BRAIN RESEARCH

Research Report

Spatial attention facilitates selection of illusory objects: Evidence from event-related brain potentials

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ABSTRACT

The relationship between spatial attention and object-based attention has long been debated. On the basis of behavioral evidence it has been hypothesized that these two forms of attention share a common mechanism, such that directing spatial attention to one part of an object facilitates the selection of the entire object. In a previous study (Martinez, A., Teder-Salejarvi, W., Vazquez, M., Molholm, S., Foxe, J.J., Javitt, D.C., Di Russo, F., Worden, M.S., Hillyard, S.A., 2006. "Objects are highlighted by spatial attention." J. Cogn. Neurosci. 18(2): 298–310) we used recordings of event-related potentials (ERPs) during a paradigm modeled after that of Egly et al. (Egly, R., Driver, J., Rafal, D.R., 1994. Shifting visual attention between objects and locations: evidence from normal and parietal lesion subjects. J. Exp. Psychol. Gen. 123(2) 161–77) to investigate this relationship. As reported in numerous studies of spatial attention, we found the typical pattern of enhanced neural activity in visual cortex elicited by attended stimuli. Unattended stimuli belonging to the same object as the attended stimuli elicited a very similar spatiotemporal pattern of enhanced neural activity that was localized to lateral occipital cortex (LOC). This similarity was taken as evidence that spatial- and object-selective attention share, at least in part, a common neural mechanism. In the present study we further investigate this relationship by examining whether this spread of spatial attention within attended objects can be guided by objects defined by illusory contours. Subjects viewed a display consisting of two illusory rectangular objects and directed attention to continuous sequences of stimuli (brief onsets) at one end of one of the objects. Stimuli occurring at irrelevant locations but belonging to the same attended object elicited larger posterior N1 amplitudes than that elicited by unattended objects forming part of a different object. This object-selective N1 enhancement was localized to lateral occipital cortex. The present data support the hypothesis that the allocation of spatial attention can be guided by illusory object boundaries and that this allocation strengthens the perceptual representations of attended objects at the level of visual area LOC.

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1.   Introduction

Visual attention may be directed voluntarily to specific locations or to specific objects within the visual fields (Scholl, 2001). Location-selective attention effects are typically demonstrated in spatial cueing experiments in which stimuli at a pre-cued (attended) location are found to be detected and discriminated more rapidly and accurately than are stimuli at uncued locations (e.g., Posner et al., 1980; Luck et al., 1994). On the other hand, evidence is mounting that attention can be allocated to entire perceptual objects defined in terms of their distinctive boundary contours or cohesive groupings. In support of such object-based selection are findings that (1) dividing attention between stimulus elements within the same object is generally more efficient than dividing attention between separate objects (e.g., Duncan, 1984; Watson and Kramer, 1999; Rodriguez et al., 2002) and (2) paying attention to one part of an object results in facilitated processing of stimuli in other parts of the object (Egly et al., 1994; Abrams and Law, 2000; Lamy and Egeth, 2002).

While there is a general agreement that visual attention has both spatial-selective and object-selective components, it is not clear how these two forms of selection are related. One hypothesis, which might be characterized as "object-guided spatial selection" proposes a direct relationship, such that directing spatial attention to one region within an object results in a top-down facilitation of sensory processing that spreads throughout the object's boundaries and thereby strengthens the sensory representation of the entire object (Weber et al., 1997; Davis et al., 2000). An alternative hypothesis accounts for object-selective attention effects by proposing that locations within a cued object's boundaries are given higher priority for target search than are locations within uncued objects (Shomstein and Yantis, 2002; Yantis and Serences, 2003). In contrast with the object-guided spatial selection hypothesis, this "attentional prioritization" mechanism is assumed to act by controlling the order of locations to be searched rather than by facilitating early sensory-level processing. A third hypothesis proposes that object-based attention selects object representations that are not coded in terms of their spatial coordinates (Duncan, 1984; Vecera and Farah, 1994). This latter hypothesis suggests that object- and space-based selections may utilize entirely different mechanisms.

1.1.   Physiological evidence

Recent physiological studies have provided support for the object-guided spatial selection hypothesis. Using a design patterned after that of Egly et al. (1994), Müller and Kleinschmidt (2003) used fMRI to examine neural activation in early visual cortical areas following an attention-directing cue to one end of a bar-shaped object. Activation was found not only at the retinotopic representation of the cued end of the bar but also (to a lesser extent) at the cortical region corresponding to the uncued end of the same bar. This object-selective fMRI activation was taken as evidence that the deployment of spatial attention is guided by the presence of objects. Due to the low time resolution of the hemodynamic response, however, it is difficult to ascertain the exact timing of object-selective processing in the different cortical regions.

He et al. (2004) recorded event-related brain potentials (ERPs) in an Egly-style paradigm, in order to study the timing of object-selective attention effects. In their design a peripheral cue directed attention to a probable target location at one end of a bar-shaped object. It was found that a posteriorly distributed N1 component (at 150–180 ms post-stimulus onset) was enhanced for targets occurring at both cued and uncued locations within the object, which provided evidence for an object-based selection mechanism based on modulation of sensory processing in the visual pathways. Similar findings of N1 amplitude modulations associated with object-selective attention have been reported in tasks where subjects attended to one of two superimposed geometric figures (Weber et al., 1997) or superimposed transparent surfaces formed by rotating dot arrays (Pinilla et al., 2001; Rodriguez and Valdes-Sosa, 2006). Rodriguez and Valdes-Sosa (2006) carried out a source localization of the enhanced N1 amplitude associated with surface selection and identified current sources in lateral occipito-temporal, superior temporal, and superior parietal lobes. They concluded that this object-based selection was based on a suppression of the sensory signals from the unattended surface in early extrastriate visual areas.

In a recent study (Martinez et al., 2006), we combined ERPs with fMRI to study both the time-course and the anatomical sources of cortical activity patterns associated with object-selective attention. In yet another variant of the Egly et al. (1994) paradigm, our subjects viewed a display consisting of two bar-shaped objects that were oriented either horizontally or vertically on different runs. The stimuli consisted of brief offsets of the bars' corners, which occurred one corner at a time in random order. The subject was cued to pay attention to the offsets in one corner at a time and to ignore the offsets at the other corners. The task was to judge the shape of the offset stimulus (concave or convex) and to press a button upon detecting the infrequent target shapes.

Attended corner offsets elicited enlarged P1 (80–128 ms) and N1 (160–196 ms) components, which is the typical pattern of ERP enhancement produced by spatial attention (e.g., Di Russo et al., 2003; Hopfinger et al., 2004). In addition, there was a smaller augmentation of the N1 elicited by the offsets at the unattended end of the attended bar relative to the offsets occurring on the unattended bar. This object-selective enhancement of N1 was significant for each of the quadrants. In contrast, the P1 wave did not show any object-selective modulations.

Topographical voltage maps of the N1 modulations produced by spatial attention (attended waveform minus unattended–different-object waveform) and by object-selective attention (unattended–same-object waveform minus unattended–different-object waveform) were nearly identical, suggesting that the two effects arose from a common cortical source. The anatomical locations of these N1 modulations, estimated by dipole modeling, were found to lie in lateral occipital cortex (LOC). These dipole localizations were supported by converging evidence from fMRI obtained in a separate session with subjects engaged in the same task. Spatial-selective and object-selective fMRI activations were found to be situated in the same LOC region as the dipoles for

the N1 amplitude modulations. The Talairach coordinates of these activations corresponded to those previously reported for the LOC (Talairach and Tournoux, 1988) region which has been implicated in object recognition processes (Grill-Spector et al., 2001; Murray et al., 2004).

The results of Martinez et al. (2006) reinforce previous behavioral (Egly et al., 1994; Abrams and Law, 2000; Lamy and Egeth, 2002) and physiological (Müller and Kleinschmidt, 2003; He et al., 2004) studies showing that paying attention to one part of an object facilitates the processing of the entire object. The similar scalp distributions and source localizations of the N1 amplitude modulations strongly suggest that the neural mechanisms of spatial- and object-selective attention overlap substantially. These mechanisms are not identical, however, because a P1 amplitude modulation was only found with spatial attention. This is in accord with previous findings that point to different roles for the P1 and N1 components of the visual ERP in spatial attention (Luck et al., 1994; Hopfinger et al., 2004). Whereas the P1 component appears to index an early stage of processing at which inputs from unattended locations are suppressed, the N1 reflects a subsequent stage of enhanced discriminative processing of attended inputs. The findings of Martinez et al. (2006) thus suggest that spatial attention becomes object-selective at the stage of discriminative processing reflected in the N1, which is in line with the proposal that object-based selection may be mediated in part by spatial attention (Weber et al., 1997; Davis et al., 2000).

The ERP data obtained by He et al. (2004) and Martinez et al. (2006) provide information about the timing of object-selective processing that is not obtainable from previous fMRI studies. The finding of N1 modulation provides critical evidence that spatial attention facilitates the selection of objects as soon as 160–196 ms after stimulus onset, rather than by means of a slower attentional control process. Moreover, the evidence that enhanced object-selective processing in this time frame takes place in the LOC region converges with a large number of fMRI (Malach et al., 1995; Grill-Spector et al., 1998a,b; Grill-Spector et al., 1999; Grill-Spector et al., 2001; Lerner et al., 2002), ERP (Murray et al., 2002; Murray et al., 2004; Rose et al., 2005) and neuromagnetic (Halgren et al., 2003) studies indicating that the LOC plays a major role in object perception and recognition. The results of Martinez et al. (2006) thus point to the conclusion that spatial attention can act to reinforce the perceptual integrity of objects that include the attended location.

1.2. Spatial attention guided by illusory objects

The above-described physiological and behavioral studies support the hypothesis that spatial attention spreads throughout an object's boundaries to facilitate processing of the entire object. An important question in this regard is whether the spread of spatial attention within an object is guided by actual low-level physical boundaries such as lines and contours or by a higher perceptual representation of the object. This question
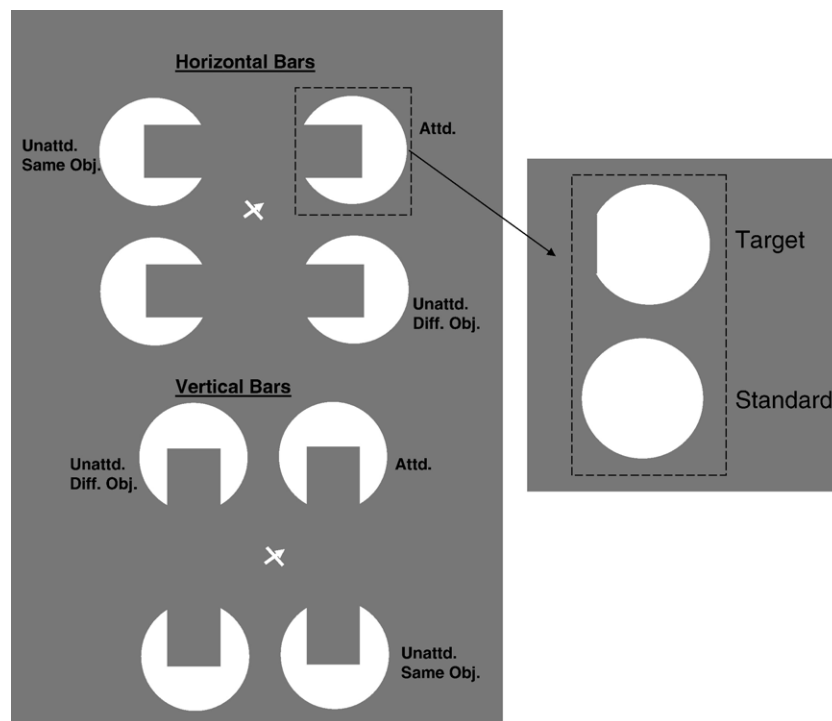

Fig. 1 – Stimulus configurations. Kanisza inducers were used to generate illusory bars. A pair of either vertical or horizontal illusory bars was continuously present on the display screen. Subjects attended to either the upper left or upper right quadrant while maintaining fixation centrally. The direction of a central arrow indicated the attended quadrant for each experimental block. Stimuli consisted of brief (100 ms) flashes that filled in the gap in the inducer, forming either a full circle (standards) or a circle with a straight edge (targets). In the example shown, the upper right quadrant was attended. The upper left and lower right quadrants could belong to the same (attended) or different (unattended) object depending on the orientation of the illusory bars.

Table 1 – Effects of spatial attention on P1 amplitudes

Quadrant	Hemispheres	P1 amplitudes		Attention		Hemisphere × Attention	
		Attended	Unattended	(Attended vs. Unattended)		(Ipsilateral vs. Contralateral × Attended vs. Unattended)	
				$F(1,11)$	$p<$	$F(1,11)$	$p<$
UR	LH	0.29	0.00	7.16	0.022	19.14	0.001
	RH	−0.10	−0.12				
UL	LH	−0.11	−0.15	15.85	0.002	9.45	0.011
	RH	0.24	0.05				

Mean amplitudes (in μV) for the P1 component elicited by stimuli in each quadrant at electrodes over left (LH) and right (RH) hemispheres. Data shown are for the latency window used in the ANOVAs (80–124 ms).

can be investigated by using stimulus arrays in which objects are formed by Kanisza inducers that produce illusory rather than real object boundaries. Since Kanisza objects do not have physically defined edges, perceptual grouping mechanisms are required in order to form a coherent representation of the object. If the facilitatory influence of spatial attention spreads throughout a Kanisza-defined object, this would imply that the object-selective process is controlled at a fairly high level, after object forms are integrated.

Moore et al. (1998) used Kanisza illusory rectangles in a design very similar to that of Egly et al. (1994). As expected, they found that targets appearing at validly cued locations were responded to faster than those occurring at all other uncued locations. In addition, as in previous studies of the Egly paradigm utilizing real objects, response times to targets at uncued locations within the attended object (an illusory rectangle) were faster than to targets at uncued locations belonging to the other, non-attended illusory rectangle. These latter findings are consistent with the view that spatial attention can spread within illusory object boundaries, thereby enhancing the perceptual representation of the illusory object.

To further study the time-course and anatomical level of object selection based on illusory contours, we recorded ERPs in an experiment nearly identical to that of Martinez et al. (2006) but with illusory horizontal and vertical bars presented as Kanisza figures (Fig. 1). The principal aim was to

compare the timing of illusory object-guided attention with the N1 modulations obtained in our previous study using real objects. We hypothesized that the generation of illusory object percepts might require additional time-consuming processing which in turn could result in longer latency attention effects. Subjects were instructed to attend to one end of one of the illusory bars and to detect infrequent shape changes (targets) of the flashed stimuli that location. For the stimuli in each visual quadrant ERPs were averaged separately for conditions (1) when the stimulus location was attended, (2) when the stimulus location was unattended but belonged to the same illusory bar as the attended location, and (3) when the stimulus location belonged to a different bar from the attended location. ERP differences associated with spatial- and object-selective attention were formed and compared in the same manner as in our previous study (Martinez et al., 2006).

2. Results

Subjects viewed a display consisting of two rectangular illusory bars oriented either vertically or horizontally. Each bar was formed by a pair of Kanisza-like figures positioned and oriented in order to generate a bar shape with illusory contours (Fig. 1).

Table 2 – Effects of spatial attention on N1 amplitudes

Quadrant	Hemisphere	N1 amplitudes		Attention		Hemisphere × Attention	
		Attended	Unattended	(Attended vs. Unattended)		(Ipsilateral vs. Contralateral × Attended vs. Unattended)	
				$F(1,11)$	$p<$	$F(1,11)$	$p<$
UR	LH	−0.76	−0.13	8.15	0.016	10.04	0.009
	RH	−0.29	−0.04				
UL	LH	−0.39	−0.01	7.37	0.020	5.63	0.037
	RH	−0.67	−0.14				

Mean amplitudes (in μV) elicited by stimuli in each quadrant in the N1 latency window (152–176 ms), as described in Table 1.

The task stimuli consisted of brief presentations of a square shape rounded on one side that filled in one of the Kanisza inducers. These stimuli were presented in a rapid, randomized sequence to the four different inducer locations. During each 20-s run the square onsets in either the upper left (UL) or upper right (UR) quadrant were designated as relevant and had to be discriminated for shape, with infrequent targets lacking the rounded edge. On average, subjects correctly detected 91.8% of the targets with a mean RT of 512 ms. Neither discrimination accuracy nor RTs differed significantly between targets in the UL and UR quadrants (P>0.05) nor between horizontal and vertical bar configurations (P>0.05).

Spatial attention effects were evaluated by comparing the ERPs elicited by the UL and UR standard stimuli when attended with the ERPs elicited by the same stimuli when the opposite field was attended (and with the bars oriented vertically, see Experimental procedures). As in many previous studies, attended stimuli elicited ERPs having significantly larger amplitudes than did the same stimuli when unattended. This difference was first observable as amplitude enhancements of the sensory-evoked P1 (80–104 ms) and N1 (152–176 ms) components. In all quadrants these enhancements were larger over the contralateral scalp (Tables 1 and 2, Fig. 2).

Object-selective attention was assessed for each of the four quadrants by subtracting ERPs elicited by unattended
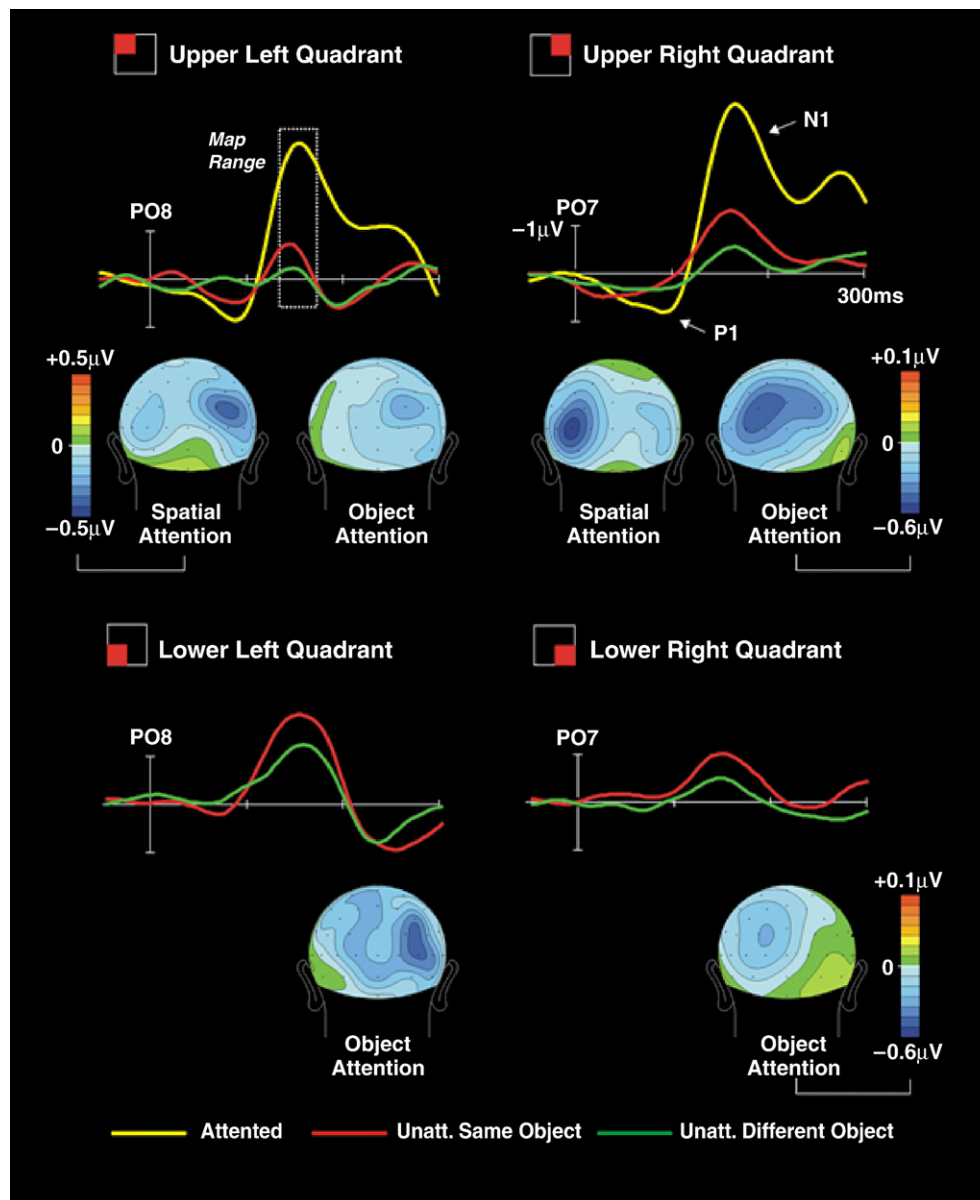

Fig. 2 – Grand-averaged ERPs to stimuli in each quadrant when attended (yellow waveforms) and unattended (red and green waveforms). ERPs elicited by attended and unattended stimuli are shown from a contralateral occipito-parietal electrode site (PO7/PO8). Voltage maps of the attention-related difference waves associated with spatial attention (yellow minus green waveforms; UL and UR quadrants only) and object attention (red minus green waveforms; all quadrants) are shown in the N1 latency range (152–176 ms) indicated by the dashed rectangle. Voltage scale on left applies to spatial attention maps. Voltage scales on right apply to object attention maps.

Table 3 – Effects of object-selective attention on N1 amplitudes

Quadrant	Hemisphere	N1 amplitudes		Attention		Hemisphere × Attention	
		Same	Different	(Same vs. Different object)		(Ipsilateral vs. Contralateral × Same vs. Different)	
				$F(1,18)$	$p<$	$F(1,18)$	$p<$
UR	LH	−0.35	−0.13	14.46	0.003		
	RH	−0.15	−0.05			5.59	0.038
UL	LH	−0.21	0.01	10.59	0.008		
	RH	−0.35	−0.14			6.27	0.029
LR	LH	−0.75	−0.53	5.38	0.041		
	RH	−0.48	−0.43			5.6	0.037
LL	LH	−0.67	−0.44	7.06	0.022		
	RH	−1.02	−0.72			16.01	0.002

N1 amplitudes elicited by unattended stimuli in each quadrant are given as mean voltage (in μV) at electrodes over LH and RH in latency window used in the ANOVA.

standard stimuli belonging to the unattended object (different-object condition, see Experimental procedures) from those elicited by the same unattended stimuli when they belonged to the attended object (same-object condition).

Unlike spatial attention, this comparison did not yield a significant amplitude modulation of the P1 component ($P>0.05$ for all quadrants). However, unattended stimuli in the same-object condition elicited significantly larger N1
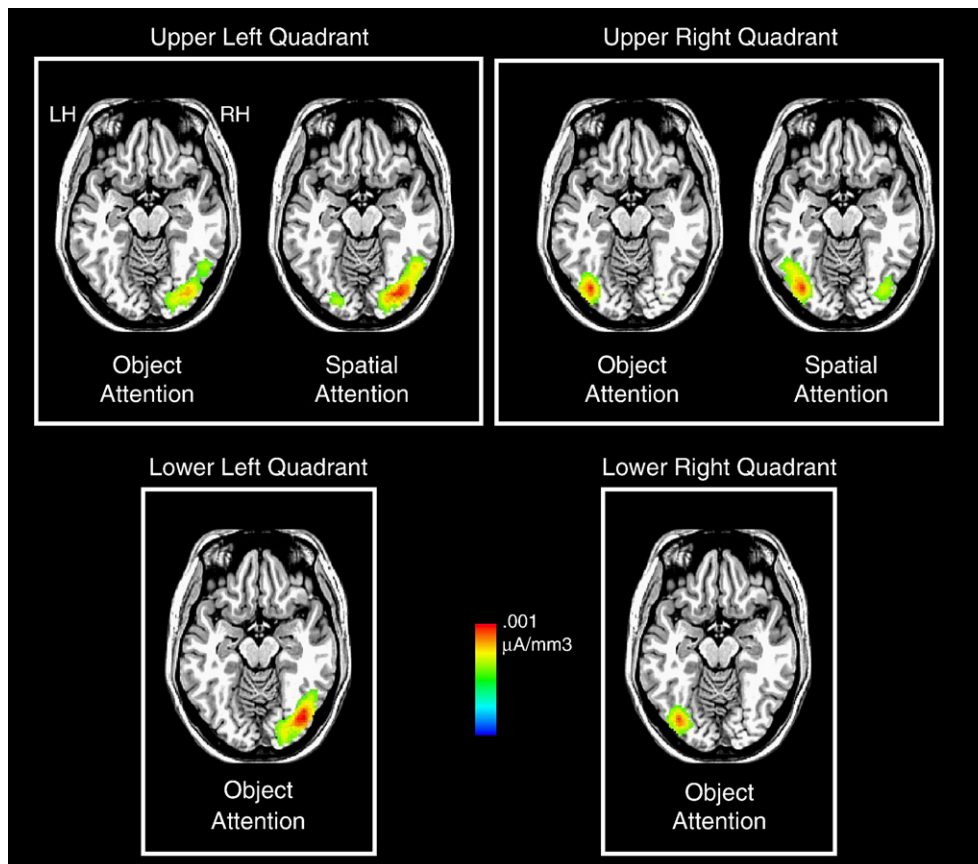

Fig. 3 – LAURA source estimations for the spatial and object N1 attention effects. The grand-averaged ERP difference waves were used to estimate the neural sources of the object and spatial attention effects in the N1 latency range (152–176). The group-averaged LAURA solutions are displayed on the brain (left hemisphere is on left). A prominent source in the contralateral LOC region was associated with both the spatial (UL and UR quadrants only) and object attention effect waveforms (all quadrants). Color bar depicts the current source intensity for all source solutions.

amplitudes than did unattended stimuli in the different-object condition. As with spatial attention, these effects were significantly larger over the contralateral scalp (Table 3, Fig. 2). Finally, we compared the amplitude of the object-selective attention effects in the N1 latency for the upper quadrants (when the same-object condition consisted of horizontal bars) vs. the lower quadrants (when the same-object condition used vertical bars). The amplitude of the N1 modulations obtained in the upper vs. lower quadrants did not differ significantly ($P > 0.05$), thus bar orientation cannot account for the attention effects.

As shown in Fig. 2, the scalp topographies of the N1 difference waves for object attention and spatial attention were very similar to one another, both having maximum amplitudes over the posterior contralateral scalp. The topographical distributions of these difference waves over the occipital scalp were compared using the procedure described by McCarthy and Wood (1985). This test revealed no significant differences between the topographies of the object and spatial attention difference waves ($P > 0.05$) for either the UL or UR quadrants. It can also be seen in Fig. 2 that the topographies of the object-selective N1 attention effects in the lower quadrants were very similar to those of their upper field counterparts.

2.1. Source localization of ERP attention effects

The linear distributed inverse solution (LAURA) technique was used to estimate the neural sources underlying the spatial and object N1 attention effects. Inverse solutions were calculated on the basis of the grand-average difference wave topographies in the N1 latency window (152–176 ms). For all quadrants, LAURA identified a primary source associated with the N1 object attention effect in the hemisphere contralateral to the eliciting stimulus. This source was situated in ventro-lateral occipital regions (Fig. 3) within the region previously described as area LOC (e.g., Malach et al., 1995). Similarly localized sources in LOC were identified for the N1 spatial attention effects in the UL and UR quadrants. The Talairach coordinates of the center of each LOC source estimated by LAURA are given in Table 4. Additional sources for the N1 spatial attention effect in the upper quadrants were identified in the contralateral inferior occipital gyrus, the fusiform gyrus and lingual gyrus. The object attention effect for the UL quadrant was also associated with a small source in the right fusiform gyrus, and the object attention

effect in the LL quadrant also had a dorsal source centered in the contralateral middle occipital gyrus. In all cases, however, the largest and most prominent sources for these N1 modulations were estimated to lie in the contralateral LOC.

3. Discussion

The present results provide evidence that directing spatial attention to one part of an object results in the facilitation of sensory processing of the entire object, even when the object is defined by illusory boundaries. This facilitation was reflected in an enhanced N1 component of the ERP, which had the same timing and source localization as the N1 increase produced by spatial attention when ERPs to attended vs. unattended locations were compared. These object-selective attention effects on the N1 component were very similar to those reported by Martinez et al. (2006) in a study that had a similar design but used objects with real boundaries. These findings provide evidence that perceived object boundaries, whether real or illusory, can guide spatial attention to facilitate the selection of entire objects. Moreover, these results suggest that this object-selective process is not guided by low-level physical boundaries but occurs at a higher level at which object forms are represented.

While the present ERP data and those of Martinez et al. (2006) suggest that spatially mediated and object-based selection share, at least in part, a common mechanism, it does not appear to be the case that spatial attention simply spreads uniformly throughout an object's boundaries. In the first place, the enhanced neural processing of the unattended region of the attended object is considerably less than for the attended region itself, which suggests a gradient of attentional allocation within the object that diminishes as a function of distance from the attended region (see also Müller and Kleinschmidt, 2003). Secondly, the ERP component modulations indicate that the spatial and object selection mechanisms, while overlapping in part, are not identical. Whereas spatial selection was associated with enlarged P1 and N1 components to attended location stimuli, the unattended stimuli within the attended object only elicited an enlarged N1. This is consistent with studies suggesting that the P1 and N1 index separate and dissociable processes involved in attentional selection (Luck et al., 1994). Specifically, it has been proposed that, while the P1 component reflects the suppression of irrelevant inputs, modulation of the N1 indexes a subsequent stage of facilitated processing and discrimination of relevant inputs (reviewed in Hopfinger et al., 2004).

Previous electrophysiological studies have shown that Kanisza figures elicit a different pattern of ERPs from those elicited by the same inducing stimuli when they are rotated such as not to produce the perception of an illusory boundary. Herrmann et al. (1999); Herrmann and Mecklinger (2000); and Herrmann and Bosch (2001), for example, found that Kanisza-induced objects, when compared to control non-objects, evoked larger posterior N1 components regardless of the type of object the subject was instructed to detect. Similar

Table 4 – Talairach coordinates of LOC sources						
	Object attention			Spatial attention		
	x	y	z	x	y	z
Upper left	38	−74	−12	35	−77	−12
Upper right	−37	−74	−13	−35	−75	−12
Lower left	38	−73	−12			
Lower right	−37	−73	−12			

LAURA source estimations for the object and spatial attention N1 effect in the latency window 152–176 ms.

amplitude enhancements in the N1 latency range have been reported in response to illusory objects using a variety of Kanisza inducers (Murray et al., 2002; Pegna et al., 2002; Proverbio and Zani, 2002; Murray et al., 2004), which suggests that this neural activity may be associated with Gestalt closure processes. Murray et al. (2002, 2004) combined fMRI with ERP recordings to show that this enhanced N1 to the perception of illusory objects had its primary generator source in area LOC. In the present experiment and in our previous study (Martinez et al., 2006), source analyses of the N1 associated with object-selective attention also indicated a principal neural generator in lateral occipital cortex (area LOC). Activation in this same LOC region has been observed in numerous object recognition studies using a variety of task stimuli, including objects defined by illusory contours (Mendola et al., 1999; Murray et al., 2004), partially occluded objects (Lerner et al., 2001) and scrambled objects (Malach et al., 1995). On the basis of these studies and others it has been suggested that the LOC region plays an important role in the encoding and recognition of objects.

The findings reported here and those of Martinez et al. (2006) suggest that the neural mechanisms underlying spatial- and object-selective attention partially overlap, consistent with models proposing that object boundaries guide the allocation of spatial attention (Weber et al., 1997; Davis et al., 2000). These ERP results appear inconsistent with attentional prioritization models (e.g., Shomstein and Yantis, 2002; Yantis and Serences, 2003) that attribute object-specific benefits to a higher priority for switching voluntary, task-driven attention within an attended object than between objects. Because the present design of sustained attention did not require any switching of attention to uncued stimuli, a prioritized switching mechanism does not seem likely to be involved. However, we cannot rule out the possibility that an automatic (i.e., reflexive) attention switching may have been triggered by stimuli at unattended locations.

In sum, the present data reveal the operation of an object-selective mechanism that may be best described as a form of object-guided spatial attention, which facilitates processing within the boundaries of attended objects. This facilitation does not occur at the earliest level of spatial attention (indexed by the P1), however, but at a higher level in cortical area LOC (indexed by the N1) at which object representations guide the allocation of attention. We propose that this allocation enhances sensory information throughout the attended object, thereby strengthening its perceptual representation in area LOC.

4. Experimental procedures

4.1. Task and stimuli

Twelve subjects (8 female, mean age 20.4 years) participated in the study. All subjects had normal or corrected-to-normal vision. Stimuli were pairs of Kanisza-like figures, each measuring 3.4° of visual angle, positioned and oriented such that each pair of inducers formed a bar shape with illusory contours (Fig. 1). These illusory bars measured 4° of visual angle in length and were continu-

ously present throughout each run. For half the runs the bars were oriented vertically (2° to the left and right of a continuously present central fixation point measuring 0.25°), and for the other half the bars were horizontal (positioned 2° above and below fixation). Task stimuli consisted of brief (100 ms) presentations of a white square shape (1.7° in height and length) that filled in the Kanisza inducer, forming either a full circle (standards, $P=0.8$) or a circle with a straight edge (targets, $P=0.2$). All stimuli were white on a gray background.

The fill-in squares were presented one at a time in continuous randomized sequences to the four different inducers, at intervals of 400–600 ms. Stimuli were delivered in 20-s blocks that alternated between the vertical and horizontal bar configuration. In both configurations, subjects were instructed to maintain fixation on a central cross while covertly directing attention to the flashed squares in the quadrant indicated by a pair of arrows presented at fixation. Detections of target squares at the attended location were reported by button presses, while squares at the other three locations were ignored. During a random half of the blocks the attention-directing cue pointed to the upper left (UL) quadrant and in the remaining half to the upper right (UR) quadrant. Thus, stimuli in the lower left (LL) and lower right (LR) quadrants were always ignored.

4.2. Electrophysiological recording and data analyses

Subjects sat in a dimly lit recording chamber while viewing stimuli presented on a video monitor at a viewing distance of 90 cm. The EEG was recorded from 62 electrode sites using a modified 10–10 system montage (Di Russo et al., 2001). All scalp channels were referenced to an electrode at the right mastoid but were algebraically re-referenced offline to the average of the left and right mastoids. Horizontal eye movements were monitored bipolarly via electrodes at the left and right outer canthi. Blinks and vertical eye movements were recorded with an electrode below the left eye, also referenced to the right mastoid.

The EEG was digitized at 250 Hz with an amplifier bandpass of 0.01 to 80 Hz (half amplitude low- and high-frequency cutoffs, respectively). Computerized artifact rejection was performed prior to signal averaging in order to discard epochs in which deviations in eye position, blinks, or amplifier blocking occurred. In addition, ERPs to standard stimuli that were preceded by a target stimulus within 1000 ms were eliminated in order to avoid contamination of the average by ERPs related to target detection and motor response. On average, 12% of the trials were rejected due to a combination of these artifact sources.

Time-locked ERPs to the standard stimuli were averaged separately according to quadrant of presentation (UL, LL, UR and LR), whether they were attended or unattended and according to the stimulus configuration (vertical or horizontal bars). ERPs to the target stimuli were not analyzed in this study. To assess effects of spatial attention, ERPs to the upper field stimuli when attended (averaged across both horizontal and vertical bar configurations) were compared to the ERPs elicited by the same stimuli when unattended. However, to

avoid confounding spatial and object attention effects, only unattended stimuli belonging to the unattended bar were included in this spatial attention comparison (e.g., an UR stimulus was considered unattended only when attention was directed to the UL quadrant and the illusory bars were vertical).

Object attention effects were assessed by comparing ERP amplitudes elicited by unattended stimuli as a function of whether they belonged to the illusory object being attended (same-object condition) or to the other, unattended object (different-object condition). For example, for the UR stimuli the same-object condition would occur when attention was directed to the UL stimuli and the bars were horizontal, and the different-object condition would occur when attention was directed to the UL stimuli but the bars were vertical. Similarly, for the LR stimuli the same-object condition would occur when the UR quadrant was attended and the bars were vertical, while the different-object condition would occur when the UR quadrant was attended and the bars were horizontal. ERPs to stimuli in the "diagonal" positions with respect to the attended quadrant were not used in these comparisons.

In all cases, the prominent P1 and N1 components of the visual ERP were quantified in terms of mean amplitudes averaged across 10 electrode sites in each hemisphere (O1/O2, PO3/PO4, PO7/PO8, P1/P2, P3/P4, P5/P6, P7/P8, CP1/CP2, CP3/CP4, CP5/CP6). These sites spanned the region of maximum amplitude over the contralateral hemisphere, and mirror image ipsilateral sites were included for comparison. All statistical analyses were conducted within specified latency windows with respect to a 100-ms pre-stimulus baseline. Mean amplitudes of the P1 (80–104 ms) and N1 (152–176 ms) components elicited by stimuli in each quadrant were subjected to repeated measures analysis of variance (ANOVA) with factors of Attention (for spatial attention, ERPs to the UL and UR stimuli when attended vs. unattended, as described above; for object attention, ERPs to unattended UL, UR, LL, and LR stimuli when attention was focused on the same vs. different object, as described above), and Hemisphere (contralateral vs. ipsilateral to the eliciting stimulus). The P values were adjusted for heterogeneity of variance and covariance by the Greenhouse–Geisser epsilon coefficient (Vasey and Thayer, 1987). The scalp distributions of the N1 amplitude modulations produced by spatial- and object-selective attention were compared for the UL and UR stimuli after normalizing their amplitudes prior to ANOVA according to the method described by McCarthy and Wood (1985).

4.3. Modeling of ERP sources

The scalp topographies of group-averaged difference waves (attended minus unattended ERPs for spatial attention; same-object minus different-object for object attention) for each quadrant were used to estimate the underlying brain sources of the attention-related modulations of the N1 component within the same latency windows used for statistical analyses. Source analyses were carried out using a distributed linear inverse solution based on a Local Auto-Regressive Average (LAURA; Grave de Peralta Menendez et al., 2001). LAURA estimates 3D current density distributions (rather than dipolar sources) using a realistic head model with a solution space of 4024 nodes equally distributed within the gray matter of the Montreal Neurological Institute's (MNI's) average template brain. This method makes no a priori assumptions regarding the number of sources or their locations and can deal with multiple simultaneously active sources (for a review, see Michel et al., 2001). The procedure was implemented using CARTOOL software (D. Brunet, Functional Brain Mapping Laboratory, Geneva, Switzerland). To estimate the anatomical regions where the N1 component was modulated by attention, the LAURA (MNI) coordinates were transformed to the standardized coordinate system of Talairach and Tournoux (1988) using the MNI2TAL formula (http://www.mrc-cbu.cam.ac.uk/ Imaging/Common/mnispace.shtml).

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