectangle targets ($M = 569.14$ ovals, $M = 580.88$ rectangles) ($F(1, 17) = 5.73$, $p < 0.05$), suggesting a speed/accuracy tradeoff when discriminating oval targets versus rectangle targets. More false alarm errors were committed during the attention to ovals condition than the attention to rectangles condition ($M = 10.28\%$ ovals, $M = 2.42\%$ rectangles) ($F(1, 17) = 21.49$, $p < 0.001$). The configuration of the stimuli (attended red, unattended red, both gray) did not have significant effects on accuracy, ($F(2,

34) = 1.33, $p = 0.28$) but did for response time ($F(2, 34)=10.28$, $p < 0.001$). Posthoc comparisons showed a significant difference between the attended red and both gray configurations ($p = 0.01$) in which participants were fastest when all of the stimuli were gray. There was also a significant difference in false alarm rate based on the configuration of the stimuli ($F(2, 34) = 4.82$, $p < 0.05$) ($M = 8.57\%$ attended red, $M = 5.41\%$ unattended red, $M = 5.07\%$ both gray) as well as an attention to shape x configuration interaction ($F(2, 34) = 5.78$, $p < 0.01$). This interaction was tested in two separate ANOVAs (attend to ovals and attend to rectangles). The effect of configuration was significant within the attend to ovals condition ($F(2, 34) = 5.19$, $p < 0.01$) with posthoc testing indicating a significant difference between the attended red and both gray conditions ($p < 0.01$). The configuration effect was also significant within the attend to rectangles condition ($F(2, 34) = 10.07$, $p < 0.001$) with significant differences between attended red and unattended red ($p < 0.05$) and unattended red and both gray ($p < 0.001$) comparisons. The interaction between attended shape and configuration of the stimuli was not significant for accuracy or response time (accuracy, $F(2, 34) = 2.02$, $p = 0.15$; response time, $F(2, 34) = 0.27$, $p = 0.77$).

Attention condition	Stimulus Configuration	Hit rate (%)	*SEM* hit rate (%)	FA Rate (%)	*SEM* FA Rate (%)	Mean RT (ms)	*SEM* RT (ms)
Attend Ovals	Att Red/Unatt Gray	64.31	5.42	14.65	3.35	580.45	10.25
	Att Gray/Unatt Red	64.86	4.93	9.26	1.85	571.31	8.63
	Att Gray/Unatt Gray	66.81	4.37	6.92	1.05	555.66	6.36
Attend Rectangles	Att Red/Unatt Gray	66.94	5.46	2.48	0.89	589.32	9.39
	Att Gray/Unatt Red	58.47	4.17	1.55	0.73	587.22	9.73
	Att Gray/Unatt Gray	68.47	4.58	3.22	0.01	566.11	9.20

Table 3.4. Mean behavioral performance for the detection of targets of the attended shape for Experiment 3. (SEM: standard error of the mean, FA: false alarm, RT: response time, Att: attended, Unatt: unattended)

ERP Results

In all three experiments, the sensory-evoked ERP waveforms elicited by the shape stimuli were consistent with typically observed waveforms in other visual experiments (Hopfinger, Luck, & Hillyard, 2004). In particular, the first prominent component, a laterally distributed occipito-parietal positivity (P1) from 60–140 ms, peaked at about 100 ms. The stimuli in this experiment did not elicit the earlier midline C1 component. The P1 component was followed by an occipito-parietal negativity (N1), from 140–190 ms, that peaked at about 160 ms, a subsequent positivity (P2) from 180–300 ms, that peaked at 230 ms, and a negativity (N2) from 300–360 ms that peaked at 325 ms.

Sensory effect of color

<u>Passive viewing condition</u>

In order to assess sensory effects of color in the absence of a task-specific attention requirement, as done in the attention to line orientation study, participants in Experiment 3 were run in a five minute passive viewing session prior to the active attention conditions. Non-target stimuli were presented with the same timing parameters as in the experimental session. A sensory effect was observed as a greater negativity between 80 -127 ms at focal, posterior midline occipital sites when the color red occurred in the display as compared to displays in which both shapes were gray (Table 3.5; Figures 3.6, 3.7). This negativity was accompanied by a broad frontal/central positivity during the same time frame (96 – 127 ms). This effect continued and extended laterally from 160 to 219 ms. The sensory effect during this passive condition became significantly different from the baseline between 90-99 ms (p < .01).

<u>Experiment 1: Full Stimulus Set</u>

The sensory effect of color was measured by subtracting the grand-averaged ERPs elicited by stimuli in which both shapes were gray from unattended-red stimuli (see Figure 3.5A for a visual depiction). As in the Schoenfeld and colleagues (2003) study, this comparison was collapsed over the "attend oval" and "attend rectangle" conditions. This sensory effect was observed as a greater negativity between 80-127 ms at focal, posterior midline occipital sites, the "early sensory effect"(Table 3.6; Figures 3.8, 3.9), and it became significantly different from the baseline at 90-99 ms post-stimulus onset ($t(12) = 3.01$, p < 0.05). This negativity was accompanied by a broad frontal/central positivity during the same

time frame (80–127 ms). These early effects were followed by a negative component between 160–219 ms, the "late sensory effect". This medial occipital negativity extended more laterally than the earlier sensory component. When the sensory effect was compared between the attend oval and attend rectangle conditions, there was a significant difference in mean amplitude for the early sensory effect at occipital electrodes (80-127 ms/occipital, $p =$ 0.02); however, there was no significant difference for the other sensory effects (80-127 ms/ central, $p = 0.11$; 160-219 ms/occipital, $p = 0.08$). The sensory effect during this experiment is similar to the sensory effect during the passive viewing session demonstrating that the comparison of "unattended red" stimuli versus "all gray" stimuli is a valid measure of the sensory effect for the presence of color in the display.

Experiment 2: Foreground/Background Counterbalanced

The sensory effect was again observed as a greater negativity at midline posterior occipital sites. However in this experiment the onset was later (96-127 ms) when the color red occurred on the unattended surface as compared to displays in which both shapes were gray (Table 3.6; Figures 3.10, 3.11). This early sensory color effect became significantly different from baseline at 100-109 ms post-stimulus onset ($t(9) = –2.67$, $p < 0.05$). This negativity was again accompanied by a broad frontal/central positivity during the same time frame (96–127 ms) followed the late sensory effect that extended more laterally during the subsequent 160–219 ms. There were no significant differences in mean amplitude when attending to ovals versus rectangles for any of the sensory effects (96-127 ms/occipital, $p =$ 0.39; 96-127 ms/ central, $p = 0.30$; 160-219 ms/occipital, $p = 0.93$).

Experiment 3: Equating Shape Difficulty

      The early sensory effect was measured from 80-127 ms and became significantly different from the baseline at 80–89 ms post-stimulus onset ($t(17) = -4.63$, $p = 0.001$) (Table 3.6; Figures 3.12, 3.13). This focal occipital negativity was again accompanied by a broad frontal/central positivity during the same time frame (96–127 ms) and was followed by a the late sensory effect, a more broadly distributed occipital negativity during the subsequent 160–219 ms. There were no significant differences in mean amplitude when attending to ovals versus rectangles for any of the sensory effects (80-127 ms/occipital, $p = 0.28$; 80-127 ms/ central, $p = 0.69$; 160-219 ms/occipital, $p = 0.57$).

      The early sensory effect difference ERP component (80-127 ms) observed during the passive viewing session was not significantly different from the sensory effect observed during the active attention session at either the occipital electrode sites (passive viewing session: $M = -0.97$ µV($SE = 0.19$); active attention session: $M = -1.01$ µV ($SE = 0.15$), ($F(1, 17) = 0.05$, $p = 0.83$) or the central electrode sites (passive viewing session: $M = 0.53$ µV($SE = 0.21$); active attention session: $M = 0.57$ µV ($SE = 0.16$), ($F(1, 17) = 0.03$, $p = 0.87$). There was also no significant difference between the sessions for the late sensory effect (160-219 ms) at either the occipital electrode sites (passive viewing session: $M = -1.13$ µV($SE = 0.18$); active attention session: $M = -1.40$ µV ($SE = 0.21$), ($F(1, 17) = 0.97$, $p = 0.34$) or the central electrode sites (passive viewing session: $M = -0.60$ µV($SE = 0.30$); active attention session: $M = 0.01$ µV ($SE = 0.19$), ($F(1, 17) = 3.09$, $p = 0.10$). Both the early and late sensory effects were similar between the passive viewing session and the active attention sessions suggesting

that the comparison of "unattended red" stimuli versus "gray" stimuli is a valid measure of

the presence of color in the display.

Time window	Electrodes Clustered	ANOVA of the Passive Sensory Effect			Passive Sensory Effect	
		Red Present µV (*SEM*)	vs.	Both Gray µV (*SEM*)	F (1,17)	$p <$
80-127 ms	OZ,IZ	-0.70(0.43)	vs.	0.27(0.43)	25.99	0.0001
80-127 ms	AFZ,FZ, FCZ,CZ,CPZ	-1.20(0.40)	vs.	-1.73(0.42)	6.63	0.05
160-219 ms	OZ,IZ,POZ, PZ	0.99(0.71)	vs.	2.03(0.72)	26.24	0.0001

Table 3.5. The sensory effect of color during the passive viewing session. Mean voltage amplitude given in µV. (*SEM*: standard error of the mean, vs.: versus)

Time window	Electrodes Clustered	ANOVA of the Sensory Effect			Sensory Effect	
		Unatt-Red / Att-Gray μV (*SEM*)	vs.	Att-Gray / Unatt-Gray μV (*SEM*)	*F*	*p*
Experiment 1					*F* (1,12)	*p* <
80-127 ms	OZ,IZ	-0.09(0.51)	vs.	0.62(0.36)	11.24	0.01
80-127 ms	AFZ,FZ,FCZ,CZ, CPZ	-1.40(0.37)	vs.	-2.09(0.28)	8.65	0.05
160-219 ms	OZ,IZ,POZ,PZ	-0.23(0.48)	vs.	1.35(0.57)	33.11	0.0001
Experiment 2					*F* (1,9)	*p* <
96-127 ms	OZ,IZ	1.92(0.83)	vs.	2.68(0.90)	5.41	0.05
96-127 ms	AFZ,FZ,FCZ,CZ, CPZ	-1.61(0.40)	vs.	(0.38)	7.98	0.05
160-219 ms	OZ,IZ,POZ,PZ	-0.41(0.79)	vs.	0.59(0.76)	18.00	0.01
Experiment 3					*F* (1,17)	*p* <
80-127 ms	OZ,IZ	0.32(0.54)	vs.	1.32(0.50)	45.38	0.0001
80-127 ms	AFZ,FZ,FCZ,CZ, CPZ	-1.95(0.38)	vs.	-2.52(0.39)	13.34	0.01
160-219 ms	OZ,IZ,POZ,PZ	-0.58(0.59)	vs.	0.55(0.61)	29.50	0.0001

Table 3.6. The sensory effect of color. Mean voltage amplitude given in μV. (Att: attended, Unatt: unattended, *SEM*: standard error of the mean, vs.: versus)
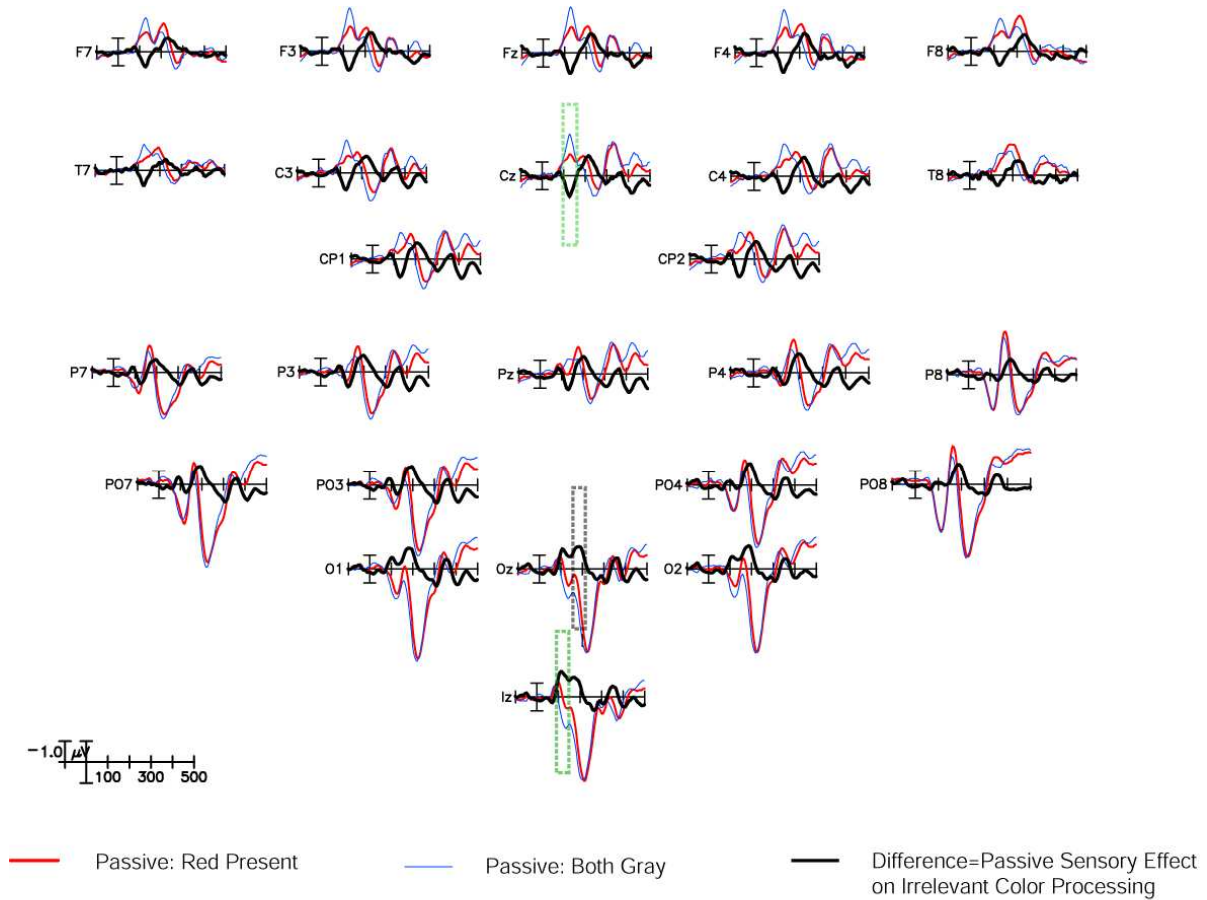
Figure 3.6. Grand-average ERPs (non-target trials) associated with the sensory effect of color during the passive viewing session. Both the ERPs elicited when red occurred in the display, when both shapes were gray, and the red minus gray difference wave indexing the sensory effect are shown. Negative voltage is plotted upward. Dotted line boxes indicate the time windows used for statistical testing.
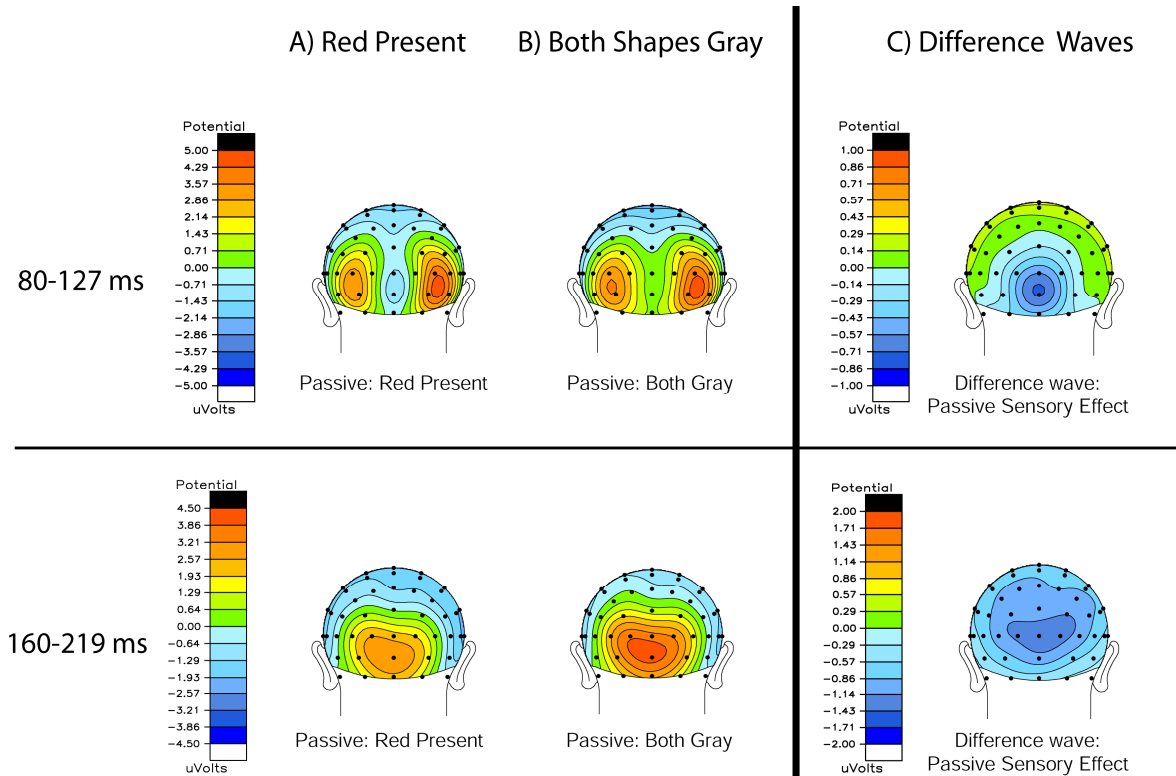
Figure 3.7. Topographical maps of ERP amplitudes indexing the sensory effect of color during the passive viewing session. A) The distribution for trials in which red occurred in the display. B) The distribution for trials in which both shapes were gray. C) The red minus gray difference wave distribution. The scale on the left is associated with columns A and B.
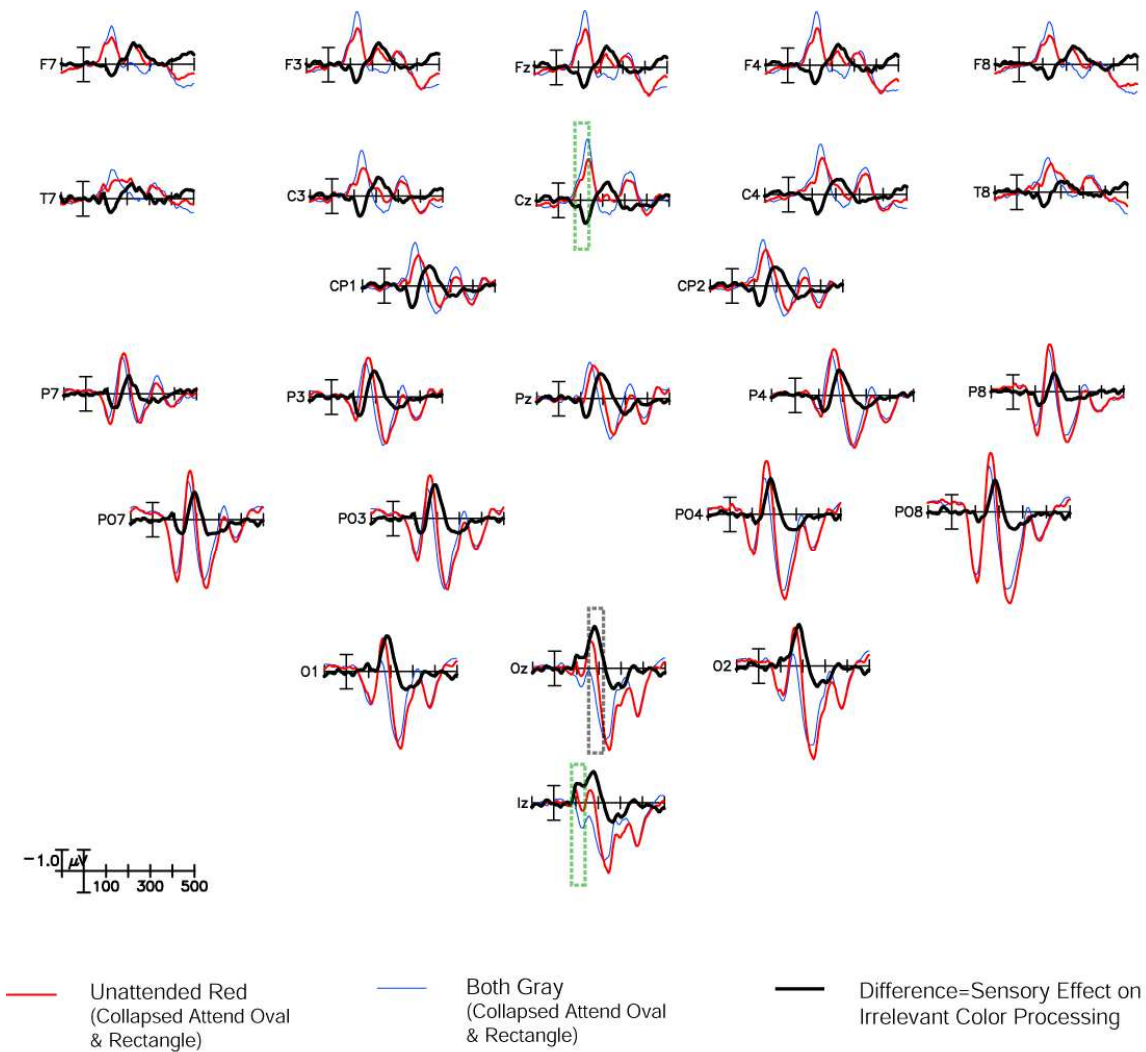
Figure 3.8. Grand-average ERPs (non-target trials) associated with the sensory effect during Experiment 1, collapsed over attend oval and attend rectangle conditions. Both the ERPs elicited when red occurred on the unattended shape, when both shapes were gray, and the red minus gray difference wave indexing the sensory effect are shown. Negative voltage is plotted upward. Dotted line boxes indicate the time windows used for statistical testing.

Figure 3.9. Topographical maps of ERP amplitudes indexing the sensory effect during Experiment 1, collapsed over attend oval and attend rectangle conditions. A) The distribution for trials in which the unattended shape was red. B) The distribution for trials when both shapes were gray. C) The red minus gray difference wave distribution. The scale on the left is associated with columns A and B. (Att: attended, Unatt: unattended)

Figure 3.10. Grand-average ERPs (non-target trials) associated with the sensory effect during Experiment 2, collapsed over attend oval and attend rectangle conditions. Both the ERPs elicited when red occurred on the unattended shape, when both shapes were gray, and the red minus gray difference wave indexing the sensory effect are shown. Negative voltage is plotted upward. Dotted line boxes indicate the time windows used for statistical testing.

Figure 3.11. Topographical maps of ERP amplitudes indexing the sensory effect during Experiment 2, collapsed over attend oval and attend rectangle conditions. A) The distribution for trials in which the unattended shape was red. B) The distribution for trials when both shapes were gray. C) The red minus gray difference wave distribution. The scale on the left is associated with columns A and B. (Att: attended, Unatt: unattended)

Figure 3.12. Grand-average ERPs (non-target trials) associated with the sensory effect during Experiment 3, collapsed over attend oval and attend rectangle conditions. Both the ERPs elicited when red occurred on the unattended shape, when both shapes were gray, and the red minus gray difference wave indexing the sensory effect are shown. Negative voltage is plotted upward. Dotted line boxes indicate the time windows used for statistical testing.

Figure 3.13. Topographical maps of ERP amplitudes indexing the sensory effect of color during Experiment 3, collapsed over attend oval and attend rectangle conditions. A) The distribution for trials in which the unattended shape was red. B) The distribution for trials when both shapes were gray. C) The red minus gray difference wave distribution. The scale on the left is associated with columns A and B. (Att: attended, Unatt: unattended)

Attention to Shape Effect

Experiment 1: Full Stimulus Set

In order to determine if there were specific effects associated purely with attention to one geometrical shape or another, in the absence of color in the display, a shape effect difference wave was computed. Trials in which rectangles were attended were subtracted from trials in which ovals were attended; both stimuli being gray (see Figure 3.5B for an illustration). A shape difference component was observed consisting of a large, midline, fronto-centro-parietal negativity between 256–367 ms in which attention to ovals resulted in a greater ERP negativity than attention to rectangles (Table 3.7; Figures 3.14, 3.15).

Experiment 2: Foreground/Background Counterbalanced

The "attention to shape difference" observed in the second experiment also contained a large, midline, fronto-centro-parietal negativity but with a later onset than in the previous experiment (Table 3.7; Figures 3.16, 3.17).

Experiment 3: Equating Shape Difficulty

In the third experiment, the attention to shape difference component was also observed within the same time frame as Experiment 1. (Table 3.7; Figures 3.18, 3.19).

		ANOVA of the Shape Effect			Shape Effect	
Time window	Electrodes Clustered	Att Oval (All Gray) µV (*SEM*)	vs.	Att Rectangle (All Gray) µV (*SEM*)	*F*	*P*
Experiment 1					*F* (1,12)	*p* <
256-367 ms	AFZ,FZ,FCZ, CZ,CPZ,PZ, POZ	-0.75 (0.72)	vs.	0.09 (0.55)	7.08	0.05
Experiment 2					*F*(1,9)	*p* <
296-367 ms	AFZ,FZ,FCZ, CZ,CPZ,PZ, POZ	-1.35 (0.52)	vs.	-0.45 (0.48)	11.70	0.01
Experiment 3					*F*(1,17)	*p* <
256-367 ms	AFZ,FZ,FCZ, CZ,CPZ,PZ, POZ	0.38 (0.75)	vs.	1.08 (0.72)	11.44	0.01

Table 3.7. The shape effect. Mean voltage amplitude given in µV. (Att: attended, Unatt: unattended, *SEM*: standard error of the mean, vs.: versus)
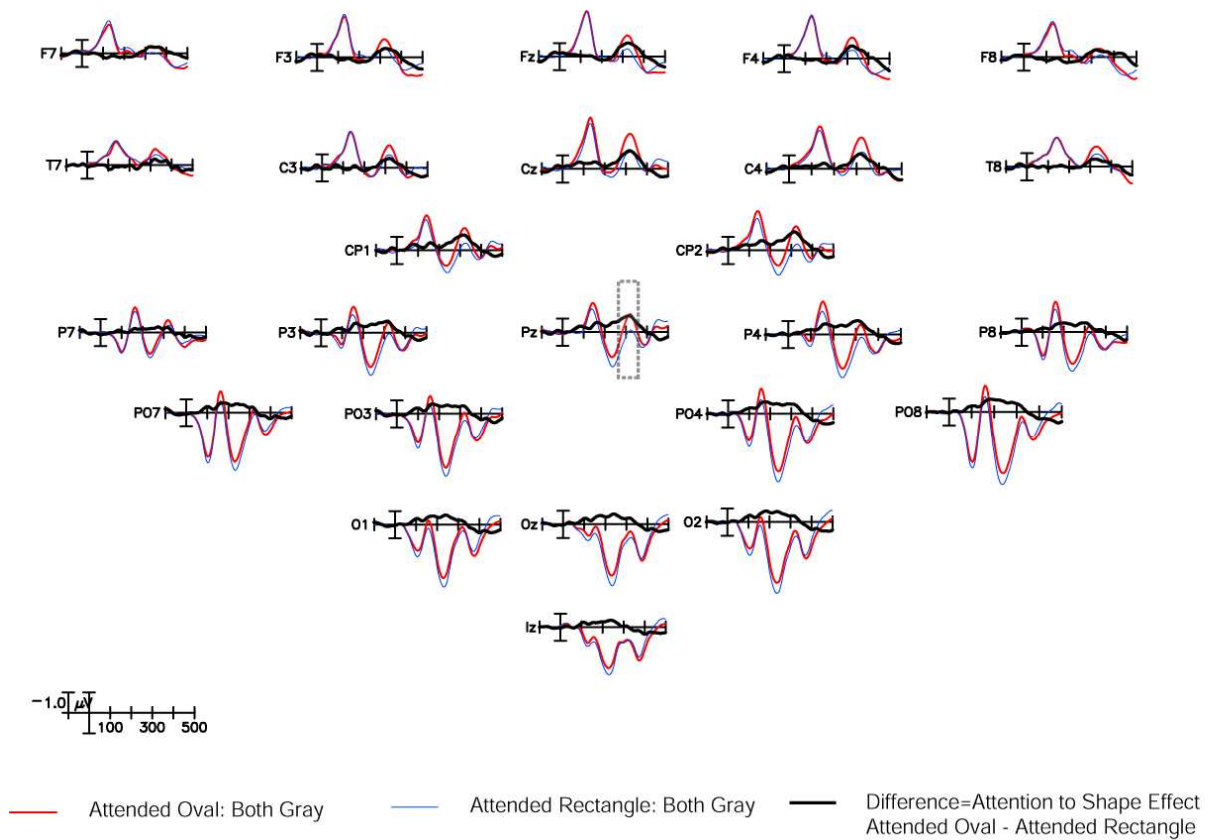
Figure 3.14. Grand-average ERPs (non-target trials) associated with the shape effect during Experiment 1. Negative voltage is plotted upward. Dotted line boxes indicate the time windows used for statistical testing.
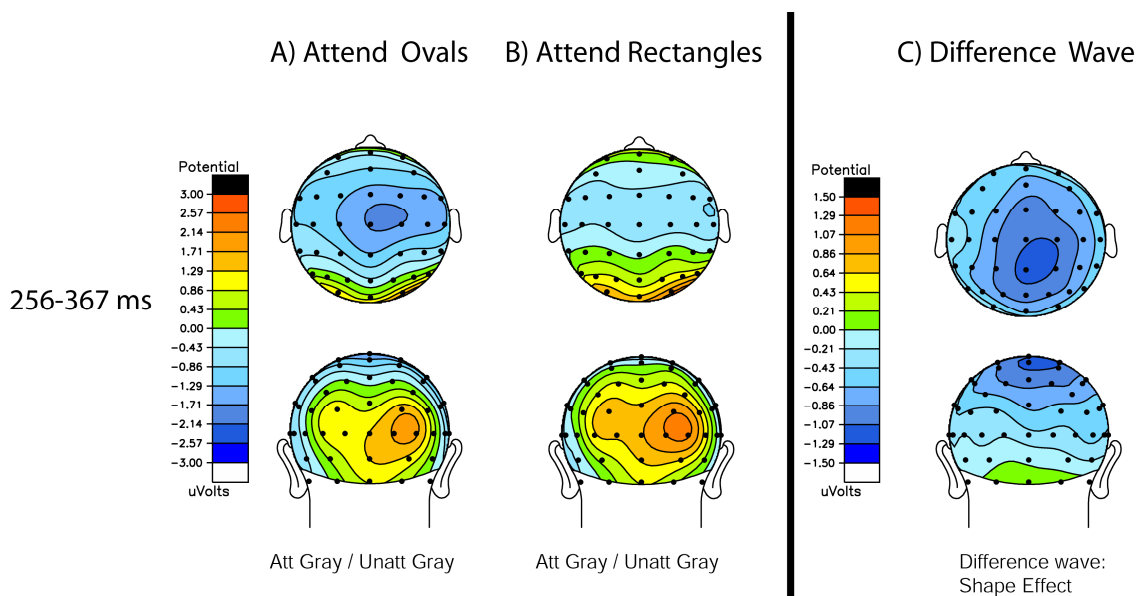
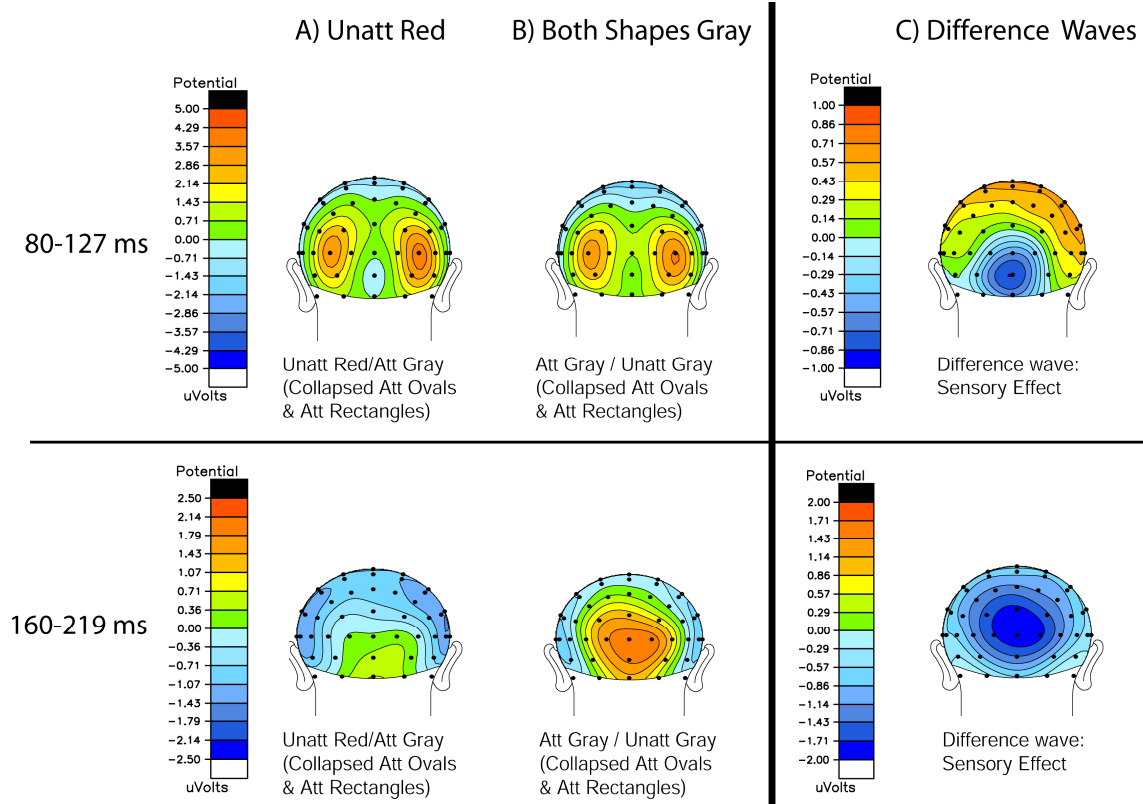Figure 3.15. Topographical maps of ERP amplitudes indexing the shape effect during Experiment 1. A) The distribution for trials during the attend oval condition when both shapes were gray. B) The distribution for trials during the attend rectangle condition when both shapes were gray. C) The attend oval minus attend rectangle difference wave distribution. The scale on the left is associated with columns A and B. (Att: attended, Unatt: unattended)
.
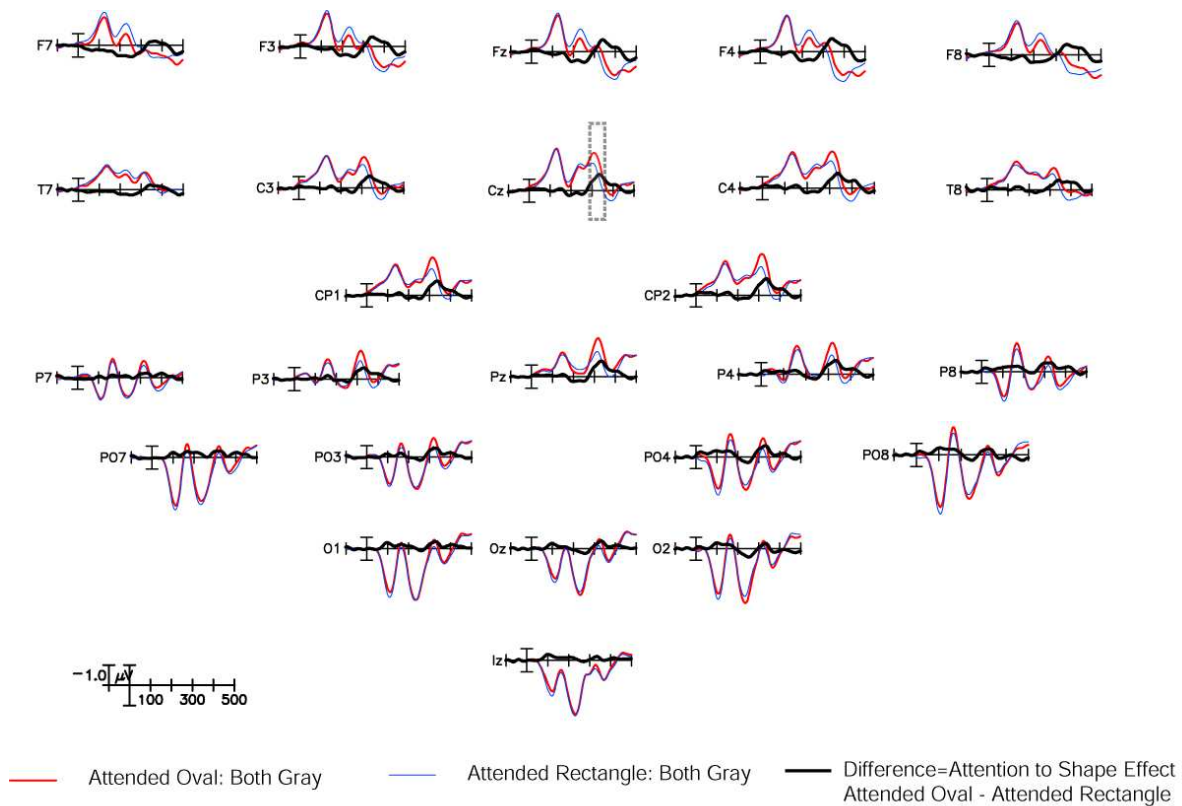
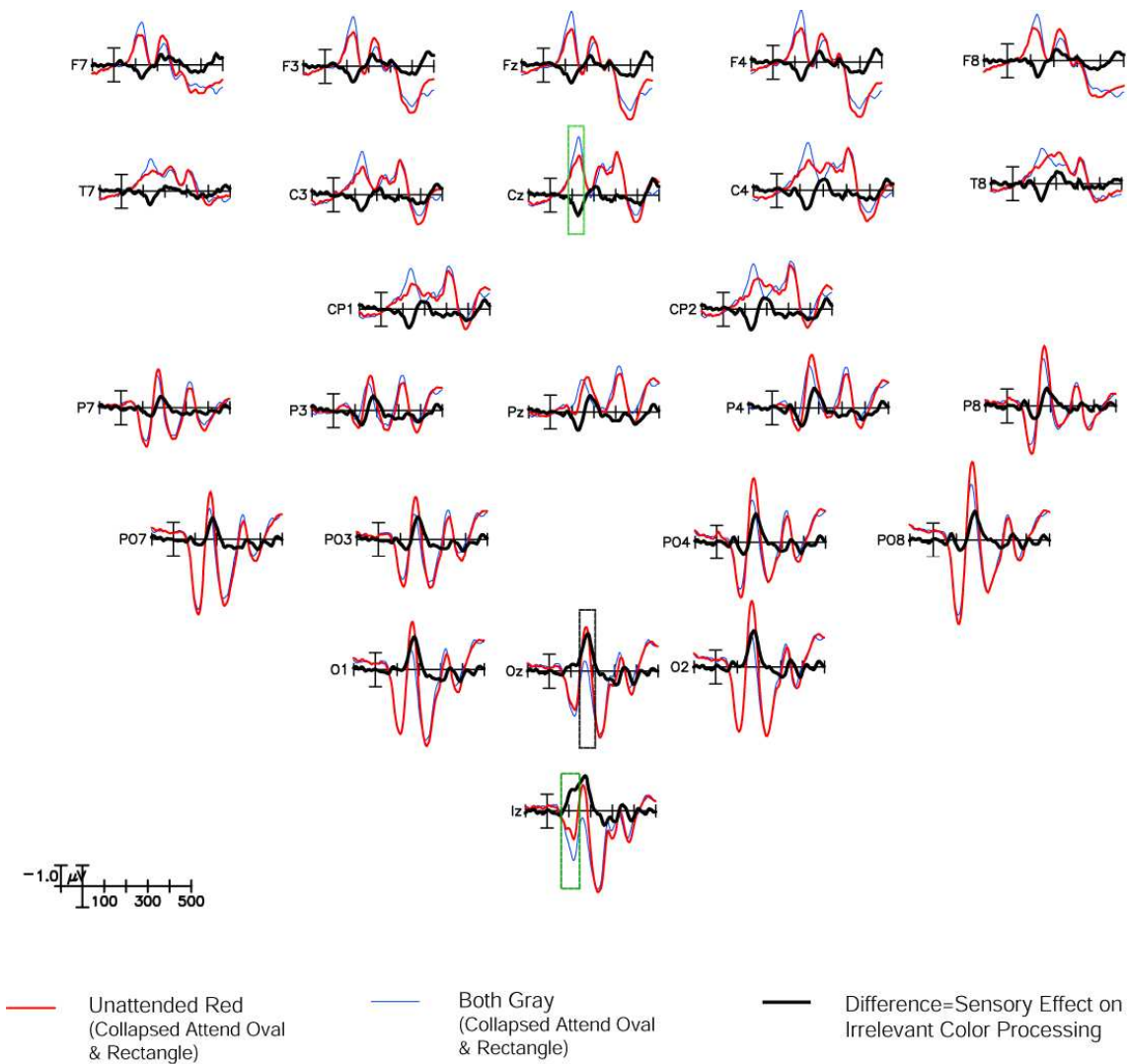Figure 3.16. Grand-average ERPs (non-target trials) associated with the shape effect during Experiment 2. Negative voltage is plotted upward. Dotted line boxes indicate the time windows used for statistical testing.

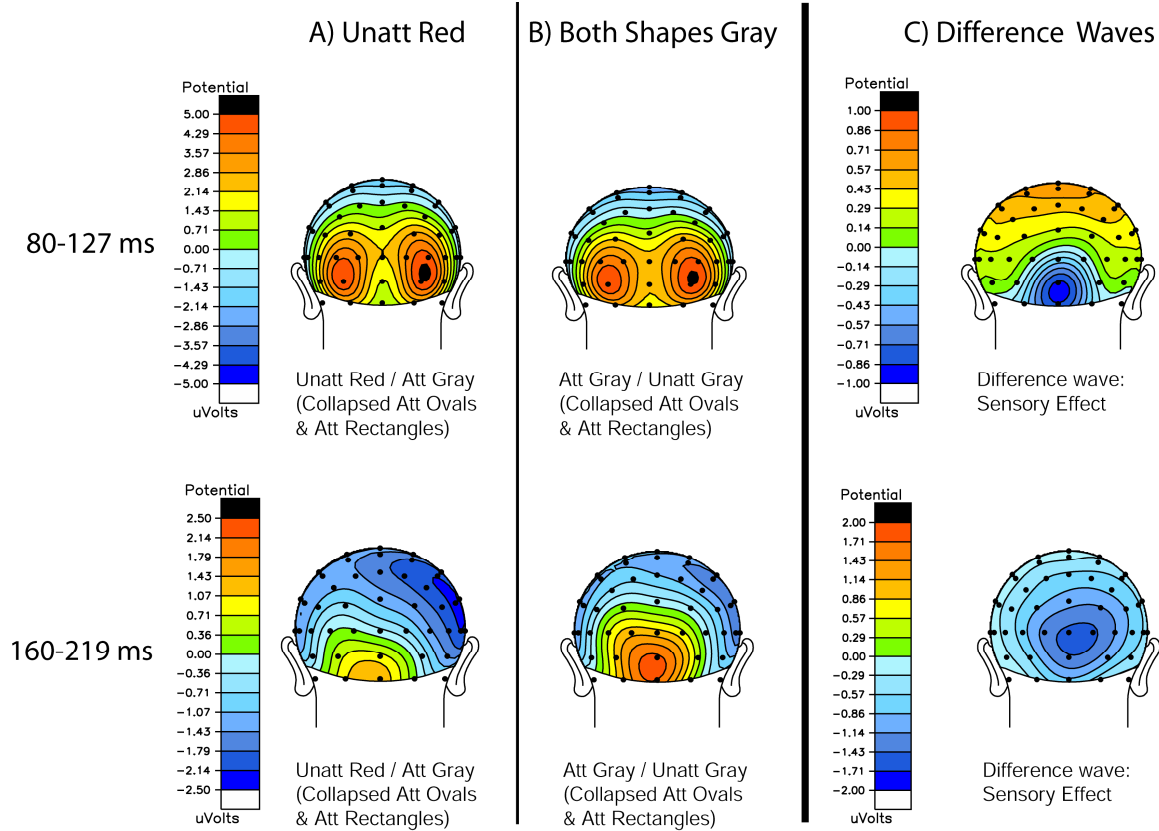Figure 3.17. Topographical maps of ERP amplitudes indexing the shape effect during Experiment 2. A) The distribution for trials during the attend oval condition when both shapes were gray. B) The distribution for trials during the attend rectangle condition when both shapes were gray. C) The attend oval minus attend rectangle difference wave distribution. The scale on the left is associated with columns A and B. (Att: attended, Unatt: unattended)
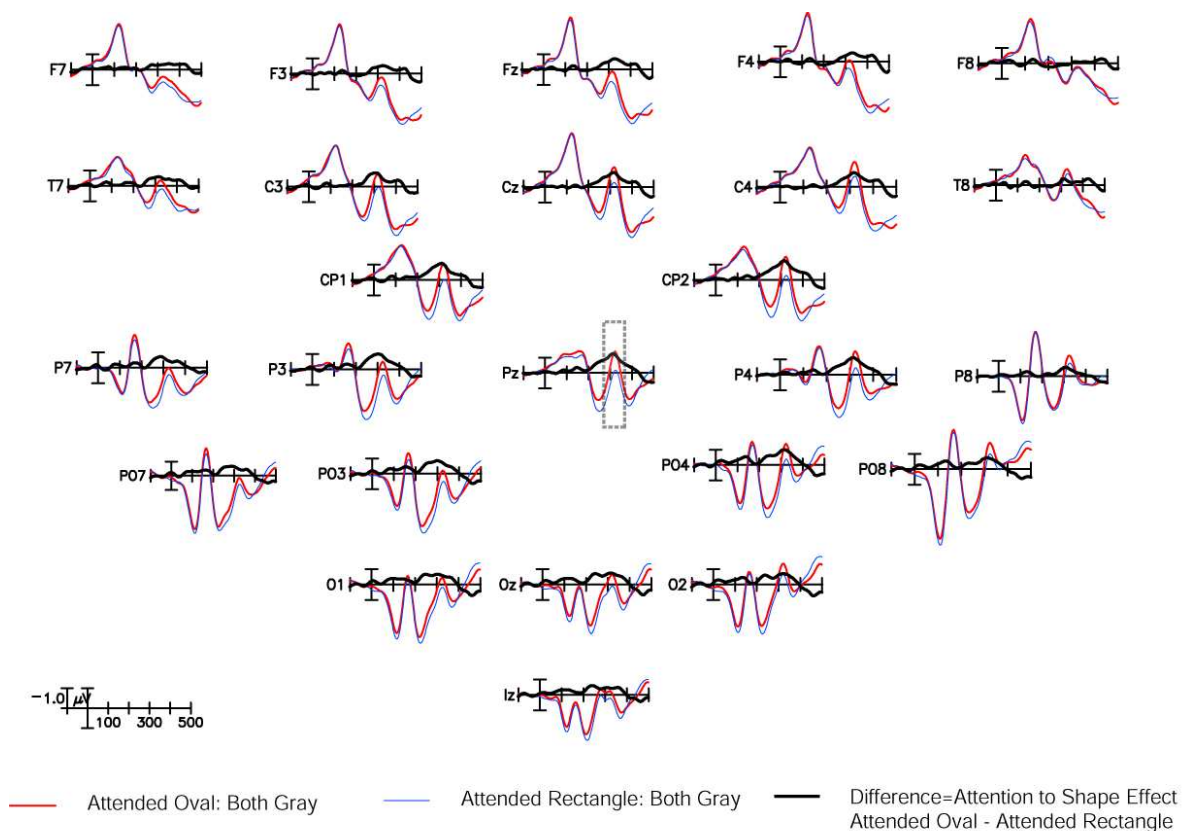
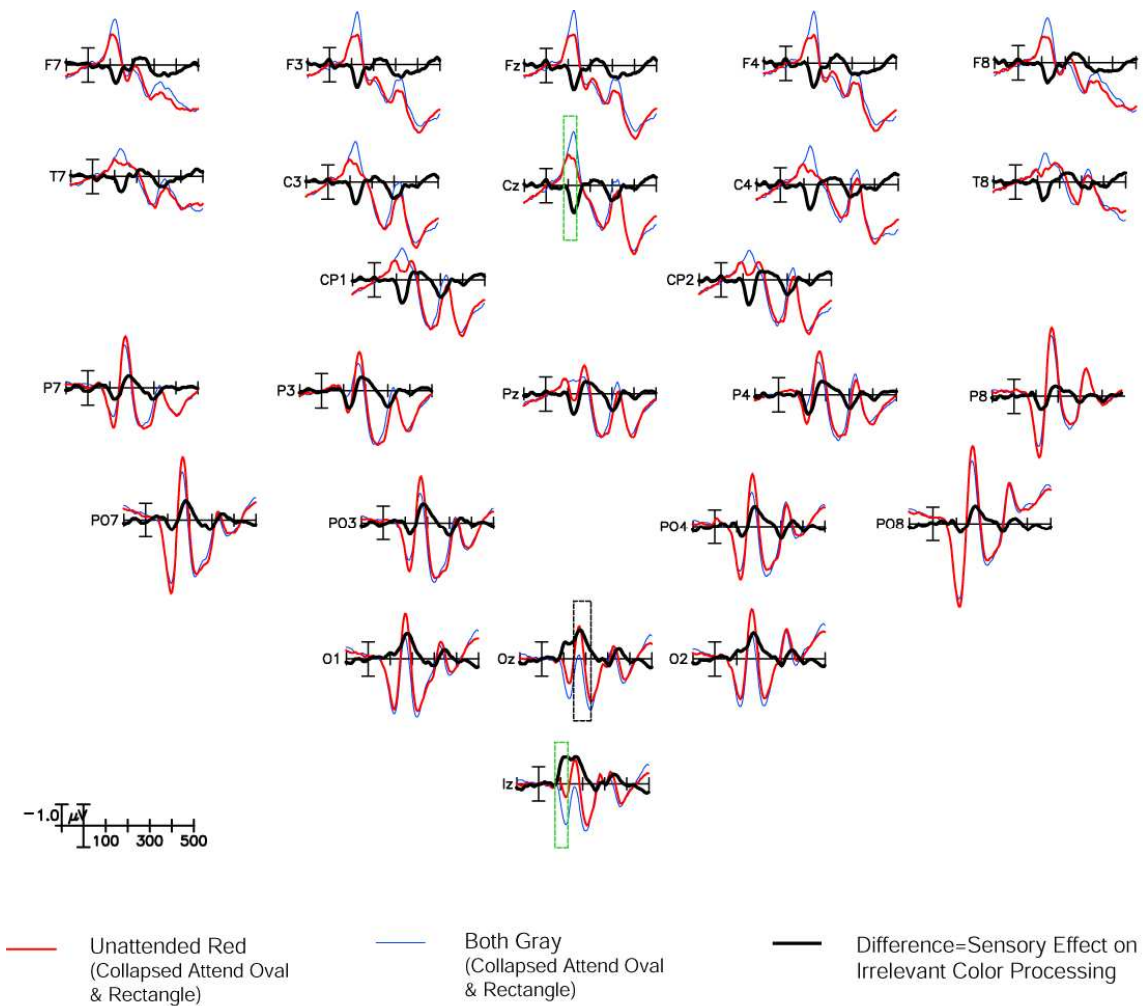Figure 3.18. Grand-average ERPs (non-target trials) associated with the shape effect during Experiment 3.   Negative voltage is plotted upward. Dotted line boxes indicate the time windows used for statistical testing.

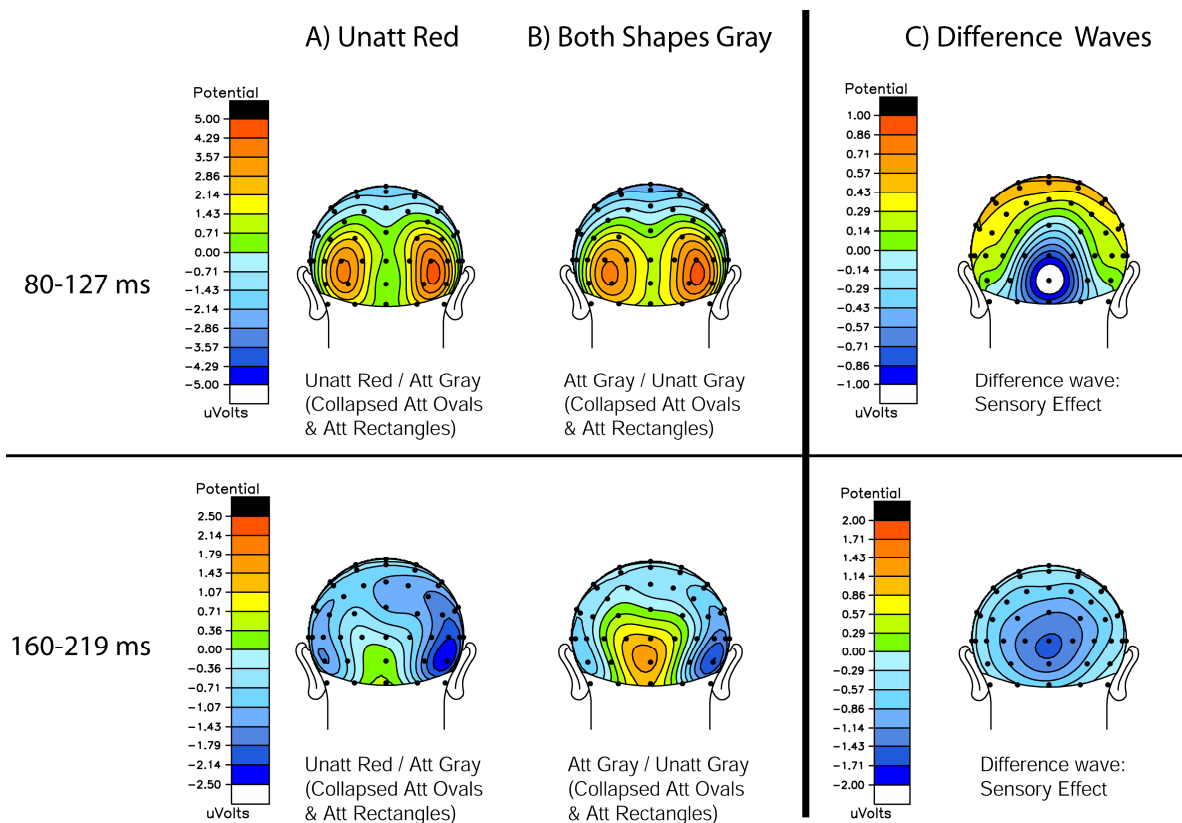Figure 3.19. Topographical maps of ERP amplitudes indexing the shape effect during Experiment 3. A) The distribution for trials during the attend oval condition when both shapes were gray. B) The distribution for trials during the attend rectangle condition when both shapes were gray. C) The attend oval minus attend rectangle difference wave distribution. The scale on the left is associated with columns A and B. (Att: attended, Unatt: unattended)

Effect of attention on task-irrelevant color processing

Experiment 1: Full Stimulus Set

In order to maintain consistency between the sensory analysis and the attention effect, Schoenfeld and colleagues (2003) analyzed the effect of attention on task-irrelevant color processing by collapsing over attended surface. Here, the same analytical approach was followed by collapsing ERP difference waves over the two attended shapes. Thus, the attention effect difference wave was isolated by subtracting ERP waveforms on trials in which the red shape was unattended from trials in which the red shape was attended (see Figure 3.5C for an illustration). Importantly, this comparison was calculated using the same stimuli under different attention conditions. As such, any differences between the two conditions should only be related to the effects of attention.

Two significant components were observed in the collapsed difference waveform (Table 3.8; Figures 3.20, 3.21). The first was a bilateral occipital positivity measured between 192–239 ms. This difference is due to a greater positive voltage when the shape containing red is attended versus when it is unattended. There was no hemispheric difference in this effect. This early attention effect became significantly different from the baseline between 210–219 ms ($t(12) = 2.54$, $p < 0.05$, left hemisphere; $t(12) = 2.27$, $p < 0.05$, right hemisphere), and was followed by a medial occipital negativity measured between 272–351 ms. This late attention effect became significantly different from the baseline between 280-289 ms ($t(12) = -2.31$, $p < 0.05$).

Experiment 2: Foreground/Background Counterbalanced

As in Experiment 1, two significant components were observed in the difference wave (Table 3.8; Figures 3.22, 3.23). The early attention effect, began earlier than in Experiment 1 and was measured between 176–239 ms. Again, there was no difference in the size of the effect between hemispheres. This effect became significantly different from the baseline between 180-189 ms ($t(9) = 2.47$, $p < 0.05$, left hemisphere; and 190–199 ms $t(9) = 2.90$, $p < 0.05$, right hemisphere). The late attention effect was also present and became significantly different from the baseline between 280-289 ms ($t(9) = -2.76$, $p < 0.05$).

Experiment 3: Equating Shape Difficulty

The early and late attention effects were again observed in the difference waveform (Table 3.8; Figures 3.24, 3.25). The early attention effect did not differ between hemispheres and became significantly different from the baseline between 210-219 ms as in the first experiment ($t(17) = 2.58$, $p < 0.05$, left hemisphere; $t(17) = 2.43$, $p < 0.05$, right hemisphere). The late attention effect became significantly different from the baseline between 300-309 ms ($t(17) = -2.53$, $p < 0.05$).

Time window	Electrodes Clustered	ANOVA of the Attention Effect			Attention Effect		Hemisphere x Attention Effect	
		Att-Red / Unatt-Gray µV (*SEM*)	vs.	Att-Gray / Unatt-Red µV (*SEM*)	*F*	*p*	*F*	*p*
Experiment 1					*F* (1,12)	*p* <	*F* (1,12)	*p* <
192-239 ms	P2,P4,P6, PO4,PO8, O2	2.60 (0.49)	vs.	2.10 (0.42)	6.98	0.05	0.63	=0.44
	P1,P3,P5, PO3,PO7, O1	2.28 (0.64)		1.70 (0.49)				
272-351 ms	OZ,IZ	1.31 (0.76)	vs.	1.72 (0.77)	8.32	0.05		
Experiment 2					*F*(1,9)	*p* <	*F*(1,9)	*p* <
176-239 ms	P2,P4,P6, PO4,PO8, O2	0.35(0.66)	vs.	-0.09(0.77)	7.18	0.05	0.08	=0.79
	P1,P3,P5, PO3,PO7, O1	1.03(0.77)		0.62(0.90)				
272-351 ms	OZ,IZ	-0.05(0.50)	vs.	0.84(0.56)	13.88	0.01		
Experiment 3					*F* (1,17)	*p* <	*F* (1,17)	*p* <
208-243 ms	P2,P4,P6, PO4,PO8, O2	2.18(0.72)	vs.	1.72(0.71)	15.32	0.01	0.32	=0.58
	P1,P3,P5, PO3,PO7, O1	3.01(0.79)		2.51(0.78)				
288-319 ms	OZ,IZ	-0.24(0.65)	vs.	0.05(0.66)	5.25	0.05		

Table 3.8. The effect of attention on task-irrelevant color processing: collapsed over attended shape. Mean voltage amplitude given in µV. (Att: attended, Unatt: unattended, *SEM:* standard error of the mean, vs.: versus)

Figure 3.20. Grand-average ERPs (non-target trials) associated with the effect of attention on the processing of task-irrelevant color during Experiment 1, collapsed over attend oval and attend rectangle conditions. Negative voltage is plotted upward. Dotted line boxes indicate the time windows used for statistical testing.
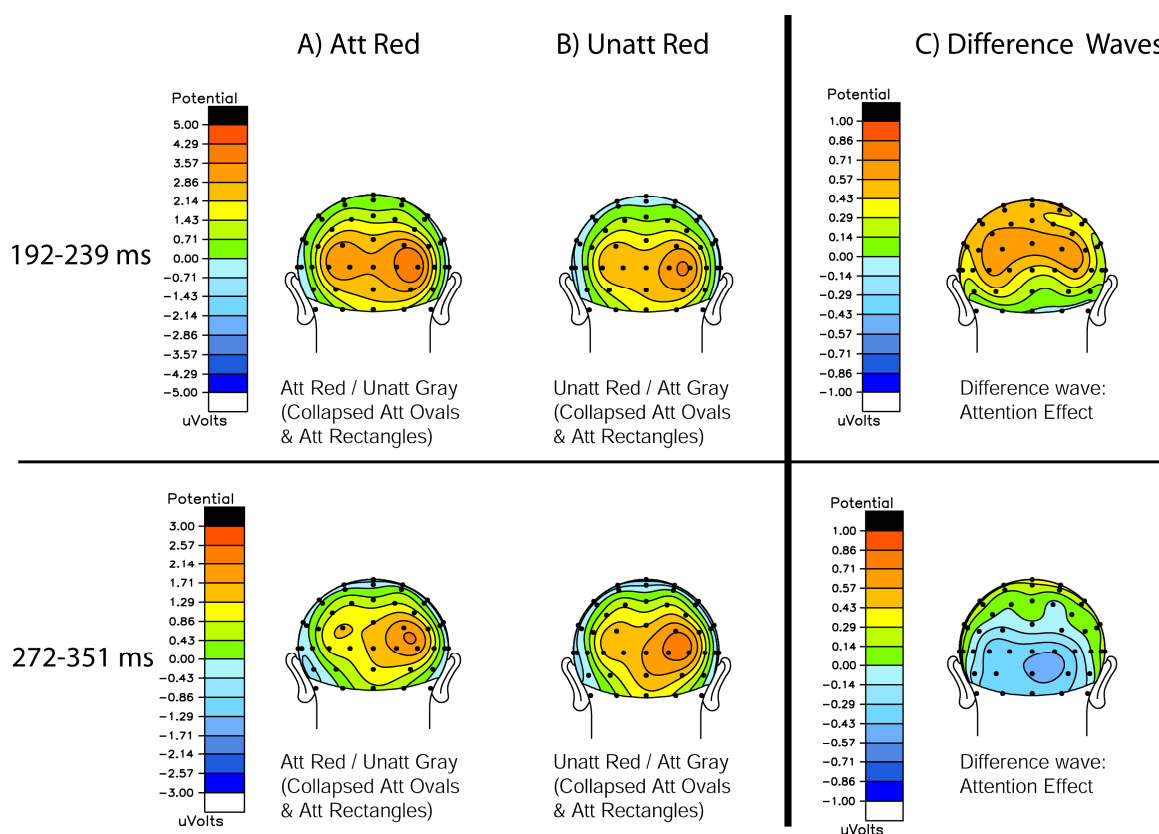
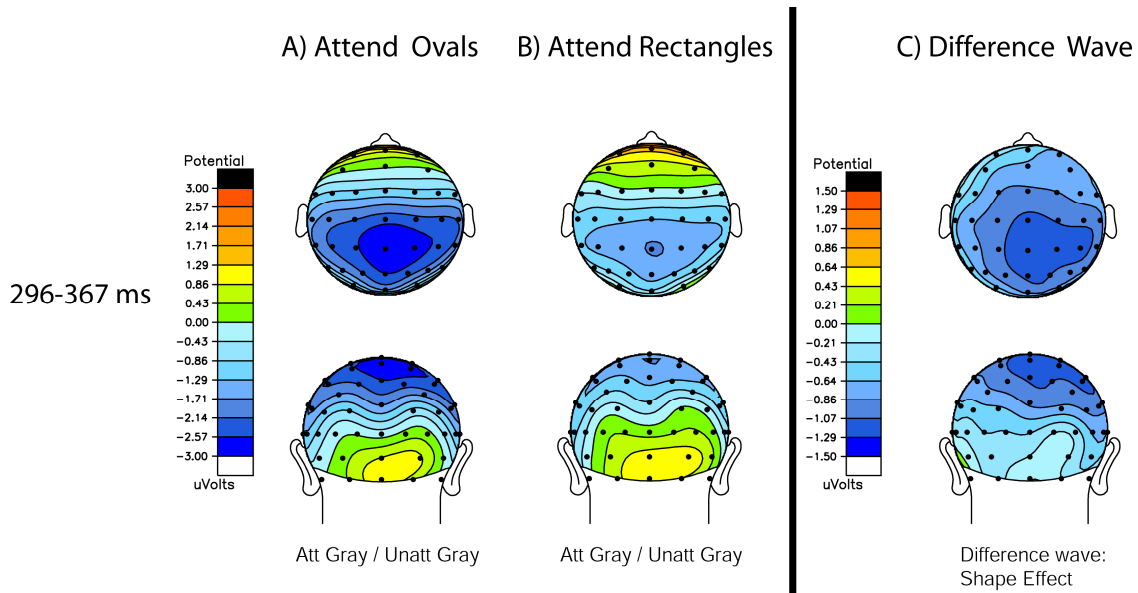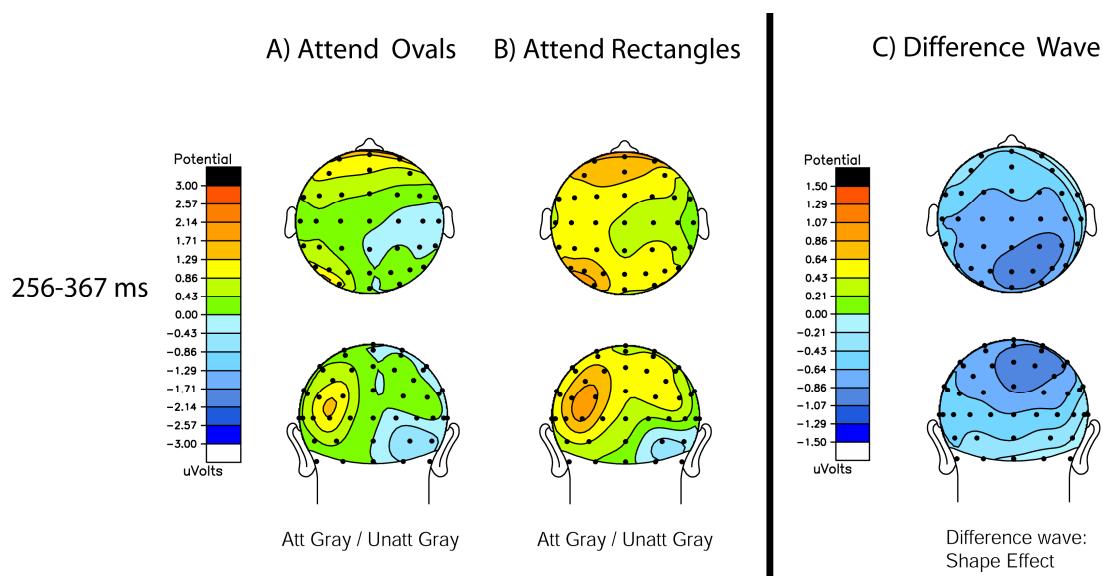Figure 3.21. Topographical maps of ERP amplitudes indexing the effect of attention on the processing of the task-irrelevant color during Experiment 1, collapsed over attend to ovals and attend to rectangles conditions. A) The distribution for trials during the "attended red" condition. B) The distribution for trials during the "unattended red" condition. C) The "attended red" minus "unattended red" difference wave distribution. The scale on the left is associated with columns A and B. (Att: attended, Unatt: unattended)

Figure 3.22. Grand-average ERPs (non-target trials) associated with the effect of attention on the processing of the task-irrelevant color during Experiment 2, collapsed over attend oval and attend rectangle conditions. Negative voltage is plotted upward. Dotted line boxes indicate the time windows used for statistical testing.
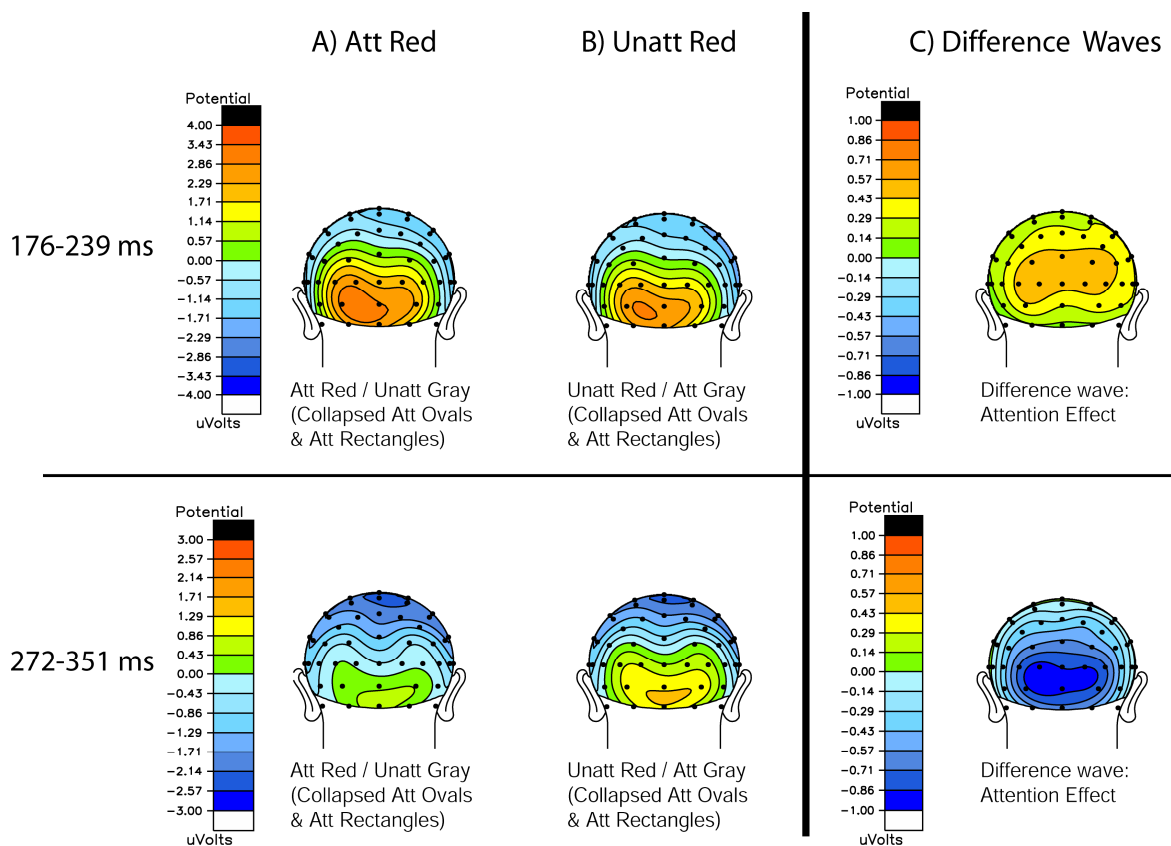
Figure 3.23. Topographical maps of ERP amplitudes indexing the effect of attention on the processing of the task-irrelevant color during Experiment 2, collapsed over attend to ovals and attend to rectangles conditions. A) The distribution during the significant time window for distribution for the "attended red" condition. B) The distribution for trials during the "unattended red" condition. C) The "attended red" minus "unattended red" difference wave distribution. The scale on the left is associated with columns A and B. (Att: attended, Unatt: unattended)
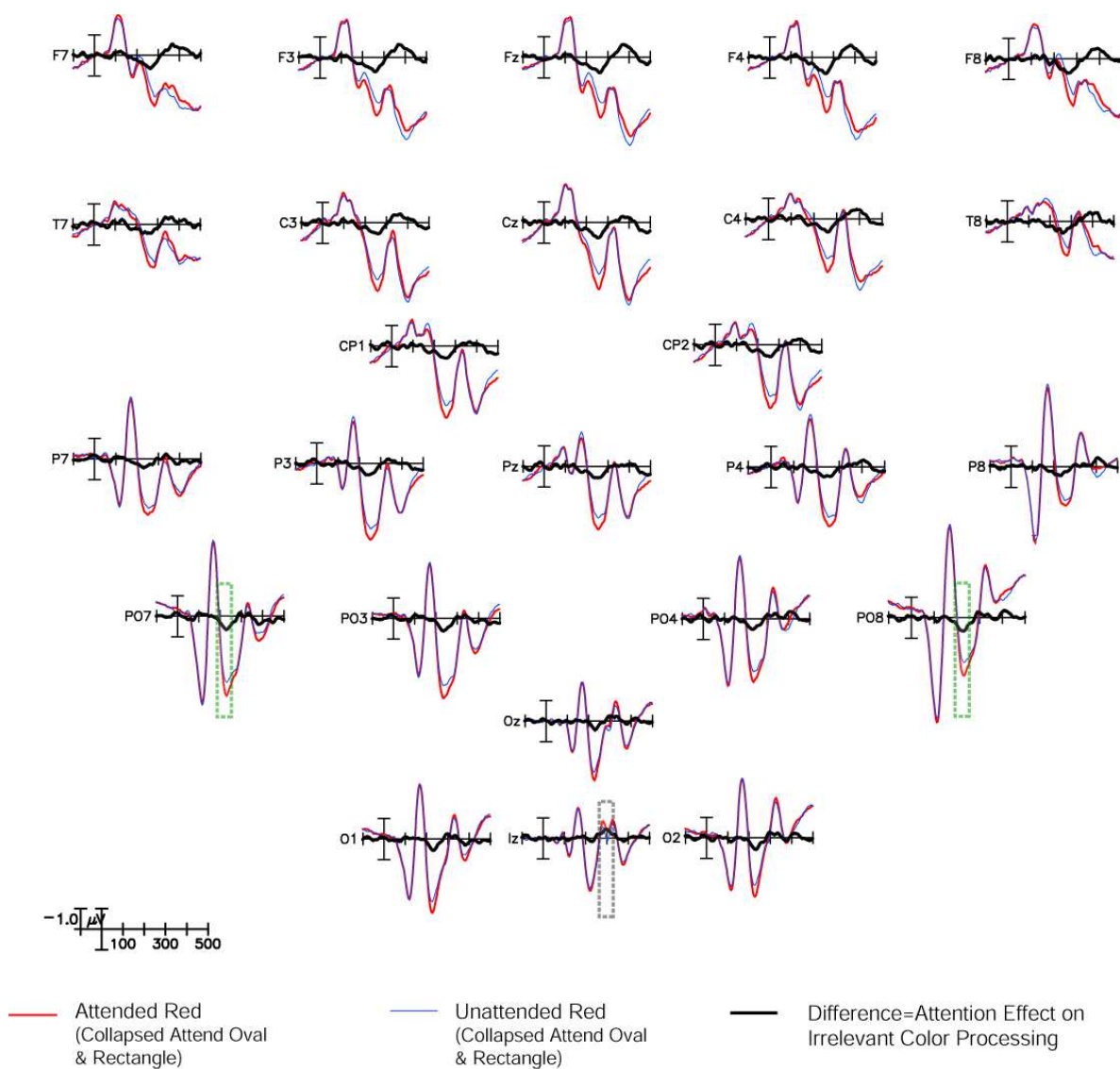
Figure 3.24. Grand-average ERPs (non-target trials) associated with the effect of attention on the processing of task-irrelevant color during Experiment 3, collapsed over attend oval and attend rectangle conditions. Negative voltage is plotted upward. Dotted line boxes indicate the time windows used for statistical testing.

Figure 3.25. Topographical maps of ERP amplitudes indexing the effect of attention on the processing of the task-irrelevant color during Experiment 3, collapsed over attend to ovals and attend to rectangles conditions. A) The distribution for the "attended red" condition. B) The distribution for trials during the "unattended red" condition. C) The "attended red" minus "unattended red" difference wave distribution. The scale on the left is associated with columns A and B. (Att: attended, Unatt: unattended)

Shape specific (oval and rectangle) attention effects on task-irrelevant color processing

The two effects of attention seen in all three experiments, the bilateral occipital positivity, "early attention effect", (beginning between 180–210 ms) and the ventral occipital negativity, "late attention effect", (beginning between 280-300 ms) can be further differentiated for specific attention effects to ovals or to rectangles. These were calculated as double

difference waves in order to remove the shape effect resulting from attention to one shape or another. Thus, differences due purely to attending to one shape or another (the shape effect) were removed by subtracting the conditions in which both stimuli were gray from the attended red and unattended red conditions.

The resulting two difference components are illustrated in Figures 3.26 and 3.27. The observed components were tested for significance at clusters of electrodes where the effects were maximal (Tables 3.9 & 3.10).

For the "attend ovals" condition, the difference between the "attended red" and "unattended red" difference waves was significant in all but one case (Experiment 2, between 210-220 ms). For the "attend rectangles" condition, only in Experiment 2 (between 280-300 ms), was there a significant difference between the "attended red" and "unattended red" conditions. The early attention effect, although noticeable in both the attend to ovals and attend to rectangles conditions in Experiment 2, is not seen in Experiments 1 and 3 when attending to rectangles. The late attention effect can be seen when attending to both ovals and rectangles in all experiments.

Time window	ANOVA of the Attention Effect			Attention Effect	
	Att-Red / Unatt-Gray Dif µV (*SEM*)	vs.	Att-Gray / Unatt-Red Dif µV (*SEM*)	*F*	*p*
Experiment 1				*F* (1,12)	*p* <
210-220 ms	-0.16(0.40)	vs.	-1.31(0.31)	8.27	0.05
280-300 ms	0.12(0.27)	vs.	0.77(0.31)	5.10	0.05
Experiment 2				*F* (1,9)	*p* <
210-220 ms	0.42(0.30)	vs.	-0.33(0.53)	2.89	=0.12
280-300 ms	-0.52(0.40)	vs.	0.41(0.24)	5.31	0.05
Experiment 3				*F* (1,17)	*p* <
210-220 ms	0.00(0.37)	vs.	-0.96(0.30)	10.90	0.01
280-300 ms	-0.81(0.34)	vs.	-0.15(0.26)	5.08	0.05

Table 3.9. The effect of attention on task-irrelevant color processing during the "attend ovals" condition for all experiments. Mean voltage amplitude given in µV. (Att: attended, Unatt: unattended, *SEM*: standard error of the mean, vs.: versus, Dif: difference wave)

Time window	ANOVA of the Attention Effect			Attention Effect	
	Att-Red / Unatt-Gray Dif µV (*SEM*) vs.	vs.	Att-Gray / Unatt-Red Dif µV (*SEM*)	*F*	*p*
Experiment 1				*F* (1,12)	*p* <
210-220 ms	-0.19(0.30)	vs.	-0.36(0.23)	0.41	=0.54
280-300 ms	0.20(0.31)	vs.	0.53(0.20)	3.28	=0.10
Experiment 2				*F* (1,9)	*p* <
210-220 ms	0.28(0.47)	vs.	-0.19(0.48)	1.48	=0.25
280-300 ms	-0.09(0.30)	vs.	0.77(0.33)	5.46	0.05
Experiment 3				*F* (1,17)	*p* <
210-220 ms	-1.01(0.29)	vs.	-0.48(0.31)	2.74	=0.12
280-300 ms	-0.30(0.17)	vs.	0.01(0.17)	3.17	=0.09

Table 3.10. The effect of attention on task-irrelevant color processing during the "attend rectangles" condition for all experiments. Mean voltage amplitude given in µV. (Att: attended, Unatt: unattended, *SEM*: standard error of the mean, vs.: versus, Dif: difference wave)
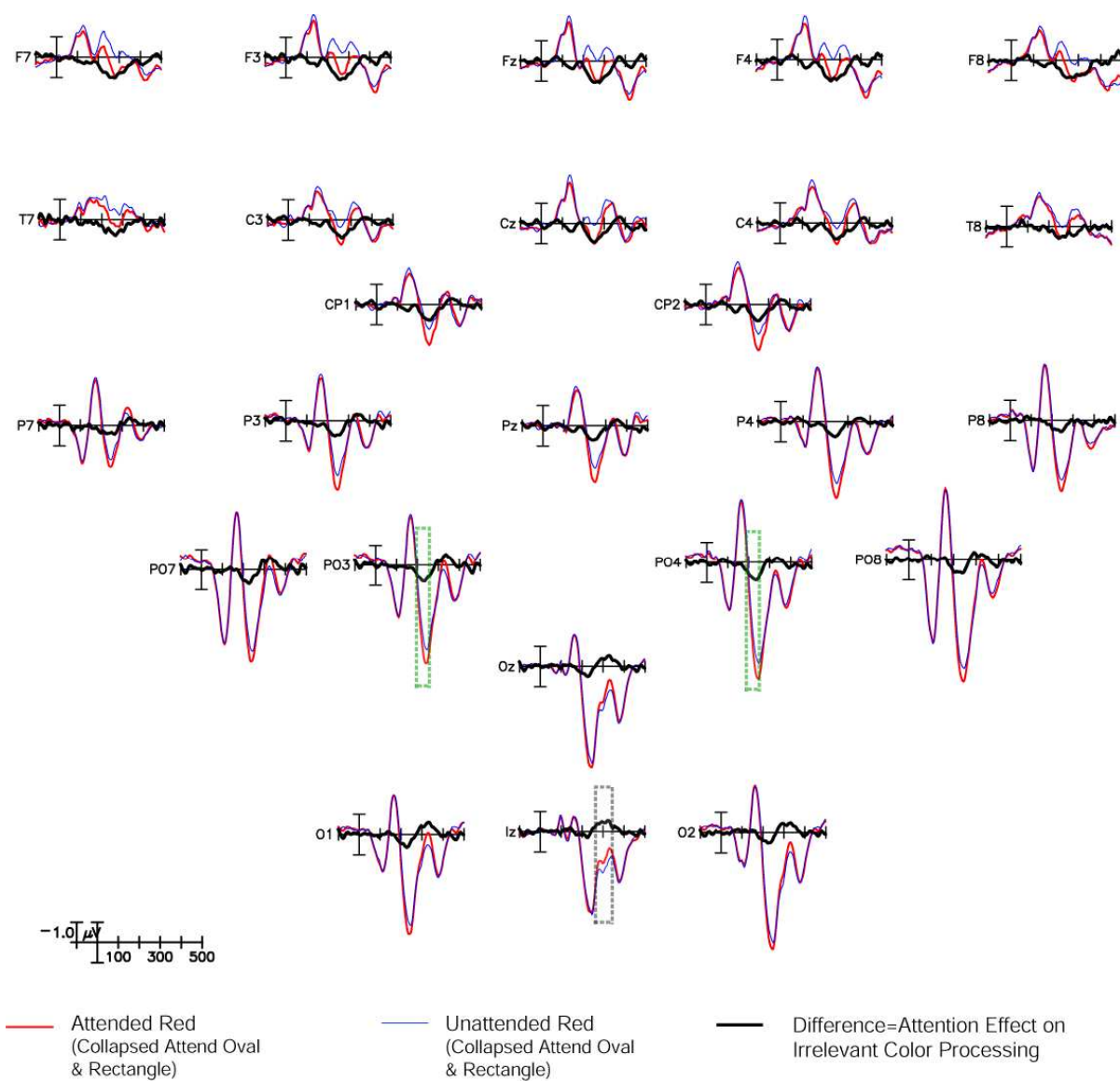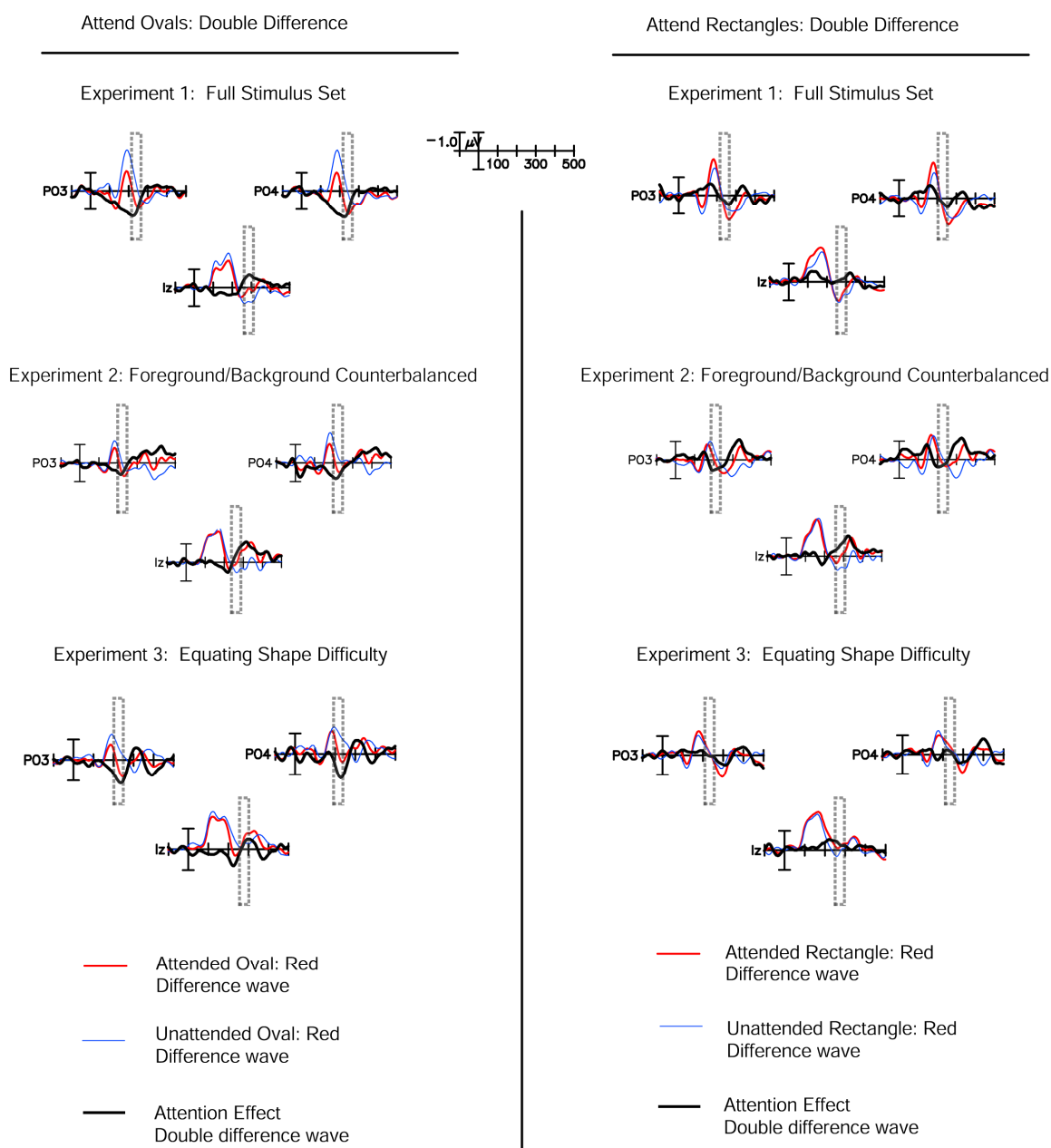
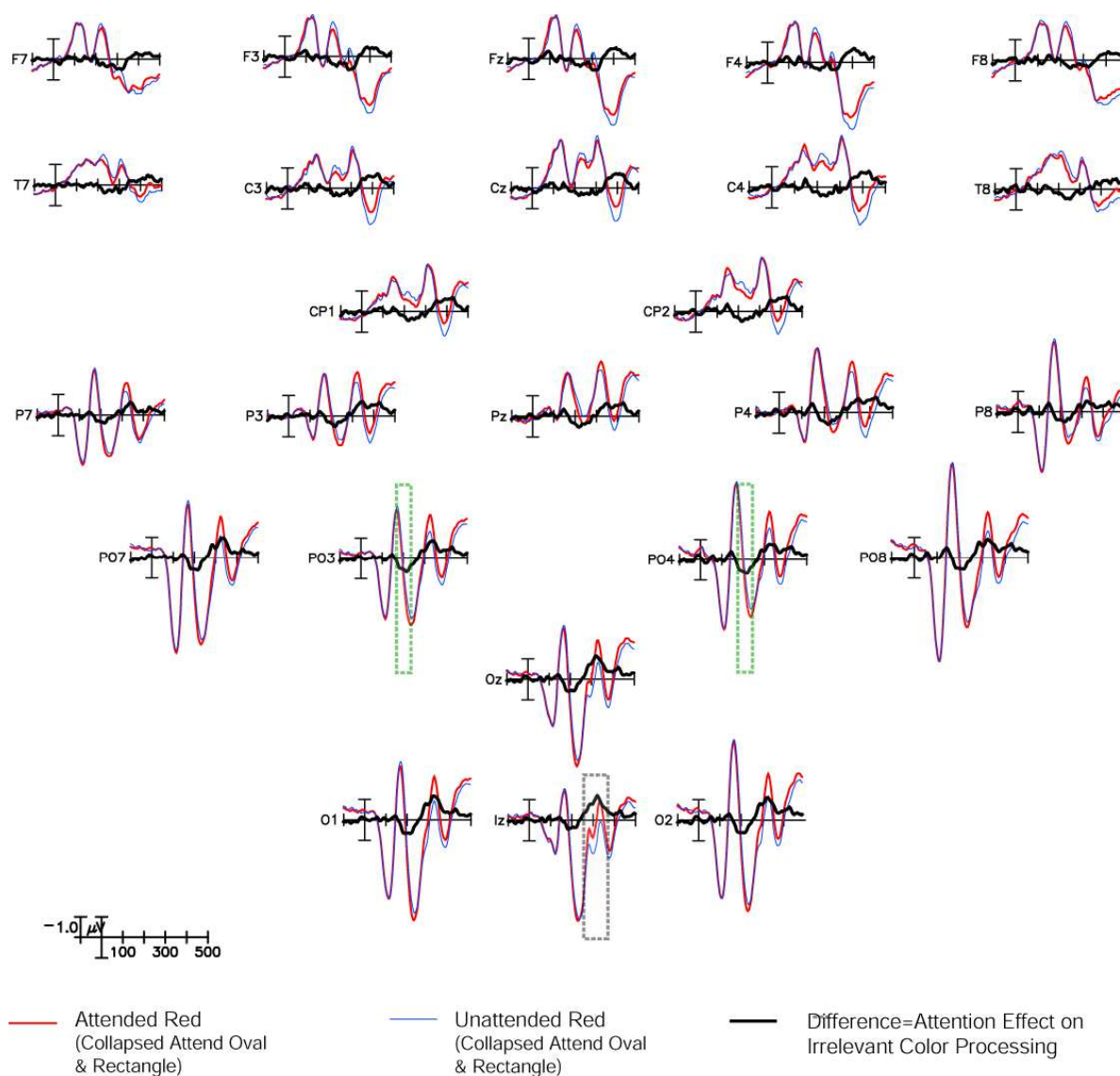Figure 3.26. Grand-average ERPs (non-target trials) associated with the effect of attention on processing of the task-irrelevant color, shown separately for the "attend ovals" and "attend rectangles" conditions for all three experiments. The "attended red" difference wave, the "unattended red" difference wave, and the effect of attention on the task-irrelevant color double difference waves are shown. Negative voltage is plotted upward. Dotted line boxes indicate the time windows used for statistical testing (210-220 ms and 280-300 ms) representing the two attention effects.
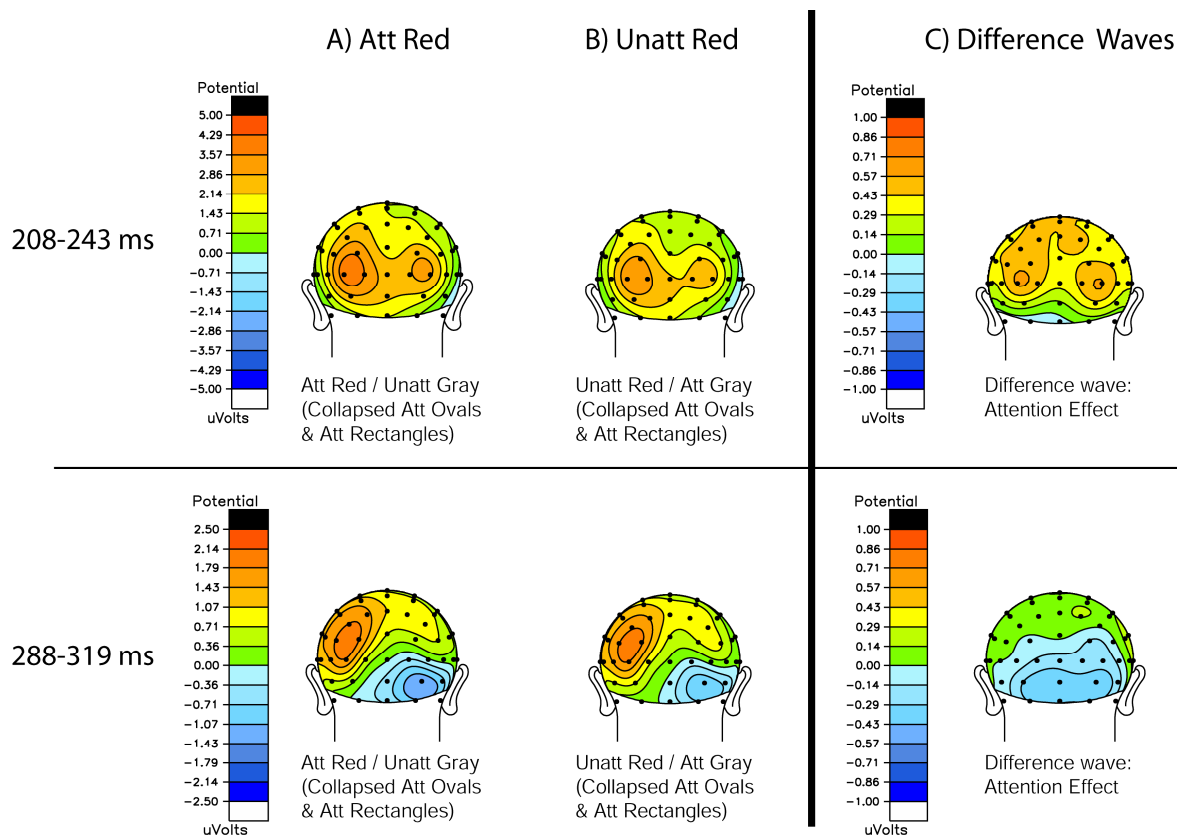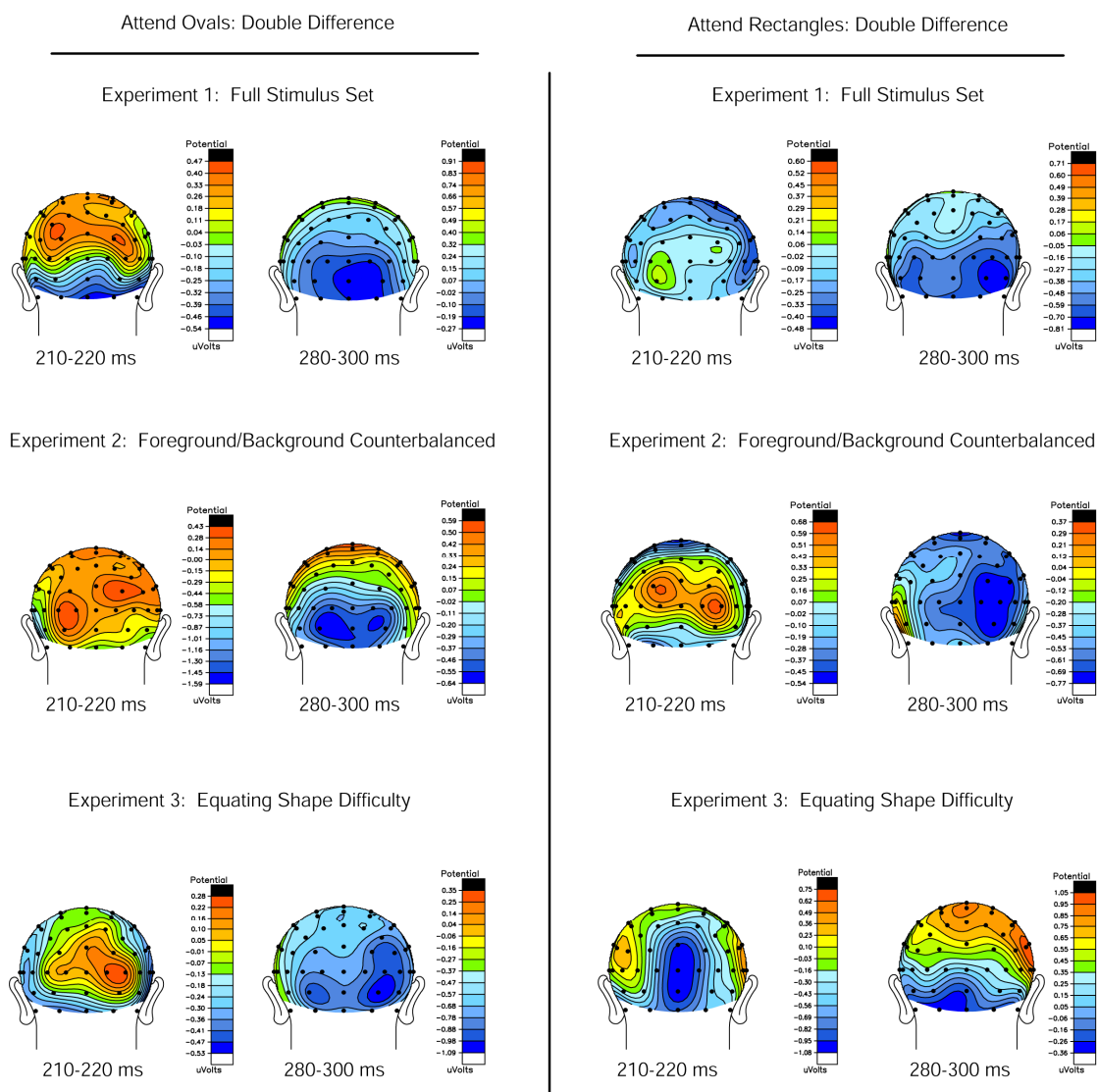
Figure 3.27. Topographical maps of ERP amplitudes indexing the effect of attention on the processing of the task-irrelevant color, shown separately for the "attend ovals" and "attend rectangles" conditions, for all three experiments. The two time windows displayed (210-220 ms and 280-300 ms) represent the time windows used for statistical testing of the two attention effects.

ERPs to target stimuli

Attended target stimuli in all three experiments elicited a P300 wave indicating that these stimuli were processed in a manner that is consistent with previously reported results obtained in other paradigms in which infrequent, task-relevant stimuli were presented (Polich, 2007). Both circle and square targets elicited this widely distributed component that peaked between 500 and 600 ms with a maximum voltage at central-parietal electrode sites (Figure 3.28). For all experiments, the amplitude of the P300 difference component was larger for attended than unattended targets in both the circle target present and square target present trials (*circle target*: Experiment 1, $F(1, 12) = 85.23$, $p < 0.0001$; Experiment 2, $F(1, 9) = 53.78$, $p < 0.0001$; Experiment 3, $F(1, 17) = 39.28$, $p < 0.0001$) (*square target*: Experiment 1, $F(1, 12) = 31.77$, $p < 0.0001$; Experiment 2, $F(1, 9) = 35.56$, $p < 0.001$; Experiment 3, $F(1, 17) = 39.28$, $p < 0.0001$). There was no significant mean amplitude difference between the circle target and square target P300 difference wave components for any of the experiments (Experiment 1, $F(1, 12) = 3.07$, $p = 0.11$; Experiment 2, $F(1, 9) = 1.91$, $p = 0.20$; Experiment 3, $F(1, 17) = 1.96$, $p = 0.18$). Interestingly, in all experiments, the shape effect can be seen in the target waveforms at 300 ms, in which the waveform elicited by circles is more negative than that elicited by squares.

Attended and Unattended Target Trials

$-2.0 \mu V$

0 ms   900 ms

Experiment 1

Circle Targets   Square Targets

Pz   Pz

Circle and Square Target
Difference Waves

Pz

—— Attended Circle Target   —— Attended Square Target

—— Unattended Circle Target   —— Unattended Square

—— Circle Target Difference Wave —— Square Target Difference
(Attended minus Unattended)   Wave

—— Circle Target Difference Wave
—— Square Target Difference Wave

Experiment 2

Circle Targets   Square Targets

Pz   Pz

Circle and Square Target
Difference Waves

Pz

—— Attended Circle Target   —— Attended Square Target

—— Unattended Circle Target   —— Unattended Square

—— Circle Target Difference Wave —— Square Target Difference
(Attended minus Unattended)   Wave

—— Circle Target Difference Wave
—— Square Target Difference Wave

Experiment 3

Circle Targets   Square Targets

Pz   Pz

Circle and Square Target
Difference Waves

Pz

—— Attended Circle Target   —— Attended Square Target

—— Unattended Circle Target   —— Unattended Square

—— Circle Target Difference Wave —— Square Target Difference
(Attended minus Unattended)   Wave

—— Circle Target Difference Wave
—— Square Target Difference Wave

Figure 3.28. Grand-average ERPs for circle and square target trials for all three experiments. Waveforms for attended and unattended circle targets and their difference waveforms are presented in the left column. Attended and unattended square targets and their difference waveforms are presented in the right column. Circle and square target difference waves are plotted in the center column. Negative voltage is plotted upward.

Summary of the main comparisons of interest across experiments

The early sensory effect (peak 115 ms)

The early sensory effect indexing the presence of color in the display peaked at about 115 ms at midline occipital electrodes and is strikingly similar in all experiments (Figure 3.29A). The similarity of the effect in all of the experiments was tested statistically by comparing the scalp topographies between groups following normalization (McCarthy & Wood, 1985). The topography of this component was not significantly different between the three experiments (Experiment x Electrode interaction: $F(74, 1406) = 0.52$, $p = 0.81$). Moreover, these topographies remained similar with the addition of the passive viewing condition (Experiment x Electrode interaction: $F(111, 2035) = 0.75$, $p = 0.97$).

The late sensory effect (peak 175 ms)

The late sensory effect indexing the presence of color in the display peaked at about 175 ms at midline occipital electrodes and is also similar across all of the experiments (Figure 3.29B). Furthermore, the topography of this component was not significantly different between the three experiments (Experiment x Electrode interaction: $F(74, 1406) = 1.18$, $p = 0.32$).

The early attention effect (peak 225 ms)

The first attention effect associated with task-irrelevant feature color processing peaked at about 225 ms at bilateral parietal-occipital electrodes (Figure 3.29C). The scalp topography of this component was not significantly different between the three experiments (Experiment x Electrode interaction: $F(74,1406) = 0.92$, $p = 0.48$) suggesting that they originated from the same underlying cortical sources.

This topography of this "early attention effect" was compared to the distribution of both the "early sensory" and the "late sensory" effects (Table 3.11). Significant *p*-values indicate a significant difference in scalp topography. The scalp topographies of the "early attention effect" and the "early sensory effect" were significantly different from one another in all three experiments. This was also the case for the comparison of the "early attention effect" and the "late sensory effect" suggesting that the early attention effect and the sensory effects may have some differences in their underlying cortical sources.

ANOVA of the Early Attention Effect Scalp Topography Analysis Effect x Electrode Interaction				
Experiment 1			F (37,444)	p
Early Attn Effect	vs.	Early Sens Effect	4.28	= 0.02
Early Attn Effect	vs.	Late Sens Effect	6.14	= 0.003
Experiment 2			F (37,333)	p
Early Attn Effect	vs.	Early Sens Effect	4.87	= 0.01
Early Attn Effect	vs.	Late Sens Effect	4.25	= 0.02
Experiment 3			F (37,629)	p
Early Attn Effect	vs.	Early Sens Effect	7.17	= 0.001
Early Attn Effect	vs.	Late Sens Effect	6.93	= 0.001

Table 3.11. Comparison of the scalp topographies of the "early attention" versus the "early sensory" and "late sensory" effects.

The late attention effect (peak 315 ms)

The late attention effect associated with task-irrelevant color processing peaked at about 315 ms at central occipital electrodes (Figure 3.29D). This component had a similar distribution across experiments (Experiment x Electrode interaction: $F(74, 1406) = 1.38$, $p = 0.24$). The scalp topography of this "late attention" effect was compared to the distribution of both the "early sensory" and "late sensory" effects (Table 3.12). The scalp topographies of the "late attention" effect and the "early" and "late" sensory effects were similar in all

experiments. In particular, the "early sensory" effect was similar to the "late attention" effect across all experiments as indicated by a $p > 0.05$. As such, the LAURA source estimates for these two difference components were further compared (Figure 3.32).

ANOVA of the Late Attention Effect Scalp Topography Analysis Effect x Electrode Interaction				
Experiment 1			F (37,444)	p
Late Attn Effect	vs.	Early Sens Effect	1.25	= 0.31
Late Attn Effect	vs.	Late Sens Effect	4.38	= 0.01
Experiment 2			F (37,333)	p
Late Attn Effect	vs.	Early Sens Effect	1.90	= 0.17
Late Attn Effect	vs.	Late Sens Effect	0.66	= 0.54
Experiment 3			F (37,629)	p
Late Attn Effect	vs.	Early Sens Effect	2.77	= 0.59
Late Attn Effect	vs.	Late Sens Effect	2.53	=0.08

Table 3.12. Comparison of the scalp topographies of the "late attention" versus the "early sensory" and "late sensory" effects.
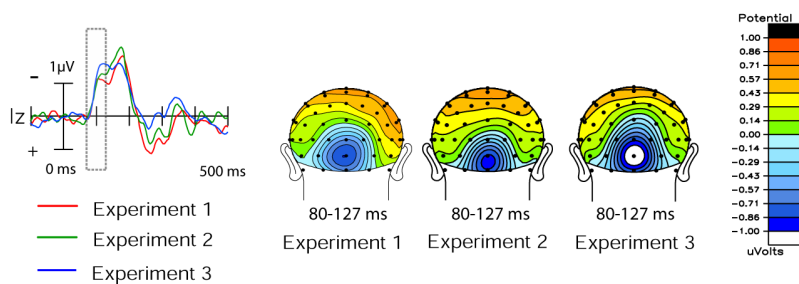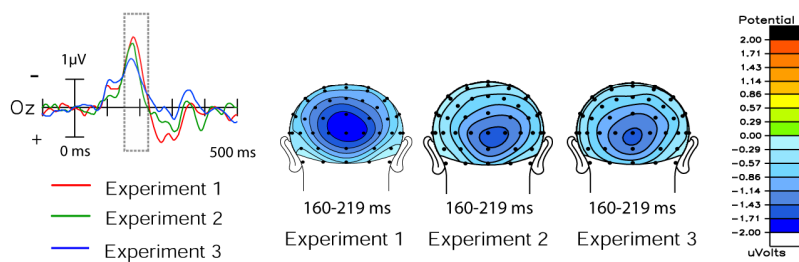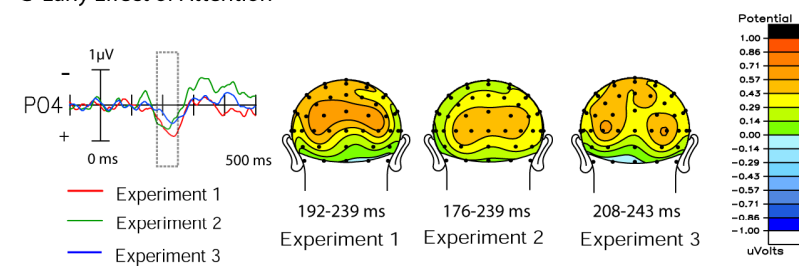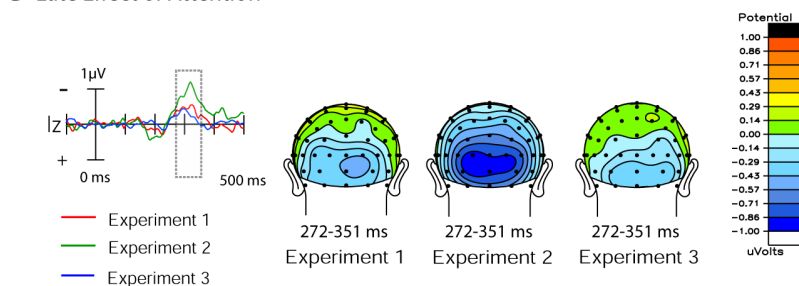
Figure 3.29. Comparison of each difference ERP effect for all three experiments. Waveforms are shown as well as the associated scalp topography of the effect.

Source Analysis

LAURA source analyses were performed on the grand-averaged difference waveforms for the early (115 ms peak) and late (175 ms peak) sensory effects, and the early (225 ms peak) and late (315 ms peak) attention effects, for all three experiments. In all cases, these analyses were performed on the difference waveforms averaged over the "attend oval" and "attend rectangle" conditions. Current source maxima for each of the conditions and experiments are given in Table 3.13. The maximal coronal slices for the estimated sources are shown for all four effects and for all three experiments in Figures 3.30 & 3.31. The sensory effect of color included bilateral source estimates throughout the lingual and fusiform gyri, for both the early and late sensory effects. The source estimates for the earlier (225 ms) effect of attention showed a maximal lateral occipital distribution in the fusiform gyrus but extending throughout the visual cortex. The later (315 ms) attention effect also included source estimates in the fusiform gyrus. Moreover, the estimate for Experiment 1 included an additional maximal source in the parietal lobe. Altogether, the combined source analysis findings point to common sources in ventral occipital cortex that are associated with processing of the sensory and attention effects. When the early sensory and late attention effects are compared for all three experiments (Figure 3.32), common sources in ventral occipital cortex are observed with additional parietal cortical sources estimated for the late attention effect.

ERP component	x (mm)	y (mm)	z (mm)	Brain region
Experiment 1				
Sensory Dif (80-127 ms)	±17	-86	-12	Left Lingual Gyrus (BA 18)
Sensory Dif (160-219 ms)	±41	-69	-11	Right Fusiform Gyrus (BA 19)
Attention Collapse Dif (192-239 ms)	±35	-75	-12	Left Fusiform Gyrus (BA 19)
Attention Collapse Dif (272-351 ms)	+23	-72	42	Right Parietal Lobe, Precuneus (BA 7)
Experiment 2				
Sensory Dif (96-127 ms)	±17	-86	-12	Left Lingual Gyrus (BA 18)
Sensory Dif (160-219 ms)	±35	-75	-12	Left Fusiform Gyrus (BA 19)
Attention Collapse Dif (176-239 ms)	±29	-80	-12	Left Fusiform Gyrus (BA 19)
Attention Collapse Dif (272-351 ms)	±23	-86	-12	Left Fusiform Gyrus (BA 18)
Experiment 3				
Sensory Dif (80-127 ms)	±17	-86	-12	Left Lingual Gyrus (BA 18)
Sensory Dif (160-219 ms)	±17	-86	-12	Left Lingual Gyrus (BA 18)
Attention Collapse Dif (208-243 ms)	±35	-75	-12	Left Fusiform Gyrus (BA 19)
Attention Collapse Dif (288-319 ms)	±35	-75	-12	Left Fusiform Gyrus (BA 19)

Table 3.13. Talairach coordinates and corresponding brain regions of the current source maxima as modeled by LAURA for the components in the sensory and attention difference waveforms, collapsed over attended shape. (Dif = Difference Wave, BA = Broadmann's Area)

A Early Sensory Effect of Color

Experiment 1	Experiment 2	Experiment 3

y = -86   0.0035 µA/mm^3

y = -86   0.0065 µA/mm^3

y = -86   0.0055 µA/mm^3

L

B Late Sensory Effect of Color

Experiment 1	Experiment 2	Experiment 3

y = -69   0.0035 µA/mm^3

y = -75   0.003 µA/mm^3

y = -86   0.0025 µA/mm^3

L
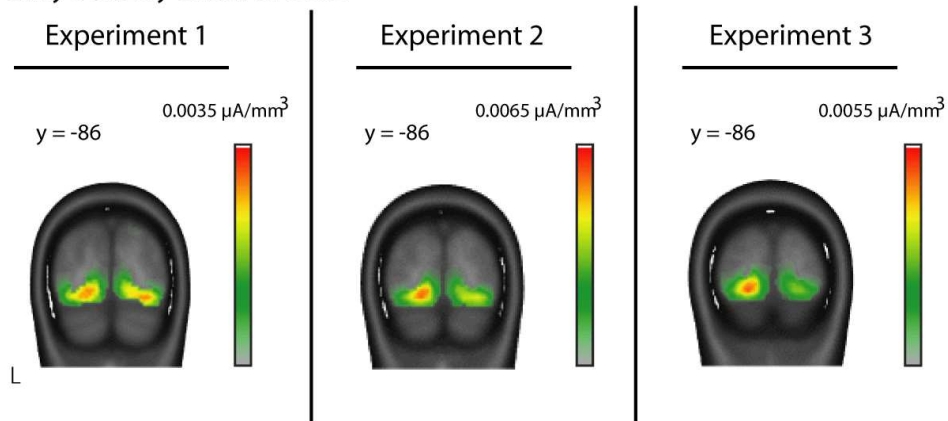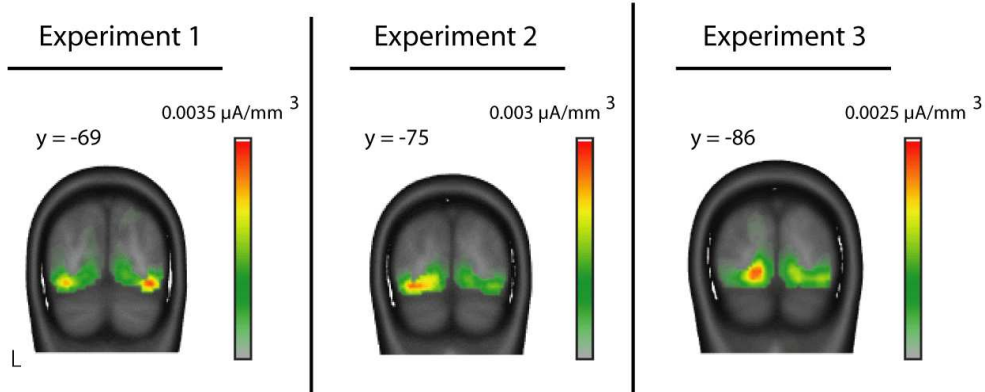
Figure 3.30. Estimated sources for the major components of the sensory effects in the grand-averaged waveforms. . LAURA inverse solutions are represented in units of current source density. (L-left hemisphere, A-anterior)
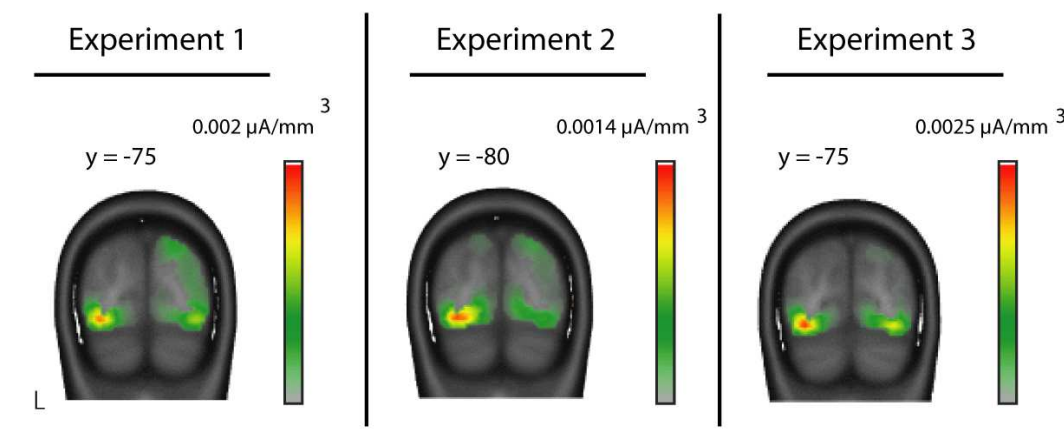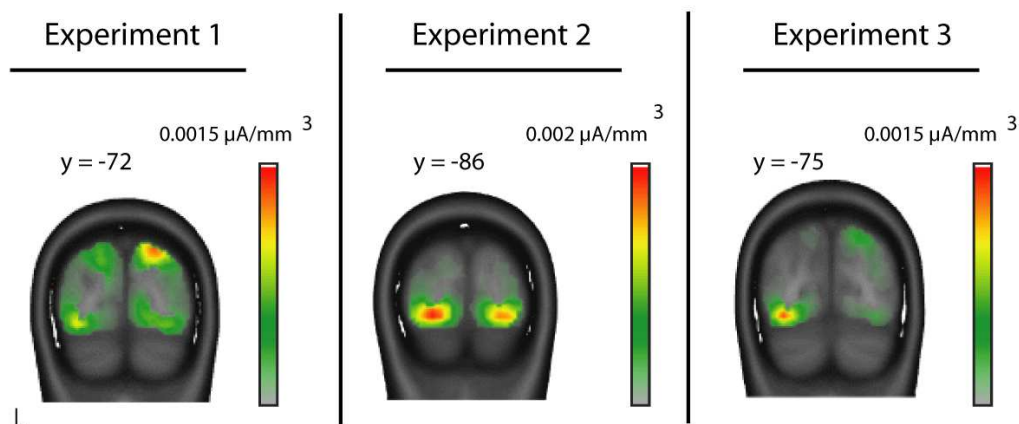
Figure 3.31. Estimated sources for the major components of the attention effects in the grand-averaged waveforms. LAURA inverse solutions are represented in units of current source density. (L-left hemisphere, A-anterior)

Comparison of Sensory and Attention Effects

Experiment 1

y = -80
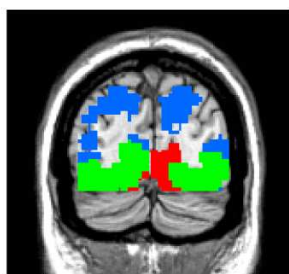
- Early Sensory Effect (red)
- Late Attention Effect (blue)
- Both Sensory and Attention Effects (green)

L

Experiment 2

y = -80
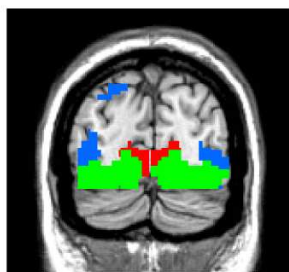
- Early Sensory Effect (red)
- Late Attention Effect (blue)
- Both Sensory and Attention Effects (green)

L

Experiment 3

y = -80
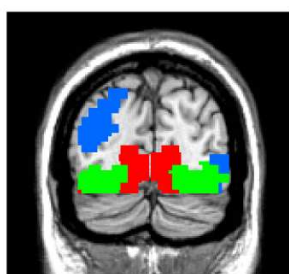
- Early Sensory Effect (red)
- Late Attention Effect (blue)
- Both Sensory and Attention Effects (green)

L

Figure 3.32. LAURA source estimates for the "early sensory" effect and the "late attention" effect indicating the common source estimates in green. Coronal slices shown. (L-left hemisphere)

DISCUSSION

This study was designed to investigate whether all of the features of an object (both task-relevant and irrelevant) are selected when that object is attended. Moreover, the aim was to assess whether the attention effects seen in previous studies would generalize to more ecologically valid stimuli consisting of features processed in the ventral stream that included more structure, such as edges and corners. In addition, this study was intended to further investigate the neural signs of selection of a task-irrelevant feature (color) of an object when the object is not defined by motion, as it was in a previous study by Schoenfeld et al. (2003). In particular, the temporal dynamics of color binding were investigated for objects defined by geometric shape. The timing of the binding of shape and color was determined by comparing two main effects of interest: 1) the sensory effect of color and 2) the effect of attention to shape on the processing of a task-irrelevant color. The sensory effect of color was defined as the neural activity associated with color processing driven by the physical color difference of the stimuli presented in the display. The effect of attention on the sensory effect of color (hereafter referred to as the "attention effect") was defined as the neural activity elicited when attention to shape resulted in selection of the task-irrelevant color feature. In other words it was investigated whether the selection of an irrelevant color would occur when a specific shape object was attended versus unattended.

Based on the previous study (Chapter 2), it was expected that the presence of color in the display would result in an early modulation of the evoked potential. However, it was unclear whether 1) paying attention to one of two overlapping shapes would result in selection of the irrelevant color feature thus providing evidence for the selection of the entire

object (spreading from task relevant to irrelevant features) and 2) if an attention effect was found, whether its distribution and timing would be similar to the sensory effect or occur later in time. Based on the findings of the prior "attention to orientation" study (Chapter 2), as well as previously reported by Schoenfeld and colleagues (2003), differential processing of the task-irrelevant color feature was expected to occur when an object was attended versus when unattended. Moreover, this attention effect was not expected to be a direct modulation of the early sensory effect; instead, the attention effect was predicted to occur later in time. In fact, this is what was observed in the current study.

In summary, the results of this study indicate that:

- The sensory effect associated with the presence of color occurs at an early stage of processing in the visual cortex.

- Paying attention to an object results in modulation of processing of its irrelevant color feature, therefore providing evidence that object-based attention spreads to task-irrelevant features.

- This modulation is delayed with respect to the initial processing of the color.

- Therefore, the binding of the task-irrelevant feature takes additional time to occur.

In order to establish the reliability of these effects, three complementary experiments were conducted. In the first experiment, a large number of overlapping ovals and rectangles of differing sizes were presented. In the second experiment, the presentation of ovals or rectangles in the foreground was counterbalanced, and only a subset of the stimuli was used.

For the third experiment, the difficulty of the discrimination of ovals and rectangles was equated in order to rule out a difference in discrimination difficulty as the reason for the observed effects.

The effect of attention on task-irrelevant color processing

The effect of attention on task-irrelevant color processing was determined by the comparison of the ERPs elicited by the color red on the attended versus the unattended shape. As presented in the results section, there were two attention-related difference components, a positivity peaking at 225 ms and a later negativity peaking at 315 ms observed in all three experiments. These results show evidence for the occurrence of object-based attention, using this paradigm.

The first attention-related component, the bilateral dorsal/occipital positivity peaking at 225 ms "the early attention effect", became significantly different from the baseline at an average of 200 ms (210 ms, Exp.1; 180 ms, Exp. 2; 210 ms, Exp. 3). This component had estimated sources in ventral occipital cortex, consistent with the sources estimated for the sensory effects. While the estimated cortical sources were consistent between the sensory effects and the early attention effect, the polarity and scalp distribution were dissimilar. It could be the case that the summation of several latent components gives rise to the distribution seen in the early attention effect, including the components related to color processing. Thus, it is likely that the scalp distribution reflects not only the projection of the activity of areas involved in color processing but also additional processing areas, perhaps of sources associated with the control of object-based attentional processing.

The "late attention" difference component, a medial occipital negativity peaking at 315 ms, was similar in scalp distribution and polarity to the "early sensory" effect indicating similar neural generators, as also observed in the LAURA source analysis. These findings support the integrated-competition model (Desimone & Duncan, 1995; Duncan, Humphreys, & Ward, 1997) which predicts that selection of an object in a visual scene containing several objects occurs as a result of enhanced activity in all of the feature modules coding the properties of the selected object, both task-relevant and irrelevant. As in the attention to orientation study (Chapter 2), these findings suggest that the binding of the task-irrelevant feature results from differential activity in similar areas that process the initial selection of color information. The integrated-competition model is the closest fitting model available to support the data presented in this study because it does not rely on space-based selection, as do other models of attention, such as feature-integration theory (Treisman & Gelade, 1980).

In sum, the results of this study present novel evidence that previously reported findings on object-based attention demonstrating the spread of attention to both task relevant and irrelevant features within the selected object can in fact be generalized to at least structured objects with different shapes. Interestingly however, post-hoc analysis parsing the effects to either oval or rectangle conditions show a more robust effect for ovals. Further investigation would be needed to adequately explore this difference. For instance, amongst other possibilities, it can be hypothesized that the continuity of the curve of the oval stimuli might allow for better integration of all of the features of the object than the jagged outline of the rectangle stimuli. Future research using a wider variety of shapes should be able to provide further insight into the novel findings observed in this study.

The timing of feature binding

As it was inferred in the Schoenfeld et al. study, it was considered here that the binding of the color and shape occurred at some point in time between the onset of the processing of color in the visual system (the sensory effects), and the onset of the attention effects. Thus, the time required for the binding of color and shape can be estimated by subtracting the sensory effect from the attention effect. In this study, this subtraction provides an average estimate of 110 ms for the binding of color and shape (Experiment 1, 120 ms; Experiment 2, 80 ms; Experiment 3, 130 ms). While this seems like a relatively large range, the variation in onset of the sensory effect alone was about 20 ms across experiments. Moreover, when considering overall performance, participants performed the best in Experiment 2, followed by Experiment 1 and lastly Experiment 3, which is interestingly consistent with the timing of their binding estimates. These results suggest that the difference in binding times may be correlated with the difficulty of target discrimination. As such, the effort required for shape discrimination may influence the amount of time it takes for the spreading of attention through the object to select its color. A delay of this kind was previously shown in a study examining the timing of selection for conjunctions of shape and color (Smid, Jakob, & Heinze, 1999). In that study, participants were instructed to press a button when a *specific* conjunction of color and shape were presented. The difficulties of shape and color discrimination were varied, and the ERP components typically elicited in that paradigm (the selection negativity, selection positivity, and N2b) were all delayed by 50 ms or more when shape or color was hard to discriminate. Similarly, it is possible that in the current study, the selection of a task-irrelevant feature is delayed when the discrimination of

shape in general is difficult. Future experiments in which the difficulty of object

discrimination is manipulated parametrically would need to be conducted in order to assess

this hypothesis.

The shape effect

An unexpected, yet consistent, finding throughout this study was the occurrence of a

shape effect. The "shape effect" was characterized by a large, broad central-parietal

difference when attending to one shape versus another when both stimuli were gray, and was

driven by a negative shift in the waveform when participants attended to ovals. It is unclear

what this effect is indexing. It is not due to stimulus differences because the effect is

calculated by comparing the same stimulus with only a change in attention from one shape to

another. While this effect has a similar distribution to the late positive component "P300",

considered to be a measure of the timing of perceptual classification of target versus non-

target stimuli (Polich, 2007), it is distinct from the P300. When examining the P300

waveforms to target stimuli (Figure 3.28), the shape effect is distinctly seen in the middle

column when comparing the circle and square target difference waves. Moreover, this shape

effect peaks at about 300 ms as seen in the greater negativity to circle targets, but it is

followed by the traditional P300. In addition, the shape effect is also seen in non-target

trials. The possibility of differential difficulty in discrimination of the ovals versus

rectangles being the cause for this effect was discarded in experiment three, where the

discrimination of circles and squares was matched and the shape effect persisted. Although

interesting, the shape effect is not directly relevant to the research question pursued here.

However, future experiments could adequately investigate what exactly the functional significance of this effect is indexing.

CONCLUSIONS

The reported findings indicate that attention can occur in an object-based manner, spreading to all features of the selected object. Furthermore, the effect of attention on a task-irrelevant color feature can be generalized to different objects and is associated with two components that occur later in time than the initial sensory processing of color. When attending to a stimulus shape, the binding of a task-irrelevant color feature takes approximately 110 ms to occur after the sensory registration of color in the display. The source of the selection of the task-irrelevant features of an object occurs in similar cortical regions to those associated with the processing of that feature. This provides evidence of biased competition in favor of all features of the attended object across cortical areas.

CHAPTER 4: GENERAL DISCUSSION AND CONCLUSIONS

A growing number of behavioral and neuroimaging studies indicate that the selection of visual items for further processing in order to achieve a given task goal may occur in an object-based manner. Such object-based selective attention complements other mechanisms of selection, such as space-based and feature-based selection. However, little is known about the extent to which all of the constituent features of an attended object are processed when that object occurs in a multi-object scene. Only a few studies have started to explore the neural basis of this phenomenon and the question of whether attention spreads through all the features (task-relevant and irrelevant) of the attended object. If so, selective object-based attention would be associated with an overall spread of attention such that all of the constituent features of an object (i.e. its color, form, orientation, etc) are bound together into a unified object, and all attended.

In order to further our understanding of this neuropsychological mechanism, this dissertation was designed to investigate: 1) The occurrence of the abovementioned attention spread within the entire selected object for various types of objects, establishing it as a potential general mechanism and 2) If in fact this spread of attention occurs, what is the associated timing for that selection and are there differences associated with each specific object type and/or dimension?

The results reported here provide evidence that object-based attention does occur for a variety of object types but that timing of the binding of a task-irrelevant feature may differ based on object type and task demands.

Previous evidence for the spread of attention

Few studies have explored the brain mechanisms for the spread of attention through all of the features of an object. The first reported study, with the use of fMRI, investigated the neural processing of overlapping face and house stimuli and concluded that attention spread to task-irrelevant features of the objects, such as motion (O'Craven, Downing, & Kanwisher, 1999). However, while providing important initial evidence that task-irrelevant aspects of objects are selected in their respective cortical areas, the timing of this selection could not be determined due to the inherent temporal limitation of the fMRI method.

The work of Schoenfeld and colleagues (2003) extended the work of O'Craven et al. (1999) by also providing evidence that when an object is attended, all of the features of the attended object are selected for further processing. In addition to the use of fMRI to determine which brain areas were involved in the selection of the task-irrelevant feature, Schoenfeld et al. (2003) also utilized EEG and MEG methods in order to gain important timing information about that selection. In that study, the processing of a given color in a display of intermixed moving dot surfaces was compared to the processing of this color when it was part of the attended surface versus on the unattended surface. The authors provided evidence that not only does selection of all of the features of a grouped array object occur, but also that the timing for selection of a task-irrelevant feature of an object takes about 50 ms from its initial sensory registration. Moreover, the attentional selection of the task-irrelevant feature was accomplished by additional processing in the same brain regions typically associated with the original processing of that feature (i.e. differential activity in color processing areas when color was the task-irrelevant feature). While this study provided

initial and fundamental spatial and temporal insights into the brain processes involved in the selection of multi-feature objects, it is unclear whether the results were specific to the particular set of stimuli/objects used, in particular, to the use of motion-defined objects. The studies in this dissertation sought to determine whether the Schoenfeld et al. (2003) findings can be generalized to different types of objects, more specifically, grouped arrays defined by orientation (Chapter II) and objects defined by geometric shape (Chapter III). Since orientation and shape are common defining and identifying features of objects in the real world, they were selected to provide ecological validity to the investigated object types.

Based on the Schoenfeld study, it was hypothesized that

I) There would be a spread of object-based attention throughout all of the features of the object, resulting in differential processing of the task-irrelevant feature when it belonged to the attended versus the unattended object.

II) The spread of attention to the task-irrelevant feature should be reflected in an ERP component having the same scalp distribution (and hence neural source) as an earlier component reflecting the sensory effect of color.

III) If the attention effects observed by Schoenfeld et al. (2003) are indicators of a general mechanism independent of the specific stimuli used and task requirements, then the timing of the binding of color to the attended object and the scalp distribution of the associated ERP should be the same as previously reported.

IV) If the timing of binding of a task-irrelevant color feature and the ERP scalp distribution is affected by the defining object feature and/or task requirements,

then it would be concluded that different mechanisms of object-based attention

are involved for different object types.

General findings

The results of the studies in this dissertation replicated and extended previous work

on object-based attention by demonstrating that:

I) Attention spreads to the task-irrelevant color feature of an object, providing evidence

for the selection of objects as wholes.

II) This spread of attention occurs for a variety of types of objects.

III) The selection of a task-irrelevant color feature by object-based attention does not

occur during the initial processing of the color, but rather its selection takes additional

time to be bound to the attended object.

IV) The timing of binding of the task-irrelevant feature may vary depending upon the

specific type of object and task demands.

V) The object-based attentional selection of the task-irrelevant feature occurs in cortical

areas that typically are associated with the processing of that feature.

Discussion of specific findings

The sensory effect

The sensory effect of color in the display was marked by an early negative deflection

in the ERP difference wave, which became significant at an average of 100 ms at focal,

occipital electrode sites and was accompanied by a broad positivity over the rest of the scalp.

This sensory effect was present in both the "attention to orientation" and the "attention to

shape" studies and was localized to lateral extrastriate sources in the lingual and fusiform

gyri, areas known to be involved in color processing (Clark, et al., 1997; Corbetta, et al., 1991).

<u>Comparison to the Schoenfeld et al. (2003) study</u>

In addition to the current study, color processing has been previously shown to occur by 100 ms using the ERP method (Paulus et al., 1984; Schoenfeld et al., 2007). However, interestingly, the sensory effect reported by Schoenfeld et al. (2003) occurred much later. In that study, the sensory effect was a positive component, delayed by at least 80 ms when compared to the current study. It is unclear why the "sensory effect" occurred so late in the Schoenfeld and colleagues study, but it is possible to consider that the specific experimental design may have influenced it. Since the ERP analysis was time-locked to the onset of dot-movement, perhaps the addition of color to the onset of the dot-movement delayed the sensory effect.

Attention effects

<u>The spread of attention to a task-irrelevant color feature: evidence for object-based attention</u>

The main effect of interest, an "attention effect" for the irrelevant color feature, was observed in all of the experiments included in this dissertation, thus providing evidence for the spread of attention through multiple features (both task-relevant and irrelevant) in various types of objects. These results suggest that attention can operate in an object-based manner, selecting not only one object over another but also, multiple features of an attended object. Even though the observed effects presented some similarities and some differences associated with each specific type of object attended, an attention effect was always present. As such, these studies extend previous findings of the selection of a task-irrelevant color

feature to a variety of object types, designed to include stimuli defined by ecologically valid features such as geometric shape and orientation.

<u>Common "attention effect" for the "attention to orientation" and "attention to shape" studies</u>

The common "attention effect" observed in both the "attention to orientation" and the "attention to shape" studies, was the presence of a ventral occipital negative component that became significant on average at 290 ms. Thus, this effect appears to be a general finding of the spread of attention to a task-irrelevant color feature, regardless of the type of object attended (grouped line arrays or shape) or the task performed. Moreover, this attention effect was localized to source maxima in the fusiform gyrus for both types of objects. Therefore, the effect of attention on task-irrelevant color processing involves cortical areas typically associated with the encoding of color, suggesting a spread of attentional modulation from the task-relevant object feature to the task-irrelevant color feature.

<u>An additional earlier attention effect</u>

The later attention effect observed in both experiments was accompanied by an earlier effect in the "attention to shape" study, indicating that some of the components associated with the effects of attention on task-irrelevant features may vary depending on specific stimulus parameters or task conditions. This earlier attention effect for shape stimuli was represented by a bilateral dorsal/occipital positive component that became significant at an average of 200 ms and was observed in all three of the experiments. This suggests that the effects of attention on task-irrelevant feature processing may consist of several components, and that some of the components may vary depending on the different types of objects that are the focus of attention.

Comparison to the Schoenfeld et al. (2003) study

The "attention effect" observed in the Schoenfeld and colleagues study was represented by a midline parietal positive component that became significant at 230 ms. The attention effect in that study has a similar distribution to the early attention effect (200 ms) observed in the attention to shape study. However, while the Schoenfeld et al. (2003) effect began at 230 ms, it persisted for another 200 ms. The Schoenfeld et al. article also does not report the scalp distribution of the later portion of the attention effect (from 300 ms – 450 ms). So it is also not known whether the distribution of the attention effect changed over that interval, which would indicate more than one attention effect, or whether the effect had a similar distribution over the entire interval of the difference waveform. This information would be crucial to assess if one or more effects were elicited by their experimental paradigm.

Comparison between the sensory and attention effects

While there is a difference in timing between the sensory and attention effects, the scalp topography between the early sensory and late attention effects are similar, suggesting that these effects originated from similar cortical sources. Importantly however, both of these effects (the two sensory and the two attention effects) were localized to color processing areas of cortex. Interestingly, the LAURA source analyses indicated that in addition to the visual areas active in the sensory comparison, the source of the "late attention" effect also included a more extensive estimation of sources including some sources in parietal cortex. This extension of the estimated cortical sources for the attention effects may be associated with a role for the parietal cortex in the selection of task-irrelevant object

features or could be associated with the fact that the attention effects occurred fairly late in

processing time, thus multiple brain areas/networks may be active in addition to those purely

involved in color processing. While the resolution of ERP source analysis methods do not

allow for precise spatial localization of effects, the results described indicate that the sensory

and attention effects do have common sources, but that the attention effects may have

engaged a broader network of cortical areas.

Feature binding times

As it was inferred in the Schoenfeld et al. (2003) study, it was also estimated here that

the timing for the binding of the task-relevant feature and the task-irrelevant color feature

occurred at some point in time between the onset of the processing of color (i.e. "the sensory

effect") and the onset of the "attention effects". As such, for each study reported here,

different estimates for the binding time of the task-irrelevant color feature were obtained.

This subtraction provides an average estimate of 180 ms for the binding of line orientation

and color and an average estimate of 110 ms for the binding of shape and color.

Comparison between the binding times for "attention to orientation" and "attention to shape"

A few hypotheses can be put forward to account for the reported difference in binding

times. One hypothesis is associated with the perceptual construction of the objects. For the

"attention to orientation" study, attention is needed to link the line segments of the grid to

form the vertical and horizontal lines. Whereas, in the "attention to shape" study, the objects

are defined by a combination of semantic memory retrieval and closure. Perhaps, the initial

segmentation process in the orientation study is more demanding than the initial

segmentation process in the attention to shape study, effecting the binding times of task-irrelevant color feature for each study.

Another hypothesis is that the specific task requirements for each study may have impacted the binding times. For the "attention to shape" study, the task required a judgment of a change in the entire shape of the object attended, in which color was incorporated, but not relevant. In the "attention to orientation" study, while the distribution of attention over the entire group of oriented lines was encouraged, target detection was specific to the thickening of a line of the attended orientation, not the whole object (i.e. ensemble of lines of the indicated orientation). Future experiments would need to be conducted to determine conclusively the impact of these variables on the feature binding process.

Timing of the attention effects compared to findings of rapid object processing

The timing of the "attention effects" and subsequent binding time estimates for the current studies occur rather late in terms of visual processing time. Recordings from human patients have demonstrated that visual stimuli can activate the frontal eye fields in as little as 45-60 ms (Kirchner et al., 2009) and in other cases as early as 100 ms after stimulus presentation (Blanke et al., 1999). In addition, object categorization may also occur relatively rapidly, for example, differences in ERPs based on the detection of the presence of an animal in a rapid stream of images, can occur within 150 ms of stimulus presentation (Thorpe, Fize, & Marlot, 1996). Those results suggest that the processing of object features for identification is complete within a rather short period of time. In the current studies, the attention effects (selection of the task-irrelevant feature) were observed 200-290 ms after stimulus presentation. This timing seems rather late in visual processing considering that an

object may be identified prior to that time. One possibility for this timing discrepancy is that in the Thorpe and colleagues study, key object features could have been identified during the 20 ms of scene presentation that could have led to a rapid detection of the target object in the display.

This hypothesis has been examined by Evans & Treisman (2005) in which they suggested that this rapid detection occurs as a result of the parallel detection of feature sets characteristic of the target, instead of due to the creation of a "high-level visual representation". For instance, in one of their studies, stimulus streams which included distractors that shared features with the task-specific object category (such as people in a stimulus stream where non-human animals were to be detected) resulted in fewer correct animal detections. In addition, fewer than half of the detected targets could be subsequently identified (e.g. I saw a rabbit.). Based on their results, they concluded that, "an initial rapid pass through the perceptual hierarchy registers many features in parallel", and this is followed by a reentry process in which focused attention selects objects of interest and binds their features to form object representations.

Timing of the attention effects as compared to the timing of the disruption of feature binding in normal subjects

The timing of the attention effects in the current studies is consistent with the timing of brain stimulation required to disrupt feature binding in normal participants. Braet & Humphreys (2009) investigated the influence of transcranial magnetic stimulation (TMS) on the report of illusory conjunctions in normal participants. As described in the introduction, illusory conjunctions are false combination of two features of two objects into the report of

one object after a rapidly presented visual search task (for example, the report of a red F

target when a red X and blue F were actually presented). Their study showed that TMS

pulses over the right parietal lobe (two pulses, one at 150ms and another at 200 ms) and later

(tested up to 250 & 300 ms after stimulus presentation) resulted in illusory conjunctions in

non-disordered (normal) participants, whereas stimulation at 0-100 ms after had no such

effect. This suggests that the findings in this dissertation of a late onset of the spread of

attention to task-irrelevant object features is similar to the late process of feature binding

found in the Braet & Humphreys (2009) study.

Comparison of the timing of the attention effects with studies of the detection of task-
relevant feature conjunctions

The timing of the attention effects in the current studies is also consistent with the

timing estimated in ERP studies investigating the detection of conjunctions of features

(Anllo-Vento & Hillyard, 1996; Previc & Harter, 1982; Smid, Jakob, & Heinze, 1999). The

ERP response to task-relevant conjunctions of features typically occurs between 145-284 ms

Karayanidis & Michie, 1997; Smid, Jakob, & Heinze, 1999). This estimate may vary

depending on the difficulty of the task performed. The findings of the current studies

indicate that for a variety of objects, the binding of a task-irrelevant feature occurs during a

similar time period as the detection of a conjunction of object features. Although, this is a

broad time estimate for feature binding, in general, the current and previous findings suggest

that the binding of object-features (task-relevant or irrelevant) occurs at a fairly late time in

the time course of object processing rather than as a direct amplitude modulation of the early

sensory effect comparison.

Significance of the findings

To enable an estimate of the time required for binding, these studies (both Schoenfeld et al. (2003) and the studies presented here) relied on the use of color versus its absence to enable a time marker of the processing of color in the display. While the use of one colored and one achromatic object was necessary to enable an estimate of binding time, this manipulation could result in the introduction of another variable, color saliency. Thus, any differences in the saliency of one object versus another were controlled by 1) equalizing the subjective luminance of the two colors and 2) by using the same stimulus for the "attention effect" comparison, such that only attention to one object versus another was manipulated. There were no differences in luminance between the two objects; however another concern could be reasoned. The presence of color itself could have an influence on attentive processing. For instance, the color itself may have captured attention even though the task required attention to remain focused on the object indicated at the beginning of a block of trials. If this were the case, when attending to a gray object while the other object was colored, attention may have initially been drawn to the colored object and then reallocated to the gray "to be attended" object.

A previous study by Weber and colleagues provides relevant insight into the possibility of the switching of attention between overlapping objects (Weber, Kramer & Miller, 1997). In their paradigm, two overlapping outlines of shapes of different colors were presented. Participants were asked to judge whether a particular color/shape conjunction was present. The two features could occur on the same or on different objects. Response times were slower and the amplitude of the N1 ERP component was larger when the features

appeared on two different objects than on the same object. One interpretation of the results of their study is that when the two features were located on different objects, it may have required a shift from the first attended object to the second to determine if both features were present in the display.

Building from this previous report, it is hypothesized here that if a shift from an unattended colored object to the "to be attended" gray object were to occur, it should be evidenced as a difference in the N1 component, with a larger negativity for the "unattended red" condition versus the "attended red" condition. This pattern of effects was not observed and no early "N1" effect was found for the "attention effect" comparisons. As such, it is reasoned that an initial, reflexive shift of attention to the red stimulus in the displays did not occur during the studies presented here. Most importantly, the results from these studies provide evidence for differential processing of a task-irrelevant color feature, thus indicating a spread of attention from the task-relevant feature to the task-irrelevant feature of the object.

Default object-attention mode?

The findings presented in this dissertation suggest that once visual information in our world is structured into objects either by being grouped by bottom-up Gestalt mechanisms such as closure, by top-down mechanisms such as attention or memory, or a combination of both mechanisms, that processing of a part of an object may lead to a spread of attention to other features of that object. This spreading of attention through multiple features of an object may play an important role in tracking objects through time as described by "object-file theory" (Kahneman & Treisman, 1984; Kahneman, Treisman, & Gibbs, 1992). An object file has been described as a temporary representation that stores information about the

features of an object that is updated with changes to the object. In the current studies, each new trial presentation would require the creation of new object files, one for each of the objects in the display. The "attention effects" found in the studies included in this dissertation suggest that the task-irrelevant features of an object may also be encoded in an object file. Why might the encoding of task-irrelevant features of an object occur? As eloquently pointed out by Melcher & Vidnyánszky (2005), " Since observers and objects in the world are frequently in motion, object representations must be equally dynamic, allowing specific features that were not previously perceived or diagnostic to become visible and heuristic markers of the same object in another instant of time." Thus, the encoding of objects as wholes may serve an important role in tracking objects throughout time and space.

There may be conditions under which this default "object-based" processing can be disrupted, for instance, when the different features of an object are assigned conflicting responses. In the current studies, the task-irrelevant feature was never assigned a behavioral response (i.e. it was always task-irrelevant). However, behavioral and ERP evidence for the suppression of a task-irrelevant feature of an object was obtained by Nobre and colleagues (Nobre, Rao, & Chelazzi, 2006) when a previously ignored object feature was repeated as the task-relevant object feature in a subsequent trial. In studies such as these, the behavioral response is slowed when the previously ignored stimulus is presented as a task-relevant stimulus (i.e. a negative priming effect). In their study, they found evidence for negative priming, which they interpreted as feature-based selection of the object. However, because the task-irrelevant feature was task-relevant in other blocks of the experiment, a slowing or suppression of the response to the previously ignored object feature, instead of selection of

that feature as predicted by object-based attention, would be expected. Thus, while we may encode the task-irrelevant features of an object by default, suppression of the response to a task-irrelevant feature may occur if that feature was previously associated with a conflicting behavioral response.

Expansion of theories of object-based attention and feature binding

The research presented throughout this dissertation suggests that attention selects objects as wholes for further processing as predicted by biased competition theory (Desimone & Duncan, 1995) and in particular, its integrated competition hypothesis (Duncan, 1996; Duncan, Humphreys, & Ward, 1997). The integrated competition hypothesis proposes that the competition between two objects for representation may be resolved by top-down goal directed behavior (e.g. selection of one or another shape). This theory predicts that there should be widespread selection of the features of the attended object, in addition to widespread suppression of the features of the unattended object. Thus, for instance, in the current shape study, it would be predicted that once the attended shape became dominant in cortical areas where shape is processed, this facilitation would then spread to the cortical areas that process the other features of the object (e.g. color processing areas if the attended object was colored).

The predictions of the integrated competition hypothesis are consistent with the effects found in the research performed for this doctoral dissertation. Differential processing of the task-irrelevant color feature was indicated based upon the "attention effects" seen when color was a part of the attended object versus the unattended object. This provides evidence that the instruction to attend to one object results in the dominance of that object,

and as such, color was also selected when it was a part of that attended object. Furthermore, these "attention effect" difference wave components were localized to occipital brain areas associated with the processing of color (i.e. the fusiform gyrus). The source estimates for these "attention effects" were similar to the source estimates for the "sensory effects" indicating that there was differential processing of color based on whether it was a part of the attended object.

Other theories that address feature binding, such as feature integration theory (Treisman & Gelade, 1980; Treisman, 1993; Treisman, 1998) could not account for the data presented here because the objects that competed for attention were completely overlapping in spatial extent. Feature integration theory relies upon a spatial focus of attention to select one object versus another in order to allow for a binding of the features of the selected object. Thus, due to the spatial overlap of the objects, the selection of color could not be based upon a linking of color and the task-relevant attended feature (shape or orientation) at a given attended location.

While the studies in this dissertation provide additional evidence for integrated-competition, they do not directly address the neural mechanisms by which selective activation spreads from one cortical area to another. It may be the case that top-down attentional goal signals derived from the frontal and parietal cortices specifically lead to enhancement of the features of the objects (see Yantis & Serences, 2003 for a review). In this model, "a top-down signal that originates in the prefrontal cortex and reflects current behavioral goals arrives at the superior parietal lobule, which responds by transiently increasing its activity. The transient switch signal is received both by extrastriate neural

populations and by the intraparietal sulcus and perhaps other structures, which then

continuously maintain the new attentive state by providing a constant biasing signal to

extrastriate cortical regions" (Yantis & Serences, 2003). LAURA source analysis in this

dissertation provides evidence for a role of the parietal cortex in object-based attention. An

extended alternative that addresses the mechanism more specifically could be the "binding-

by-synchrony" hypothesis, which proposes that synchronous oscillations in the gamma range

(30-60 Hz) allow for the perceptual binding of various features or segments of an object to

occur by synchronizing activity in separate neural populations (Gray & Singer, 1989). This

hypothesis provides a temporal means of binding the features of an object. Research within

the next decade should provide further insight into the neural mechanisms of feature binding.

FUTURE RESEARCH

There are still several open questions associated with the nature of object-based attention to be pursued in future research. Amongst other possible avenues of research, two questions seem to be logical next steps as discussed below.

Are other types of task-irrelevant features of an object selected? If so, with what timing and cortical localization?

In the current studies, the selection of a task-irrelevant *color feature* was tested. Would the selection of other features for example, spatial frequency or motion also occur in a paradigm such as this one? The results of several behavioral studies suggest that a variety of task-irrelevant features may be selected when one feature of an object is selected (Kristjánsson, 2006; Melcher, Papathomas, & Vidnyánszky, 2005; Melcher & Vidnyánszky, 2006; Sohn, Papathomas, Blaser, & Vidnyánszky, 2004). However, an indication of the neurophysiological mechanisms of the attention effect using different task-irrelevant features would provide further insights into the timing and cortical networks involved in such selection.

Under what conditions does the selection of task-irrelevant features of an object occur?

Only a few studies have sought directly to determine the conditions under which feature-based versus object-based attentional selection is dominant (Chen & Cave, 2006; Wegener, Ehn, Aurich, Galashan, & Kreiter, 2008). Although, the studies presented here were not designed to discriminate which specific conditions can lead to either feature or object-based attention, they can provide some insights. Both in the current study and in the

Schoenfeld et al. (2003) report, the experimental design included objects in which the task-irrelevant feature was incorporated into the defining characteristic of the object (for example, the outline of the shape). As such, in the attention to shape study, whether or not the selection of the task-irrelevant feature arises due to this specific stimulus configuration is a question that merits future investigation as well as other potential factors that would determine the selection of an entire object rather than just a task-relevant feature.

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