Available online at www.sciencedirect.com

Vision Research 45 (2005) 3004–3014

Vision Research

www.elsevier.com/locate/visres

Exogenous attentional selection of transparent superimposed surfaces modulates early event-related potentials

W. Khoe [a,*], J.F. Mitchell [b], J.H. Reynolds [b], S.A. Hillyard [a]

[a] *Department of Neurosciences, University of California, San Diego, La Jolla, CA, USA*
[b] *Systems Neurobiology Laboratory, The Salk Institute for Biological Studies, La Jolla, CA, USA*

Received 23 September 2004; received in revised form 8 April 2005

Abstract

Using a transparent motion paradigm, [Valdes-Sosa, M., Bobes, M. A., Rodriguez, V., & Pinilla, T. (1998). Switching attention without shifting the spotlight object-based attentional modulation of brain potentials, *Journal of Cognitive Neuroscience, 10*, 137–151; Valdes-Sosa, M., Cobo, A., & Pinilla, T. (2000). Attention to object files defined by transparent motion, *Journal of Experimental Psychological: Human Perception and Performance, 26*, 488–505] found that when attention is endogenously directed to one surface, observers can more reliably report the direction of a brief translation of the cued than the uncued surface. Using a similar design [Reynolds, J. H., Alborzian, S., & Stoner, G. R. (2003). Exogenously cued attention triggers competitive selection of surfaces, *Vision Research, 43*, 59–66] found that even in the absence of an endogenous cue, the first translation acted as a potent exogenous cue that impaired the observer's ability to discriminate a subsequent translation of the other surface. We investigated the neural basis of this exogenous cueing effect by recording visual event-related potentials (ERPs) elicited by translations of the cued and uncued surfaces. Subjects were given the task of judging whether or not the first and second translations were identical in direction, and their performance was impaired when the second translation occurred on the uncued, as compared to the cued surface. The posterior C1 (75–110 ms) and N1 (160–210 ms) components of the ERP elicited by the second translation of the cued surface were larger than those elicited by translation of the uncued surface. These behavioral and ERP cueing effects were present even when the two surfaces were identical in color and thus could not be attributed to attention-related modulations of the gain of color channels. These findings provide evidence that exogenous cueing results in preferential selection of the cued surface at both early and intermediate stages of visual-cortical processing.

Keywords: Attention; Object; Evoked-potential; Extrastriate cortex; Striate cortex

1. Introduction

Although substantial progress has been made in identifying and characterizing the neural mechanisms of spatial attention (reviewed by Hopfinger, Luck, & Hillyard, 2004; Reynolds & Chelazzi, 2004), less is known about the mechanisms underlying object-based attention (Muller & Kleinschmidt, 2003; Schoenfeld et al., 2003). Valdes-Sosa and colleagues have developed a novel transparent motion paradigm that shows great promise for analyzing object-selective attention un-confounded by spatial attention effects (Valdes-Sosa, Cobo, & Pinilla, 2000). In this paradigm, subjects view two superimposed random dot fields (one red, one green) rotating in opposite directions around a common central fixation point, yielding the percept of two transparent rigid surfaces sliding across one another. The fixation point color endogenously directs the observer to attend to one of the surfaces. Following a period of rotation of both surfaces, the cued surface undergoes a brief translation in one of eight directions, after which both surfaces resume their original rotations.

---

[*] Corresponding author. Tel.: +1 858 534 5562.
E-mail address: wkhoe@sdepl.ucsd.edu (W. Khoe).

0042-6989/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2005.04.021

After a variable interval a second translation occurs of one on the two surfaces, selected at random. The observer's task is to report the direction of both translations. Valdes-Sosa and colleagues found that observers could reliably discriminate the direction of both translations if they occured on the cued surface, but observers were strongly impaired in judging the second translation if it occurs on the uncued surface. This impairment was strongest when the second translation immediately followed the first translation and gradually decayed over approximately 600 ms (Valdes-Sosa et al., 2000). These findings provided evidence that the cued surface was selected as an integrated object.

Endogenously cued attention has been found to modulate event-related potentials (ERPs) in observers performing this surface-selection task. Valdes-Sosa and colleagues (1998) found that when attention is endogenously cued to one surface for a sustained period both the P1 (134–203 ms) and N1 (244–293 ms) ERP components elicited by translations of the uncued surface were diminished in amplitude. However, only the N1 has been found to be consistently modulated in studies that used trial-by-trial cueing in this paradigm (Lopez, Rodriguez, & Valdes-Sosa, 2004; Pinilla, Cobo, Torres, & Valdes-Sosa, 2001; Valdes-Sosa et al., 2004). The intracranial source of this N1 attentional effect was localized to bilateral generators in ventral-lateral extrastriate visual cortex in the vicinity of areas MT/MST and V4 (Valdes-Sosa et al., 2004). On the basis of these findings, Valdes-Sosa and colleagues concluded that surface selection occurs at relatively early levels of the visual processing pathway.

Extending the original Valdes-Sosa paradigm, Reynolds, Alborzian, and Stoner (2003) found that the first translation is sufficient in itself to engage surface-selection mechanisms. On randomly selected trials they replaced the endogenous cue (colored fixation point) with a non-informative grey fixation point and found that this did not measurably change behavioral performance. Observers judged both translations accurately on trials when the same surface translated twice but were impaired in judging the second translation if first one, then the other surface translated. As on endogenously cued trials, this impairment was greatest when the second translation occurred shortly after the first and diminished with greater temporal separation. This suggests that the first translation acts an exogenous cue that automatically engages attention to the translating surface while suppressing neuronal signals driven by the subsequent translation of the other surface. In the original paradigm of Valdes-Sosa et al. (2000), it is difficult to separate the influences of exogenous and endogenous attentional cueing on surface-selective processing, given that both types of cues were present.

In the present study, we sought to determine the behavioral and neural consequences of purely exogenous cueing in the Valdes-Sosa paradigm. To identify the stage of processing at which exogenously cued attention influences surface-based attention, ERPs were recorded from observers who judged the direction of two successive translations that could occur unpredictably either on the same or on different surfaces in the absence of an endogenous cue. A further aim was to evaluate the role of color as a feature for exogenous surface selection. Accordingly, the experiment was conducted under two conditions: when the two rotating dot populations differed in color (Experiment 1) or were identical in color (Experiment 2).

2. Experiment 1

2.1. Subjects

Twelve right-handed normal adults from the University of California, San Diego community (6 males and 6 females; age range 19–35, mean $= 24$ years) served as paid volunteers in the experiment. All participants had normal or corrected to normal visual acuity. No subjects reported any history of neurological injury or disease.

2.2. Stimuli

Stimuli were displayed on a 21. color monitor at a distance of 57 cm in a darkened room. Prior to the experiment, each subject performed a heterochromatic flicker fusion task (flicker rate of 60 Hz) to establish equiluminance between the red and green guns of the monitor. The red gun was held constant at maximum intensity (5.1 cd/m^2) and the green gun was adjusted until minimal flicker was reported. The procedure was repeated 10 times and the results averaged. The resulting green value was used for that individual throughout the remainder of the experiment.

The experimental display consisted of a high-contrast fixation point on a black background. The fixation point consisted of a black inner disk of radius 0.1 deg visual angle superimposed upon a larger white disk of radius 0.5 deg. The luminance values of the white and black disks were 24.2 and 0.05 cd/m^2, respectively. Surrounding the fixation point were two overlapping random dot patterns, one green and one red. The density of each dot field was 3.3 dots per square degree, and each dot subtended 0.1 deg. Stimuli were viewed through a circular aperture 4.3 deg in diameter. The two dot patterns rotated rigidly in opposite directions around the central fixation point. On half the trials, selected at random the red dots rotated clockwise, while green dots rotated clockwise on the other half. Both patterns rotated at 40 deg/s. The patterns of dots gave rise to the percept of two superimposed transparent surfaces formed by the red and green dots, rotating in opposite directions. To prevent the apperance of a particular depth ordering between the surfaces, potential occlusion cues caused by the dots from different surfaces occasionally falling on the same image pixels were eliminated by blacking out those pixels.

2.3. Experimental design

Subjects performed a translation direction discrimination task (Fig. 1A). Each trial began with the continuous rotation of both populations of dots for 800 ms. After this period of rotation, one of the surfaces underwent a brief translation in one of four directions. The duration of this translation was 100 ms and 60% of the dots translated coherently while the remaining dots moved in randomly assigned directions. The dots translated at a speed of 4 deg of visual arc per second. Subjects were told that the translation would occur with

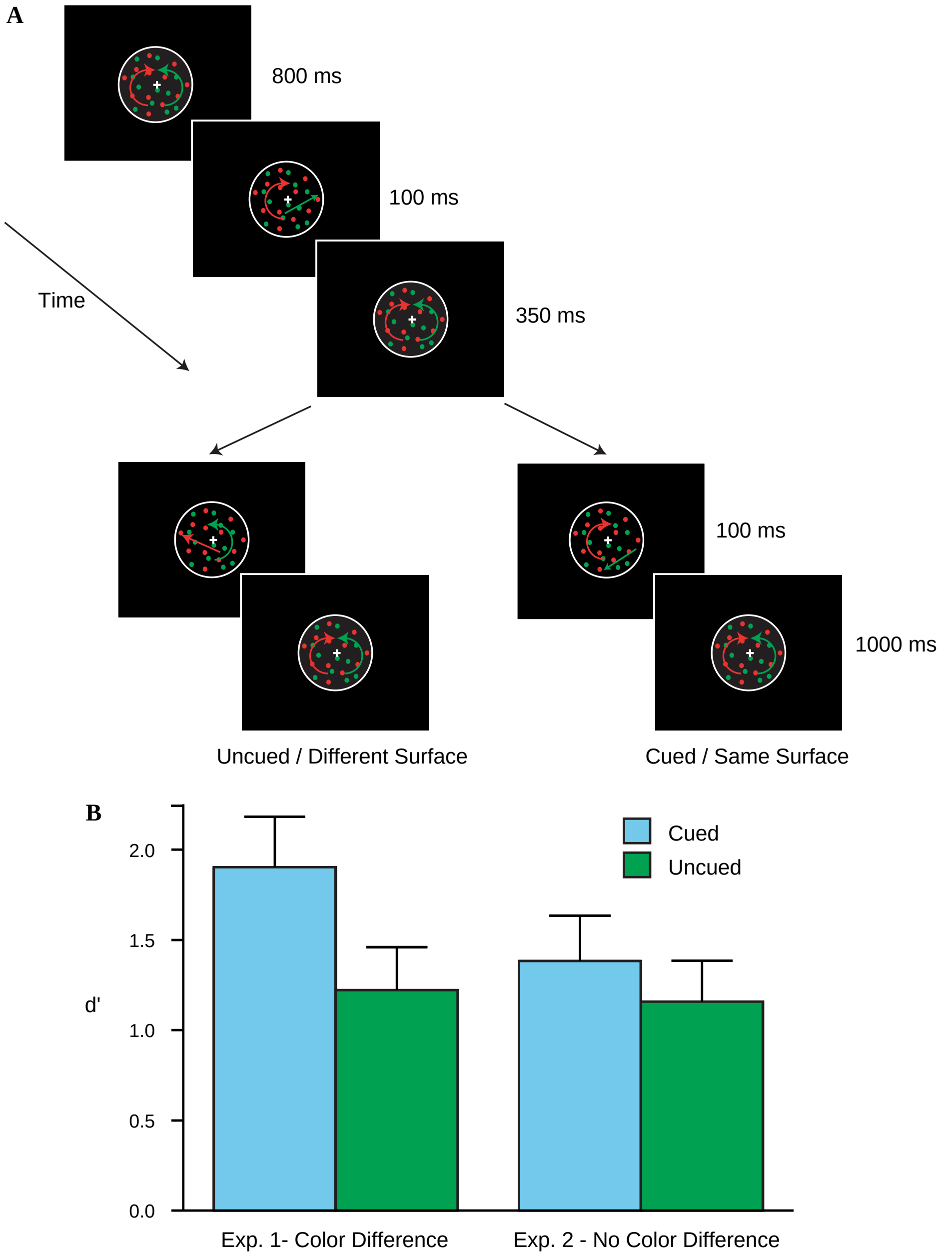

Fig. 1. Stimuli and observers' performance. (A) Example sequence of events used for the experiment. The trial began with two random overlapping dot patterns that rotated in opposite directions, thus generating a percept of two surfaces sliding across one another. After 800 ms, one of the two surfaces translated in one of four directions (100 ms). Following translation one (T1), the surfaces continue rotating for 350 ms before translating a second time (T2). T2 occurred with equal probability on both surfaces. T2 was cued if it occurred on the same surface as T1 and T2 was uncued if it occurred on the other surface from T2. Subjects responded when the T2 and T1 were in the same direction. (B) Abrupt translation on one surface for 100 ms results in higher detectability (mean d') for second translation of cued ($M = 1.90$) vs. uncued ($M = 1.22$) color difference surface and cued ($M = 1.38$) vs. uncued ($M = 1.15$) no color difference surface pooled across all subjects. Standard errors of the mean are plotted for each cueing condition.

equal probability across the two surfaces. The design incorporated an unpredictable first translation to avoid possible endogenous cueing effects. Following the first translation (T1), the two surfaces continued rotating, and a second translation of one of the surfaces (T2) occurred at a stimulus-onset asynchrony (SOA) of 450 ms. T2 occurred with equal probability on the two surfaces. On 25% of these trials, both translations were in the same direction. For the remainder 75% of the trials, T2 moved in one of the other three cardinal directions not taken by T1, selected at random with equal probability. Following T2, the two surfaces continued rotating for 1000 ms. Subjects were instructed to respond within the interval of continued rotation after the second translation to prevent overlap with the subsequent trial. After 1500 ms of blank screen the next trial began. Subjects were instructed to respond with a button press when the two translations were in the same direction. A correct response was categorized as a "hit." A non-response during trials with translations of different directions was categorized as "correctly rejected." An incorrect response for trials in which the translation directions were different was classified as a "false alarm." The hit and false alarm rates were used to derive the sensitivity estimate d'(Macmillan & Creelman, 1991). Subjects were run in 10 experimental blocks. Each block contained 128 trials.

2.4. ERP data acquisition and analysis

Scalp potentials were recorded from 60 tin electrodes mounted in a custom cap that were distributed evenly over the scalp (Electro-Cap International). Electrodes in the 60 channel cap are labeled in reference to the 10–20 electrode location system. The scalp recordings were referenced to the right mastoid during recording. Scalp and mastoid electrode impedance was maintained below 5 and 2 KΩ, respectively. Vertical eye movements were recorded by placing an electrode below the left eye and referenced to the right mastoid. Horizontal eye movements were recorded by placing an electrode over the right outer canthus referenced to the left outer canthus. All electroencephalographic (EEG) and electrooculographic (EOG) activity was amplified at a band pass of 0.1–80 Hz (SA Amps—Model SAH BA 64), digitized on-line at a sampling rate of 500 Hz with a gain of 10,000, and stored on a computer hard drive for off-line analysis. ERPs were algebraically re-referenced to the averaged left and right mastoid, and low-pass filtered prior to analysis.

ERPs were averaged over epochs beginning 1500 ms before T2 and extending 1500 ms after T2 onset. Offline, automated artifact rejection was used to reject trials that contained large eye movements (>5 deg of visual angle), blinks, muscle potentials, or amplifier blocking. To rule out any effects of small residual eye movements, the EOG was averaged and quantified in the interval 0–400 ms after T2 with respect to the pre-T2 baseline. The averaged EOG deflections were less than 2 μV, corresponding to an ocular deviation of <0.2 deg (Luck & Hillyard, 1994), and did not differ between cued and uncued T2 translations. As a result of this analysis, eye movement contamination can be ruled out as the source of the ERP modulations discussed below.

Only "correct rejection" trials were included in the ERP analysis. In these trials, T1 and T2 were in different directions, and the subjects did not erroneously respond with a button press. The ERPs for all subjects were pooled together to create the grand average waveform. To quantify the ERP elicited by T2, mean amplitude measures over specified time windows were taken referenced to a baseline of 100 ms pre-stimulus to 50 ms post-stimulus onset. Measurement windows were chosen by centering the window at the peak latency of the ERP component taken from the grand average waveform. Latency ranges of 75–110 ms for the C1, 110–160 ms for the P1, and 170–220 ms for the N1 were used to calculate the mean amplitudes. For the C1, measurements were taken from a group of midline occipital electrodes that included Pz, POz, and Oz. For the P1 and N1, measurements were taken from lateral occipital electrode sites that include P5/P6, PO3/PO4, and PO7/PO8. The ERP data were entered into a repeated measures ANOVA with surface (cued vs. uncued) and color (red vs. green) as the factors. For the P1 and N1 ANOVAs, an extra factor of hemisphere was added (left hemisphere vs. right hemisphere) to the analysis. The p values were adjusted for heterogeneity of variance and covariance using the Greenhouse-Geyser epsilon method. To visualize the scalp distributions of the ERP modulations with attention, voltage topographical maps were constructed of the cued minus uncued difference waves using spherical spline interpolation (Perrin, Pernier, Bertrand, & Echallier, 1989).

2.5. Behavioral results

The sensitivity estimates (d' values) for comparing the directions of the first and second translations were entered into a repeated measures ANOVA with surface (cued vs. uncued) and color (red vs. green) as factors. The main effect of cueing on d' was highly significant [$F(1,12) = 23.06$, $p < 0.0005$] (Fig. 1B), indicating that subjects were impaired in their discrimination when the second translations occurred on the uncued surface. The main effect of color was not significant [$F < 1$], nor was the interaction between surface and color [$F < 1$].

2.6. ERP Results

The ERPs elicited on trials where T2 was cued or uncued are superimposed on Fig. 2A. Since color was not a significant factor, the ERPs elicited by translations of

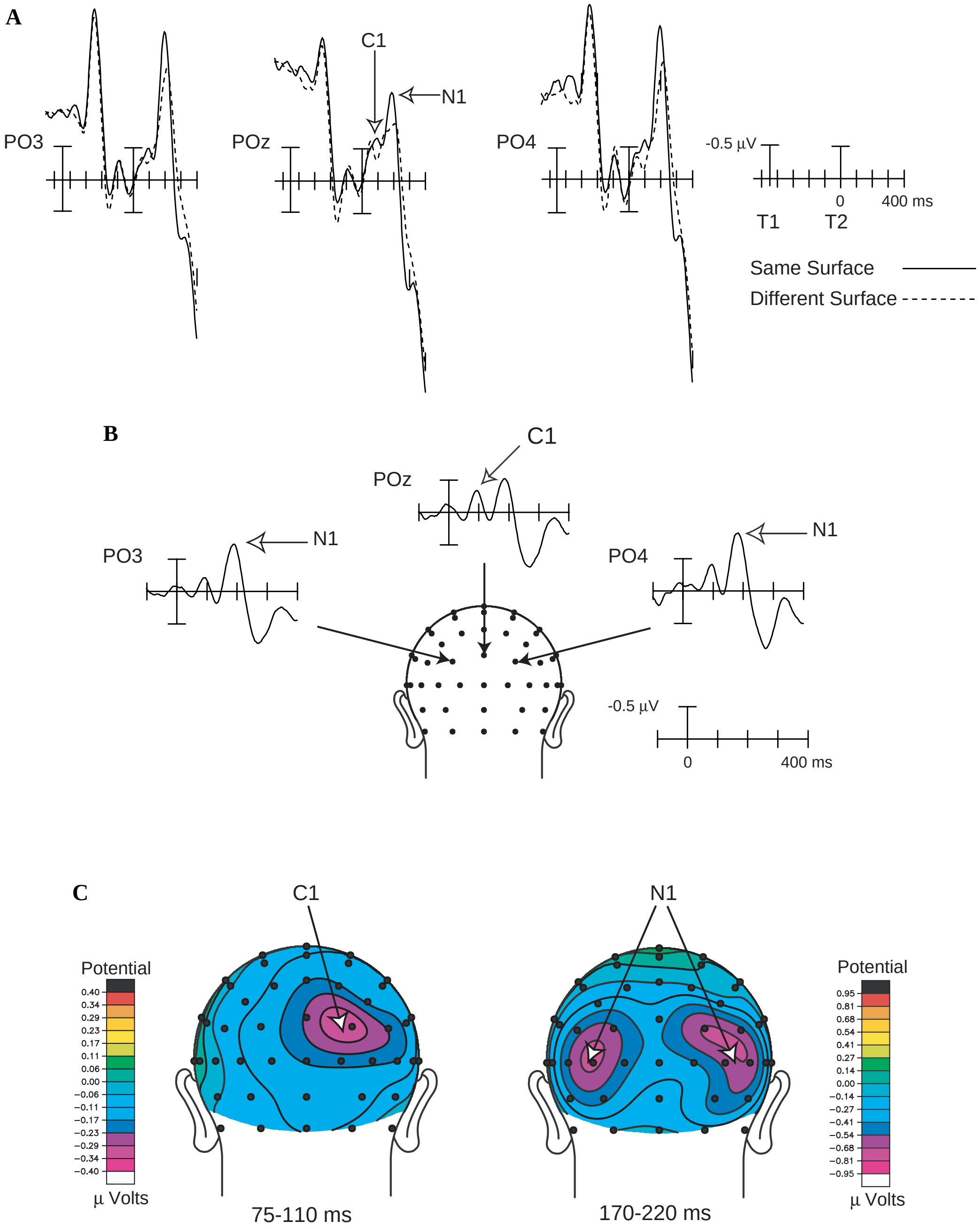

Fig. 2. Grand average ERPs during competitive selection of different colored surfaces with an exogenous cue. (A) ERPs to cued vs. uncued second translations from three parietal-occipital electrode sites (PO3, POz, PO4). The solid line represents the ERP for the cued second translation (i.e., when T2 occurred on the same surface as the first translation). The dotted line corresponds to the ERP elicited for the uncued second translation (i.e., when T2 occurred on the other surface). (B) Difference wave subtractions of cued minus uncued surface translations. The peaks of the C1 and N1 components are indicated with arrows. (C) Scalp maps of the C1 (80–90 ms) and N1 (180–190 ms) computed from the difference wave.

the red and green surfaces were collapsed. The effect of cueing can be seen more clearly by subtracting the ERPs elicited by the uncued surface from the ERP elicited by the cued surface on a point-by-point basis across the waveform (Fig. 2B). This difference waveform included C1 (peak latency—92 ms), P1 (peak latency—135 ms), and N1 (peak latency—195 ms) components. The C1 amplitude measure was significantly larger for the second translation of the cued surface compared to the uncued surface [$F(1,12) = 5.64$, $p < 0.03$]. There were no significant effects of color or interaction between color and cue for the C1. In contrast, the P1 did not show any significant effects of cueing. A pattern similar to the C1 was seen for the N1. The N1 component was significantly larger for second translation of the cued surface relative to the uncued surface [$F(1,12) = 15.52$, $p < 0.002$]. There were no significant effects of color or interaction between color and cue for the N1.

2.7. ERP scalp topography

A comparison between the topographies of the difference ERPs showed that the surface attention effect at 75–110 ms (the C1) was localized to midline occipital sites and slightly lateralized to the right hemisphere. In contrast, the attention effect at 170–220 ms (the N1) was distributed with bilaterally symmetrical foci over lateral occipital electrode sites (Fig. 2C).

2.8. Discussion

In Experiment 1, we found that exogenous attention modulated ERP amplitudes in the latency ranges of the C1 (75–110 ms) and N1 (170–220 ms) components. In particular, the amplitudes of the C1 and N1 elicited by the second translation were larger for the cued surface than for the uncued surface. These attentional modulations can be interpreted as exogenous attention influencing surface-specific selection processes. However, the two surfaces differed in color, raising the possibility that these effects might instead have resulted from a feature-based attention mechanism, such as reducing the gain of the color channel selective for the color of the uncued surface (Mitchell, Stoner, Fallah, & Reynolds, 2003). Such a reduction in gain would be expected to reduce the salience of the uncued dots, thus accounting for the reduced ERP components and the impairment in discriminating the motion of the uncued surface. Single-unit recordings in animals and human fMRI studies have shown that feature-based attentional mechanisms can modulate neuronal responses in the visual processing pathways (Saenz, Buracas, & Boynton, 2002; Treue & Martinez-Trujillo, 1999). To rule out such a feature-based explanation, we conducted an additional experiment in which the two surfaces were equated for color. A feature-based attentional mechanism based on color can be rejected if the behavioral deficit and the attentional modulations of the C1 and N1 components remain after removal of the color difference.

3. Experiment 2

3.1. Subjects

Twelve right-handed normal adults from the University of California, San Diego community (4 males and 8 females; age range 19–35, mean = 24 years) served as paid volunteers in the experiment.

3.2. Stimuli and experimental design

The stimuli and experimental design of Experiment 2 were identical to Experiment 1, except that the two random dot patterns were the same color (both red). The red gun in the monitor was held at constant maximum intensity (5.1 cd/m^2).

3.3. ERP data acquisition and analysis

Collection and analysis of ERP data were performed as in Experiment 1. The C1 and N1 amplitudes were entered into a repeated measures ANOVA with a main factor of surface (cued vs. uncued). For the N1 analysis, the additional factor of hemisphere (left vs. right) was included.

3.4. Behavioral results

The sensitivity estimates (d' values) were entered into a two-tailed paired sample t test. Subjects were significantly impaired when the second translation occurred on the uncued surface [$t(12) = 2.73$, $p < 0.01$] (Fig. 1B). The degree of impairment (16% reduction in d'), however was significantly less than in Experiment 1 (37% reduction in d') [$F(1,22) = 7.63$, $p < 0.01$].

3.5. ERP results

As in Experiment 1, the C1 amplitude measure was significantly larger for the second translation of the cued surface compared to the uncued surface [$F(1,11) = 7.26$, $p < 0.02$] (Figs. 3A and B). Similarly, the N1 amplitude elicited by the second translation was significantly larger for the cued surface than for the uncued surface [$F(1,11) = 23.23$, $p < 0.0005$], and this effect did not interact with the hemisphere factor [$F < 1$]. The P1 did not show any significant effects of cueing.

3.6. ERP scalp topography

The topographies of the difference ERP components were similar to those of Experiment 1 (Fig. 3C). The C1 was largest over midline parietal-occipital electrode sites with a slight bias to the right hemisphere, while the N1 was distributed bilaterally over occipital electrode sites.

3.7. Discussion

In Experiment 2, the color differences between the two surfaces were removed, thereby eliminating color as a possible feature for selection. As in Experiment 1, exogenous cueing significantly modulated the C1 (80–115 ms) and N1 (170–220 ms) components. The amplitude measures of the C1 and N1 elicited by the second translation were larger for the cued surface than for the uncued surface. The size of the behavioral effect was reduced in Experiment 2, however, suggesting that the additional color cue in Experiment 1 may have contributed in some way to the selection between the surfac-

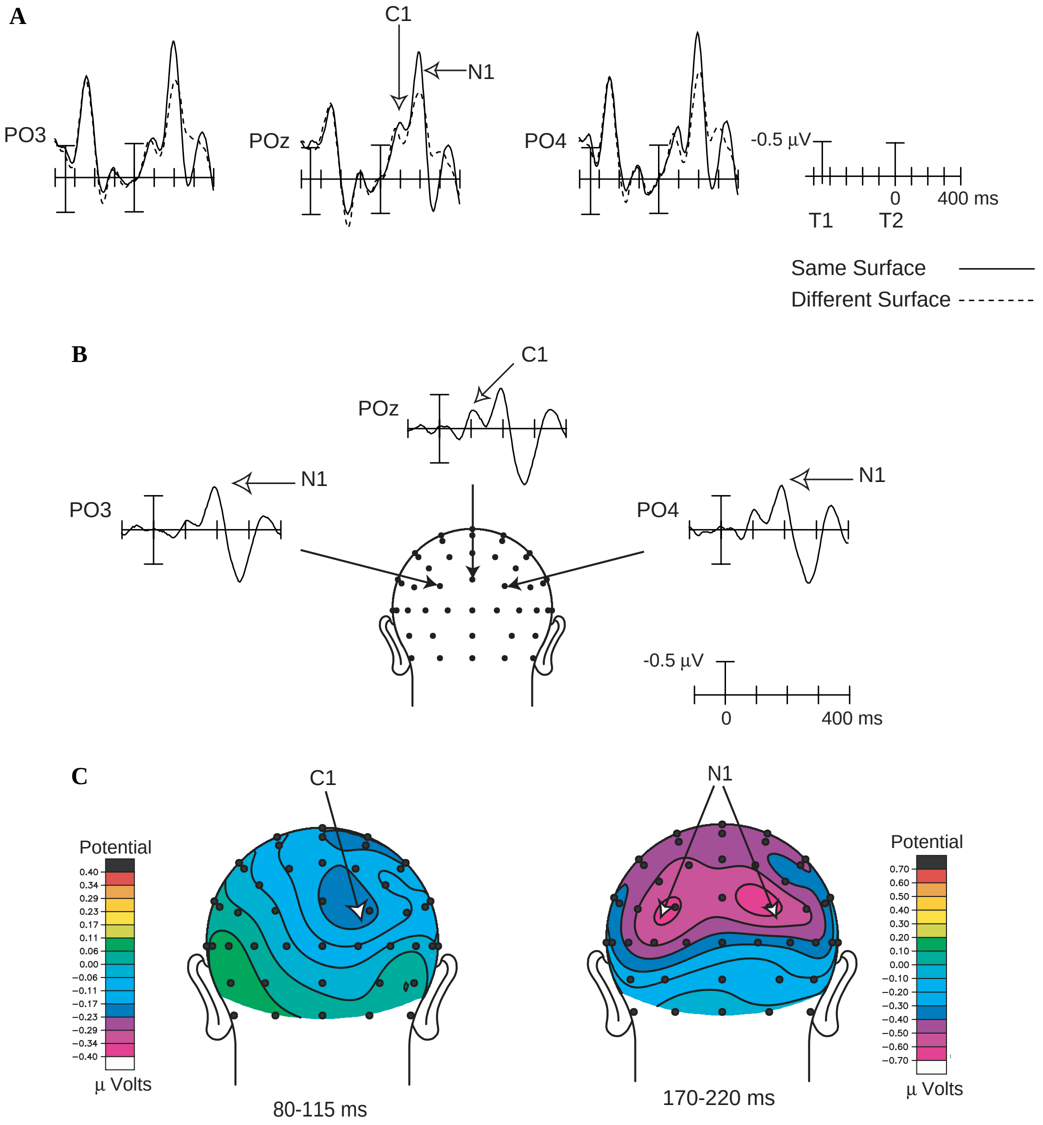

Fig. 3. Grand average ERPs during competitive selection of same colored surfaces with an exogenous cue. (A) ERPs to cued vs. uncued second translations from three parietal-occipital electrode sites (PO3, POz, PO4). The solid line represents the ERP for a cued second translation (T2). The dotted line corresponds to the ERP elicited for an uncued T2. (B) Difference wave subtractions of cued minus uncued surface translations. The C1 and N1 components are indicated with arrows. (C) Scalp maps of the C1 (90–100 ms) and N1 (180–190 ms) computed from the difference wave.

es. Nonetheless, these results rule out the possibility that the ERP and behavioral effects of cueing observed in Experiment 2 were the result of a change in the sensitivity of color selective neurons following the exogenous cue.

4. General discussion

4.1. Summary

The present study found that a purely exogenous cue consisting of a brief translation of one of two superimposed, counter-rotating surfaces produced a relative impairment at judging the direction of a subsequent translation of the uncued surface. In association with this perceptual cueing effect, the early C1 (75–110 ms) and later N1 (170–220 ms) components of the visual ERP elicited by the uncued surface were reduced in amplitude relative to those elicited by the cued surface. The scalp topography of the C1 amplitude modulation was focused over midline occipital sites, whereas the N1 modulation was distributed bilaterally at lateral occipital sites. A second experiment demonstrated that similar modulations of the C1 and N1 components and of perceptual sensitivity were produced by exogenous cueing when the two surfaces were identical in color, thereby ruling out a color-based selection mechanism. Because the rotating surfaces were spatially superimposed, a spatial-selection mechanism can also be ruled out. Instead, these results are consistent with a surface-selection model in which populations of neurons driven by the two surfaces compete with one another and the population that responds to the exogenously cued surface temporarily wins the competition at an early stage of visual processing.

4.2. Related studies

In the original ERP study of Valdes-Sosa, Bobes, Rodriguez, and Pinilla (1998), attention was cued endogenously and was sustained over runs of 1.5–2.5 min. Under these conditions, both the P1 and N1 amplitudes were found to be larger in response for translations of the attended versus the unattended surface. However, in experiments where attention was cued on a trial-by-trial basis only the N1 showed a consistent modulation (Lopez et al., 2004; Pinilla et al., 2001). As mentioned in Section 1, these previous trial-by-trial cueing studies included both endogenous and exogenous cues. The present study thus provides the first clear evidence that purely exogenous cueing also modulates ERP amplitudes. The bilateral occipital scalp distribution of the N1 cueing effect observed in the present study was very similar to that previously reported by Valdes-Sosa's group (Rodriguez, Valdes-Sosa, Bobes, & Jas, in press; Valdes-Sosa et al., 2004), which was localized to a ventral-lateral occipital source in the general vicinity of visual areas MT/MST and V4. The present findings thus suggest that an unpredictable exogenous cue modulates visual processing at this same level in ventral-lateral visual cortex.

Our finding that the first surface acts as an exogenous cue is consistent with previous psychophysical studies (Mitchell et al., 2003; Mitchell, Stoner, & Reynolds, 2004; Reynolds et al., 2003). Recently, Lopez and colleagues (2004) presented behavioral and ERP evidence that top-down endogenous control of attention is able to modulate the potency of an exogenous cue. In the present study, however, no endogenous cues were present, and the translations were randomly assigned to each surface on a trial-by-trial basis. Subjects could not know in advance which surface would translate and thus could not benefit from endogenously attending to one surface over another. Since the task required discriminating both translations, each of which was equally likely to appear on either surface, observers had an incentive to attend to both surfaces. Thus, the demands on endogenously controlled attention were constant across cueing conditions, and we can safely attribute the differences observed in the C1 and N1 component amplitudes to exogenous cueing.

4.3. The C1 component

The modulation of neural activity in the latency range of the C1 component observed in the present paradigm was unexpected. Considerable evidence supports the hypothesis that the C1 component reflects the early phasic activity in striate cortex elicited by a stimulus onset (reviewed in Di Russo, Martinez, & Hillyard, 2003). Prior ERP studies have not found any evidence of C1 modulation by spatial or feature-selective attention (Anllo-Vento, Luck, & Hillyard, 1998; Di Russo et al., 2003; Fu, Fan, Chen, & Zhuo, 2001; Martinez et al., 2001a; Martinez, DiRusso, Anllo-Vento, & Hillyard, 2001b; Noesselt et al., 2002). An important difference between stimuli used in the current and in past studies is that here the surfaces remained present throughout the entire trial period, whereas past studies presented stimuli with abrupt luminance onsets. The abrupt onset of a new stimulus is likely to evoke strong phasic responses in early visual areas. Single unit recording studies have found that paying attention to a stimulus has little, if any, effect on such onset transient responses (Fries, Reynolds, Rorie, & Desimone, 2001; Reynolds, Pasternak, & Desimone, 2000). In the current study, we measured the ERPs elicited by a change in motion (from rotation to translation) of a perceived surface that was present for several hundred milliseconds prior to the translation. Although this event produced measurable ERPs, their amplitudes were considerably smaller than those previously reported using stimulus onsets. Unlike a luminance onset, a motion onset would be less likely to elicit a robust onset transient in early visual areas, which may enable attentional modulations to be observed in the C1 component.

Previous ERP studies of surface selection did not observe any attentional modulation of the C1 component (reviewed in Lopez et al., 2004 and Valdes-Sosa et al., 2004). The earliest component reported to be modulated by attention was the P1 (134–203 ms) (Valdes-Sosa et al., 1998). These studies may have used higher contrast stimuli than the ones used in the current study. Such higher contrast stimuli could have saturated the response of the underlying neuron population that gives rise to the C1. In line with this proposal, Reynolds et al. (2000) reported that the effect of attention on evoked neural activity in monkey visual cortex was largest for stimuli of intermediate contrast than at high contrasts, particularly during the initial onset transient. Presumably, an increase in neuronal firing rate due to attention would not be seen using higher contrast stimuli if they saturated the underlying neural response. As discussed earlier, another possible reason that the C1 was affected by cueing in the present study but not in previous studies may be that the previous experimental designs did not produce purely exogenous cueing of attention.

Although the C1 modulation reported here was similar in its scalp voltage topography and timing to the C1 component observed in prior studies (e.g. Di Russo et al., 2003), it is not clear whether these components arise from a common cortical source. As noted above, the surface-translation stimuli used in the current study are quite different from the luminance onset stimuli employed in earlier experiments, and the current C1 modulation has a somewhat later onset (70–80 ms) than in previous studies (50–60 ms). Moreover, the C1 observed here was clearly evident only in the cued-surface ERPs (and hence in the cued minus uncued difference waves), suggesting that the effect of cueing was not a simple amplitude enhancement of an evoked C1 component. The scalp distribution of this C1 modulation would also be consistent with a cortical source in more dorsal parieto-occipital areas. Further studies are required to determine whether this component corresponds to the previously reported C1 that has been localized to striate cortex.

4.4. Possible mechanisms of the exogenous cueing effects

Among the various mechanisms that might account for the modulations of ERP amplitudes and improved perceptual selectivity produced by exogenous cueing, the main candidates we shall consider are feature-based selection on the basis of color or motion cues, low-level sensory interactions and surface-based selection.

4.5. Feature-based selection

The amplitude modulations of the C1 and N1 components produced by exogenous cueing were found to be very similar, regardless of whether the two rotating surfaces were of the same (Experiment 2) or different (Experiment 1) colors. These ERP modulations could thus not be explained by a color-selective process induced by the first translation. The psychophysical cueing effect (greater d' for discriminating same-surface than different-surface second translations) was also found to be present in Experiment 2, where the surfaces were identical in color, indicating that this effect cannot be explained entirely on the basis of feature-based attention to color. The psychophysical cueing effect was reduced in size relative to that observed in Experiment 1, however, suggesting that cueing was more effective when the two surfaces differed in color. This is a notable difference from the findings of Mitchell et al. (2003), who found no such color-dependent difference in the magnitude of the psychophysical cueing effect. The reason for this discrepancy is not entirely clear, but the two studies differed in several ways, including the task (reporting the direction of the two translations separately versus comparing directions in the present study) and the psychophysical measure (percent correct in judging directions versus d' in the present study). In any case, comparing the results of Experiments 1 and 2 does indicate a dissociation between ERP amplitudes (which did not differ between experiments) and the behavioral index of surface discriminability, suggesting that the psychophysical and electrophysiological measures may be influenced differentially by stimulus and task factors in this experiment.

The design of the present experiments makes it highly unlikely that feature selection on the basis of direction of rotation could underlie the exogenous cueing effects. Although it has been shown that features of superimposed stimuli can remain selected if they change smoothly over time (Blaser, Pylyshyn, & Holcombe, 2000), the motion features in our task changed abruptly from rotation to translation. Because the direction of motion of each onset event was unpredictable (each of the four directions was equally likely) and each direction of translation was equally correlated with either of the two directions of rotation, it is unlikely that the selection of the cued surface's rotation direction could selectively enhance the subsequent translation of that surface. Indeed, the only link between the cued rotation and subsequent translation was surface identity.

4.6. Low-level sensory interactions

Another factor that merits consideration is sensory adaptation to the rotation of the stimuli. Because the first translation briefly interrupted the rotation of the cued surface, neurons selective for the rotation of the cued surface might be expected to be less strongly adapted than neurons selective for the rotation of the uncued surface. A second translation of the cued surface would then occur against a more strongly adapted rotation than would translation of the uncued surface. If neurons selective for rotation were to inhibit the responses evoked by translation, the less adapted rotation-selective neurons might more effectively inhibit neurons selective for translation, resulting in poorer discrimination performance and reduced neuronal responses for translations of the uncued surface. Arguing against such a mechanism, however, are control experiments related to a recent psychophysical study (Reynolds, Stoner, & Mitchell, 2004), which found that exogenous surface cueing effects remain even when motion adaptation is equated across conditions. Moreover, single-unit studies in macaque area V1 are inconsistent with such an adaptation mechanism at the level of striate cortex, as they find that the responses of V1 motion-selective neurons are not significantly influenced by the competing motion signals of transparent stimuli (Qian & Andersen, 1994, 1995). It remains possible, however, that the early ERP modulations observed here could originate from extrastriate sources. Neurons in extrastriate areas are known to integrate the competing motion signals of transparent surfaces, and could be sensitive to the differences in adaptation of the background rotation (Qian & Andersen, 1995). Further studies are required to determine whether these early ERP modulations might be influenced by low-level sensory interactions.

4.7. Surface-based attention

The above considerations argue against proposals that the present cueing effects are the result of: (1) feature-based attention to color; (2) feature-based tracking of motion features; or (3) motion adaptation. Accordingly, we consider the most plausible interpretation of these cueing effects to involve a mechanism of surface selection—that is, selection of an ensemble of coherently moving dots that is perceived as a uniform, transparent surface. This selection of an integrated, unitary surface formed by the moving dots would appear to be a form of object-based attention. One of the hallmarks of object-based attention is that observers are characteristically better at discriminating two features of the same attended object than they are at discriminating features of two different spatially superimposed objects. This has been found to be true when the features are of different dimensions, such as color and orientation (Blaser et al., 2000; Duncan, 1984; Rodriguez, Valdes-Sosa, & Freiwald, 2002), or are of the same dimension, such as translation (Reynolds et al., 2003; Valdes-Sosa et al., 2000). Consistent with this interpretation, our observers were better able to compare translations of one surface than of two different surfaces. The underlying neuronal mechanisms involved in binding different visual features into a coherent surface representation are unknown and are controversial (Castelo-Branco, Goebel, Neuenschwander, & Singer, 2000; Thiele & Stoner, 2003). The C1 modulation observed in the current paradigm would suggest that surface-based selection mechanisms influence short latency visual responses at much earlier stages in visual processing than previously reported.

Acknowledgments

We thank Ayrielle Goins for assistance in testing subjects. Funding provided by NIMH Grant MH-25594 awarded to S.A.H., NIH Training Grant in Cognitive Neuroscience to J.F.M., and NEI Grant 5R01EY13802 and a grant from the McKnight Foundation to J.H.R.

References

Anllo-Vento, L., Luck, S. J., & Hillyard, S. A. (1998). Spatio-temporal dynamics of attention to color: Evidence from human electrophysiology. *Human Brain Mapping, 6*, 216–238.

Blaser, E., Pylyshyn, Z. W., & Holcombe, A. O. (2000). Tracking an object through feature space. *Nature, 408*, 196–199.

Castelo-Branco, M., Goebel, R., Neuenschwander, S., & Singer, W. (2000). Neural synchrony correlates with surface segregation rules. *Nature, 405*, 685–689.

Di Russo, F., Martinez, A., & Hillyard, S. A. (2003). Source analysis of event-related cortical activity during visuo-spatial attention. *Cerebral Cortex, 13*, 486–499.

Duncan, J. (1984). Selective attention and the organization of visual information. *Journal of Experimental Psychology: General, 113*, 501–517.

Fries, P., Reynolds, J. H., Rorie, A. E., & Desimone, R. (2001). Modulation of oscillatory neuronal synchronization by selective visual attention. *Science, 23*, 1560–1563.

Fu, S., Fan, S., Chen, L., & Zhuo, Y. (2001). The attentional effects of peripheral cueing as revealed by two event-related potential studies. *Clinical Neurophysiology, 112*, 172–185.

Hopfinger, J. B., Luck, S. J., & Hillyard, S. A. (2004). Selective attention: Electrophysiological and neuromagnetic studies. In M.S. Gazzaniga (Ed.), *The cognitive neurosciences* (Vol. 3). Cambridge, MA: MIT Press.

Luck, S. J., & Hillyard, S. A. (1994). Spatial filtering during visual search: Evidence from human electrophysiology. *Journal of Experimental Psychological: Human Perception and Performance, 5*, 1000–1014.

Lopez, M., Rodriguez, V., & Valdes-Sosa, M. (2004). Two-object attentional interference depends on attentional set. *International Journal of Psychophysiology, 53*, 127–134.

Macmillan, N. A., & Creelman, C. D. (1991). *Detection theory: A user's guide*. New York: Cambridge University Press.

Martinez, A., DiRusso, F., Anllo-Vento, L., Sereno, M. I., Buxton, R. B., & Hillyard, S. A. (2001a). Putting spatial attention on the map: Timing and localization of stimulus selection processes in striate and extrastriate visual areas. *Vision Research, 41*, 1437–1457.

Martinez, A., DiRusso, F., Anllo-Vento, L., & Hillyard, S. A. (2001b). Electrophysiological analysis of cortical mechanisms of selective attention to high and low spatial frequencies. *Clinical Neurophysiology, 112*, 1980–1998.

Mitchell, J. F., Stoner, G. R., Fallah, M., & Reynolds, J. H. (2003). Attentional selection of superimposed surface cannot be explained by modulation of the gain of color channels. *Vision Research, 43*, 1323–1328.

Mitchell, J. F., Stoner, G. R., & Reynolds, J. H. (2004). Object-based attention determines dominance in binocular rivalry. *Nature, 429*, 410–413.

Muller, N. G., & Kleinschmidt, A. (2003). Dynamic interaction of object- and space-based attention in retinotopic visual areas. *Journal of Neuroscience, 23*, 9812–9816.

Noesselt, T., Hillyard, S. A., Woldorff, M. G., Hagner, T., Jaencke, L., Tempelmann, C., Hinrichs, H., & Heinze, H. J. (2002). Delayed striate cortical activation during spatial attention. *Neuron, 35*, 575–587.

Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. F. (1989). Spherical splines for scalp potential and current density mapping. *Electroencephalography and Clinical Neurophysiology, 72*, 184–187.

Pinilla, T., Cobo, A., Torres, K., & Valdes-Sosa, M. (2001). Attentional shifts between surfaces: Effects on detection and early brain potentials. *Vision Research, 41*, 1619–1630.

Qian, N., & Andersen, R. A. (1994). Transparent motion perception as detection of unbalanced motion signals II: Physiology. *Journal of Neuroscience, 14*, 7381–7392.

Qian, N., & Andersen, R. A. (1995). V1 responses to transparent and nontransparent motions. *Experimental Brain Research, 103*, 41–50.

Reynolds, J. H., Alborzian, S., & Stoner, G. R. (2003). Exogenously cued attention triggers competitive selection of surfaces. *Vision Research, 43*, 59–66.

Reynolds, J. H., & Chelazzi, L. (2004). Attentional modulation of visual processing. *Annual Review of Neuroscience, 27*, 611–647.

Reynolds, J. H., Pasternak, T., & Desimone, R. (2000). Attention increases sensitivity of V4 neurons. *Neuron, 26*, 703–714.

Reynolds, J. H., Stoner, G. R., & Mitchell, J. F. (2004). Both continuity of motion and continuity of motion and of texture elements contribute to object-based selection in binocular rivalry. Abstract presented at Society for Neuroscience Annual Meeting.

Rodriguez, V., Valdes-Sosa, M., Bobes, M. A., & Jas, J. (in press). Sensory suppression during shifts of attention between surfaces in transparent motion. *Cognitive Brain Research*.

Rodriguez, V., Valdes-Sosa, M., & Freiwald, W. (2002). Dividing attention between form and motion during transparent surface perception. *Cognitive Brain Research, 13*, 183–193.

Saenz, M., Buracas, G. T., & Boynton, G. M. (2002). Global effects of feature-based attention in human visual cortex. *Nature Neuroscience, 5*, 631–632.

Schoenfeld, M. A., Tempelmann, C., Martinez, A., Hopf, J. M., Sattler, C., Heinze, H. J., & Hillyard, S. A. (2003). Dynamics of feature binding during object-selective attention. *Proceedings of the National Academy of Sciences of the United States of America, 100*, 11806–11811.

Thiele, A., & Stoner, G. (2003). Neural synchrony does not correlate with motion coherence in cortical area MT. *Nature, 421*, 366–370.

Treue, S., & Martinez-Trujillo, J. C. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. *Nature, 399*, 575–579.

Valdes-Sosa, M., Bobes, M. A., Rodriguez, V., & Pinilla, T. (1998). Switching attention without shifting the spotlight object-based attentional modulation of brain potentials. *Journal of Cognitive Neuroscience, 10*, 137–151.

Valdes-Sosa, M., Bobes, M. A., Rodriguez, V., Acosta, Y., Perez, P., Iglesias, J., & Borrego, M. (2004). The influence of scene organization on attention: Psychophysics and electrophysiology. In N. Kanwisher & J. Duncan (Eds.), *Attention and performance XX: Functional neuroimaging of visual cognition* (pp. 321–344). Oxford: Oxford University Press.

Valdes-Sosa, M., Cobo, A., & Pinilla, T. (2000). Attention to object files defined by transparent motion. *Journal of Experimental Psychology: Human Perception and Performance, 26*, 488–505.