ERP evidence that surface-based attention biases interocular competition during rivalry

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J. F. Mitchell, G. R. Stoner, and J. H. Reynolds (2004) observed that exogenously cuing one of two superimposed transparent surfaces resulted in an enhanced perceptual bias for the cued surface during binocular rivalry. We investigated the neural bases of this effect by recording event-related potentials (ERPs). Subjects viewed two superimposed rotating transparent surfaces and compared the directions of two successive translations, either both of the same surface or one of each surface. Following the first translation, which cued attention to the translating surface, two surface images were removed—one from each eye (dichoptic viewing) or both from one eye (monocular viewing). Subjects were impaired at comparing the first and second translations when they occurred on different surfaces, and the impairment was greater during dichoptic viewing (rivalry). The P1 component (110–160 ms) of the ERP elicited by the second translation of the same surface was larger than for the different surface during dichoptic but not monocular viewing. Larger cueing effects were also observed for the subsequent posterior N1 (160–220 ms) and P2 (250–300 ms) components during rivalry than during monocular viewing. These results are in line with a hybrid model of rivalry whereby cuing one surface initiates an earlier interocular selection process when the competing surfaces are presented to separate eyes.

Keywords: object-based attention, binocular rivalry, ERPs, visual cortex

Introduction

During binocular rivalry, perception alternates between the two mismatched images that are presented separately to the left and right eyes. An issue that has been of particular interest is whether binocular rivalry reflects the outcome of competition at an early or a late stage of visual processing (reviewed in Blake & Logothetis, 2002). Recent fMRI studies of binocular rivalry support the viewpoint that rivalry arises from interocular competition at an early stage of visual processing. These studies have reported changes in neural activity associated with rivalry in visual areas as early as the lateral geniculate nucleus (LGN) and primary visual cortex (Büchert et al., 2002; Haynes, Deichmann, & Rees, 2005; Lee, Blake, & Heeger, 2005; Menon, Ogawa, Strupp, & Uğurbil, 1997; Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001; Wunderlich, Schneider, & Kastner, 2005). These findings are consistent with the hypothesis that the perceptual fluctuations experienced during rivalry are the result of reciprocal inhibition between monocular neurons in primary visual cortex (Tong, 2001). However, fMRI provides limited information about the timing of the processes involved in rivalry, and it is unclear whether modulation of activity in these early visual areas reflects local inhibition as opposed to variation in the strength of excitatory feedback.

Other lines of evidence, however, support the view that rivalry arises from competition between incompatible higher-order stimulus representations at later stages of perceptual processing. Studies in awake behaving monkeys have found that perceptual reports are better correlated with single-unit activity in later visual areas than in early visual areas. Correlations have been observed in approximately 20% of neurons in V1/V2,

40% of neurons in areas V4 and MT, and 90% of neurons in the inferotemporal cortex (Leopold & Logothetis, 1996; Logothetis & Schall, 1990; Sheinberg & Logothetis, 1997). Because the largest effects of rivalry were observed in areas where objects are encoded, binocular rivalry may be closely related to multi-stable perceptual phenomena that involve competition between high-level stimulus representations such as a bistable cylinder or Necker cube (Grunewald, Bradley, & Andersen, 2002; Kornmeier & Bach, 2005; Parker, Krug, & Cumming, 2002; Tong, Nakayama, Vaughan, & Kanwisher, 1998).

In view of the substantial evidence favoring both low and high level accounts of binocular rivalry, it has been suggested that a combination of interocular and pattern competition contributes to the perceptual alternations associated with rivalry (Blake & Logothetis, 2002). Within a hybrid model of rivalry (Tong, Meng, & Blake, 2006; Wilson, 2003), inhibitory interactions can occur both at the level of monocular neurons and between binocular pattern-sensitive neurons. One of the model's predictions is that partial monocular suppression at an early level of processing is passed along to a higher stage of processing, where visual competition can continue. A second prediction is that the initial rivalry-related modulations generated at early levels of processing are amplified at higher areas. Furthermore, the strength of neural inhibition can be modulated by selective attention via feedback projections from pattern sensitive neurons to monocular neurons. This hybrid model of rivalry provides a useful framework in which to understand the competitive interactions between different stages of visual processing.

A recent psychophysical study investigated the relationship between binocular rivalry and surface-based selective attention (Mitchell, Stoner, & Reynolds, 2004). In this study, a brief motion transient (translation in one of eight directions) drew attention to one of two spatially superimposed transparent surfaces that were defined by counter-rotating patterns of dots. After this cueing event, the image of one of the surfaces was removed from the left eye, and the image of the other was removed from the right eye. This dichoptic viewing condition resulted in binocular rivalry. As an objective measure of the effect of cuing, observers judged the direction of a second translation of the same (cued) or the different (uncued) surface. Subjects were strongly impaired in judging the direction of the translation of the uncued surface. Since the cue was binocular, it could not directly have led to suppression of the eye that was later randomly selected to view the cued surface during subsequent dichoptic viewing. Instead, the effect of the cue was to favor the cued surface.

In a comparison monocular condition, Mitchell et al. (2004) removed both surface images from one eye after the cueing event, resulting in a percept that was similar to continuous binocular viewing. Thus, this condition also involved removal of two surface images but differed in that it did not induce interocular competition. This made it possible to dissociate the behavioral effect of surface-based selection from that of interocular competition. The behavioral impairment for the uncued surface was stronger and longer lasting when interocular competition was introduced compared to the monocular viewing control. These results suggest that interocular competition was biased by feedback favoring monocular neurons driven by the eye whose image matched the cued surface, and that this biased interocular competition augmented and extended the selection of the cued surface. However, it remains to be determined whether the mechanisms engaged during dichoptic viewing act at relatively late stages of selection where surfaces and patterns are represented or instead act at earlier stages where neurons are sensitive to eye-of-origin information.

Using ERPs, we investigated whether surface-based selection in this paradigm occurs earlier in dichoptic than in monocular viewing conditions. Previous ERP studies of exogenously cued surface selection under normal binocular viewing conditions have consistently reported the posterior N1 (150–250 ms) to be modulated by surface cueing (Khoe, Mitchell, Reynolds, & Hillyard, 2005; López, Rodríguez, & Valdés-Sosa, 2004; Rodríguez & Valdés-Sosa, 2006; Valdés-Sosa et al., 2004). However, in the case of dichoptic viewing, it is unknown which ERP component(s) might be modulated. One possibility is that during dichoptic viewing surface cueing may modulate an earlier ERP component prior to the N1 modulation; that is, interocular competition between surfaces may engage selection mechanisms at an earlier stage of visual processing where eye-of-origin is encoded. We tested this prediction by recording ERPs in the dichoptic and monocular conditions. The major visual ERPs associated with T2 were analyzed to measure the effect of surface cueing and rivalry in early and late stages of visual processing.

Methods

Subjects

Fourteen right-handed normal adults from the University of California, San Diego community (8 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. All procedures and protocols for participants were approved by the University of California, San Diego Human Research Protections Program.

Stimuli

Subjects viewed stimuli through a mirror stereoscope in a darkened quiet room. Stimuli were presented at a

distance of 57 cm on a color monitor. Prior to the experiment, the subject adjusted the mirrors to allow binocular fusion of two nonius lines displayed dichoptically. A chin and forehead rest stabilized the subject's head.

The experimental display consisted of a high-contrast fixation point on a black background presented to both eyes. The fixation point consisted of a black inner disk of radius 0.1 degrees of visual angle (dva) superimposed upon a larger white disk of radius 0.5 dva. The luminance values of the white and black disks were 24.2 and 0.05 cd/m^2, respectively. Centered on the fixation point were two circular superimposed random dot patterns of diameter 4.3 dva. The average density of each dot field was 3.3 dots per square dva, and each dot subtended 0.1 dva. All dots were red, with the red gun of the CRT held at maximum intensity and the green and blue dots set to minimum intensity, resulting in luminance of 5.1 cd/m^2. The two dot patterns rotated rigidly in opposite directions around the central fixation point at 50 deg per second, giving rise to the percept of two superimposed transparent surfaces rotating in opposite directions. To screen subjects for strong pre-existing ocular biases, subjects were asked to discriminate brief translations of the surfaces during rivalrous presentation. If mean accuracy between the two eyes differed by greater than 15%, subjects were excluded from the experiment. Two subjects (from an original pool of 16) were excluded on this basis.

Experimental design

Each trial began with the appearance of the two surfaces rotating in opposite directions for 800 ms, presented binocularly (Figure 1). After this period of rotation, the dots that defined one of the surfaces, selected at random, underwent a brief shift 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 dva per second. Subjects were told that the translation would be equally likely to occur on either surface. The design incorporated an unpredictable first translation in order to avoid possible endogenous cueing
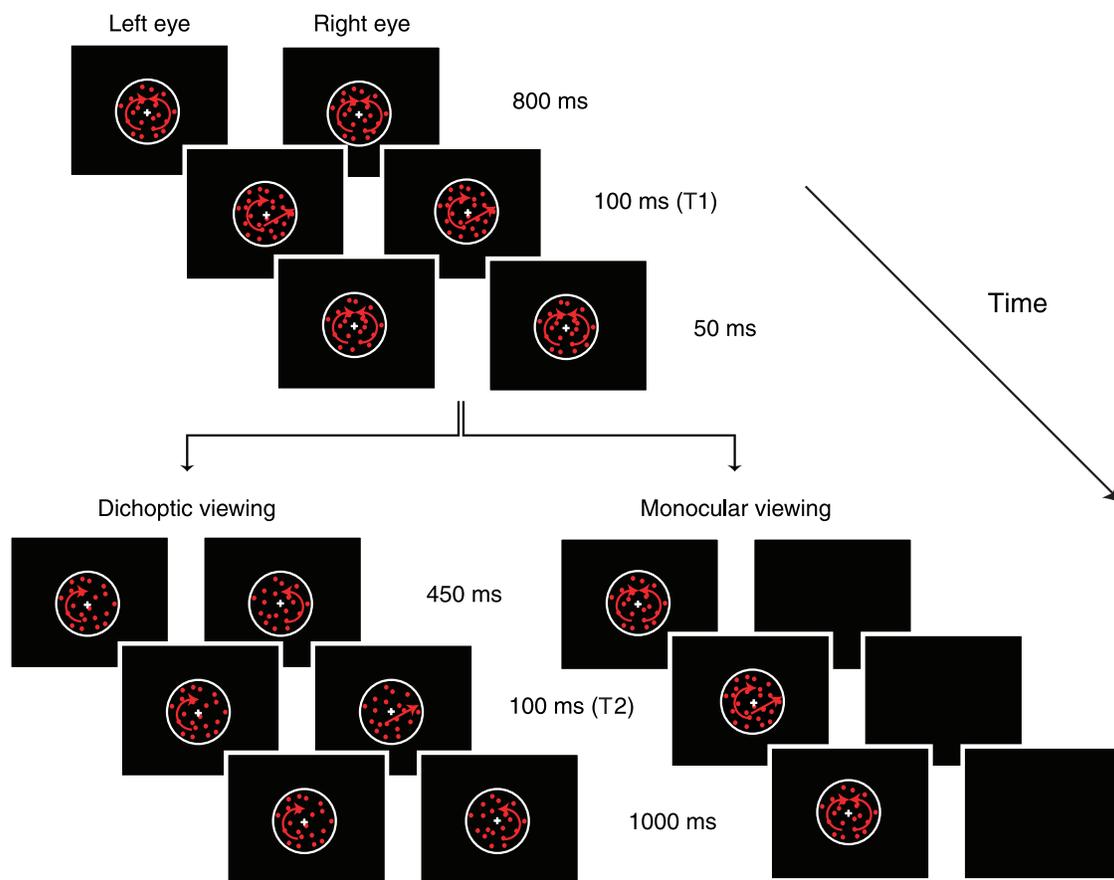

Figure 1. Each trial began with two random superimposed dot patterns that rotated in opposite directions presented to both eyes, thus generating the percept of two transparent surfaces. After 800 ms, one of the two surfaces translated in one of four directions, and the surfaces continue rotating for 50 ms before viewing became dichoptic or monocular. Following the switch in viewing the surfaces rotated for 450 ms, whereupon a second translation (T2) (100 ms) occurred on either the same or different surface selected at random. Subjects responded with a button press when T1 and T2 were in the same direction.

effects. After the first translation (T1), the surfaces continued rotating for 50 ms. Two surface images were then removed, either one from each eye (dichoptic viewing condition) or both from one eye (monocular transparency condition). Following this double image deletion, 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 relative to T1. T2 occurred with equal probability on the two surfaces. On 25% of these trials, both translations were in the same direction. For the remaining 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 run in ten experimental blocks, each composed of 128 trials.

Behavioral data acquisition and analysis

Subjects were instructed to respond within the interval of continued rotation after the second translation in order to prevent their response from overlapping with the subsequent trial. After each trial, the screen went blank for 1500 ms before 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). Sensitivity estimates were entered into a repeated measures ANOVA with factors of cueing condition (same vs. different surface), viewing condition (dichoptic vs. monocular), and eye of origin (left vs. right).

Differences between cueing conditions were normalized by computing an attentional modulation index (AI) for each subjects' mean performance. The AI was defined by $(d'_S - d'_D) / (d'_S + d'_D)$, where d'_S and d'_D are the d' values obtained in the same and different surface cueing conditions, respectively.

ERP acquisition and analysis

Scalp potentials were recorded from 60 tin electrodes that were distributed over the entire scalp and mounted in a custom cap (Electro-Cap International). Electrodes were placed according to the 10–20 location system. The scalp recordings were referenced to the right mastoid during recording, with the left mastoid recorded as an active electrode site. Scalp and mastoid electrode impedances were maintained below 5 and 2 kΩ, respectively. Vertical eye movements were recorded by an electrode placed below the left eye and referenced to the right mastoid.

Horizontal eye movements were recorded with an electrode over the right outer canthus referenced to the left outer canthus. Electroencephalographic (EEG) and electro-oculographic (EOG) activity was amplified with a gain of 10,000, band-pass filtered at 0.1–80 Hz, digitized online at a sampling rate of 500 Hz, and stored on a computer hard drive for off-line analysis. ERPs were algebraically re-referenced to the average of left and right mastoid and low-pass filtered to attenuate signals at and above 57 Hz.

ERPs were averaged off-line over epochs beginning 1500 ms before T2 and extending 1500 ms after T2 onset. Automated artifact rejection was used to reject trials that contained eye movements, blinks, muscle potentials, or amplifier blocking. To rule out any systematic 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 degrees (Luck et al., 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.

To avoid possible motor response-related contamination, only "correct rejection" trials were included in the ERP analysis. To quantify the ERP components elicited by T2, mean amplitude measures over specified time windows were taken with respect 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, and electrode clusters were chosen for which component amplitudes were maximum. For posterior components, the latency ranges of 110–160 ms for the P1 and 170–220 ms for the N1 were used to calculate the mean amplitudes. These measurements were taken from lateral occipital electrode sites P5/P6, PO3/PO4, and PO7/PO8. For the anterior N1 component, the latency range of 170–200 ms was used at electrode sites F3/F4, FC1/FC2, Fz, and FCz. For the anterior P2 component, the latency range of 230–280 ms was used at electrode sites FC3/FC4, FC1/FC2, C1/C2, and C3/C4. The ERP data were analyzed using a repeated measures ANOVA with cueing condition (same vs. different surface), viewing condition (dichoptic vs. monocular), and hemisphere (left vs. right) as factors. The ANOVA for the anterior N1 component did not include the factor of hemisphere due to its diffuse bilateral distribution. An ANOVA was also performed on the peak latencies of the posterior N1. The P values were adjusted for heterogeneity of variance and covariance using the Geisser–Greenhouse epsilon method. Since testing the modulations of the major ERP components was based on a priori hypotheses (see Introduction), corrections for multiple tests were not necessary.

To visualize the scalp distributions of the ERP modulations with attention, voltage topographical maps were

constructed from the attentional difference waves, formed by subtracting the ERPs to T2 of the uncued surface from that of the cued surface, using a spherical spline interpolation which accounts for the curvature of the scalp and non-uniform spacing of the electrodes (Perrin, Pernier, Bertrand, & Echallier, 1989). A statistical comparison of the attentional difference waves under the two viewing conditions was performed for the N1 and P2 components to compare the neural generator sources between the two conditions. The ERP amplitudes were rescaled prior to ANOVA comparisons using the procedure described by McCarthy and Woods (1985). Scaling the voltages in each experimental condition by its corresponding vector length (i.e., square root of the sum of squared voltages over all electrode location) ensures that overall amplitude differences associated with each condition are eliminated while differences between the shapes of distribution across conditions are retained. A significant interaction in the ANOVA between experimental condition and scalp distribution provides evidence for qualitatively different spatial configurations of the underlying generators among experimental conditions. ANOVA factors in the N1 scalp topography analysis included viewing condition (monocular vs. dichoptic), location (parietal vs. occipital), and electrode. A time

window between 170 and 220 ms was specified to calculate the mean amplitude of the posterior N1 component from parietal electrode (CP3/CP4, CP5/CP6, P3/P4, P1/P2, P5/P6, and PO3/PO4) and occipital electrodes (TP7/TP8, P7/P8, PO7/PO8, O1/O2, I5/I6, and I3/I4). Factors used in the P2 topography analysis included viewing condition (monocular vs. dichoptic), location (frontal/central vs. central/parietal), and electrode. Mean amplitudes were obtained from frontal/central electrodes (FC1, FC2, FCz, C1, C2, Cz) and central/parietal electrodes (CP1, CP2, CPz, P1, P2, Pz) and a time window of 240–280 ms.

Results

Behavior

Subjects were impaired at comparing the translation directions when T2 occurred on the different (uncued) versus the same (cued) surface as T1, as reflected by the lower d' values ($F(1, 13) = 25.31$, $p = 0.0002$) (Figure 2A). In addition, sensitivity estimates were significantly greater
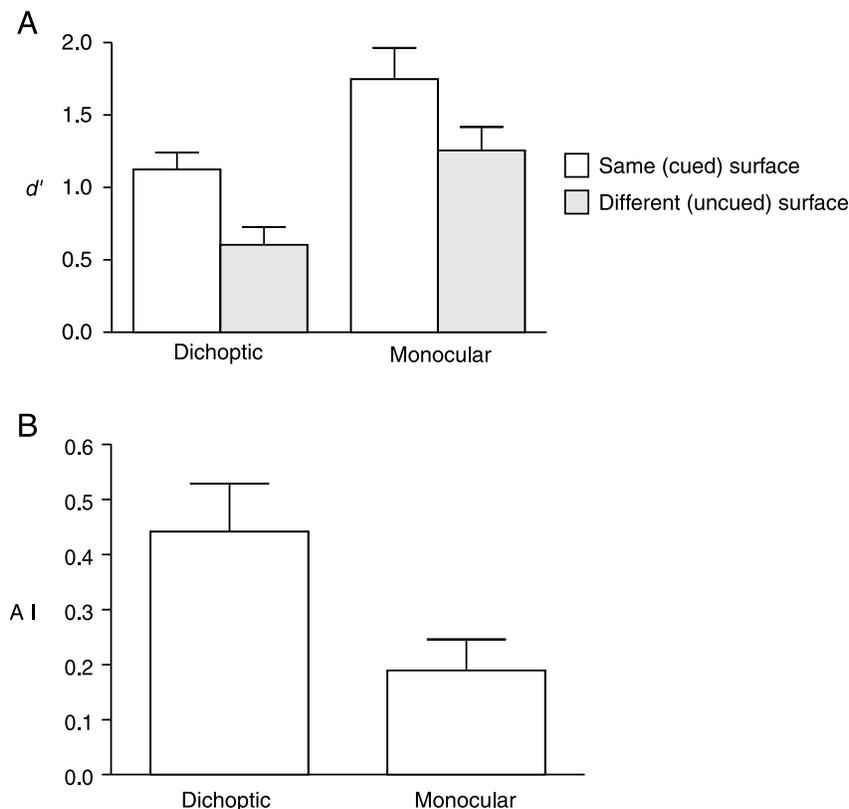

Figure 2. (A) Abrupt translation on one surface for 100 ms results in higher detectability (higher d') for T2 of cued vs. uncued surface during both rivalry and monocular viewing conditions, averaged across all subjects. Standard errors of the mean are plotted for each cueing condition. (B) Calculation of attentional modulation index (AI) revealed that suppression of the uncued surface was proportionally greater during dichoptic than monocular viewing.

for monocular than for dichoptic viewing ($F(1, 13)$ = 35.45, p = 0.00005). Eye of stimulation was not a significant factor ($F < 1$) nor were any of the interactions ($F < 1$). Analysis of the AI values found that the proportional suppression of the uncued surface was significantly greater in the dichoptic than the monocular viewing condition (paired $t(13)$ = 2.49, p = 0.01) (Figure 2B).

ERPs

Because eye of stimulation was not a significant factor in the behavioral analysis, the ERPs elicited by T2 to the left and right eye were collapsed. At posterior electrode sites, the effect of cueing condition (same vs. different surface) was evident in modulations of the P1 (110–160 ms) and N1 (190–230 ms) components (Figure 3).

A significant interaction between cueing and viewing conditions was observed for the P1 amplitude measure ($F(1, 13)$ = 5.07, p = 0.04). During rivalry, the P1 was larger in response to T2 of the cued surface than T2 of the uncued surface ($F(1, 13)$ = 5.22, p = 0.031). In contrast, the P1 was not modulated by cueing during monocular

viewing ($F < 1$). The posterior N1 was significantly larger overall when elicited by T2 of the cued surface than of the uncued surface ($F(1, 13)$ = 14.82, p = 0.002). In addition, there was a significant interaction between cueing and viewing condition ($F(1, 13)$ = 5.14, p = 0.041). This interaction resulted from the cueing effect on the N1 (larger amplitude for the same surface T2 than different surface T2) being greater during rivalry ($F(1, 13)$ = 11.08, p = 0.0055) than monocular viewing ($F(1, 13)$ = 6.55, p = 0.024).

At central and anterior electrode sites, the P2 component (250–300 ms) was significantly larger for T2 of the cued surface than of the uncued surface ($F(1, 13)$ = 10.49, p = 0.0065). Moreover, the effect of cueing on the P2 was larger during rivalry (dichoptic) than for transparency (monocular) viewing ($F(1, 13)$ = 5.70, p = 0.032). The anterior N1 (160–200 ms) evoked by T2 of the cued surface was also larger than for the uncued surface ($F(1, 13)$ = 11.59, p = 0.0047), but this effect did not differ between rivalry and monocular viewing ($F < 1$) (Figure 4).

An analysis of the peak latencies of the posterior N1 elicited by T2 revealed an interaction between cueing and viewing condition ($F(1, 13)$ = 10.09, p = 0.00073). The
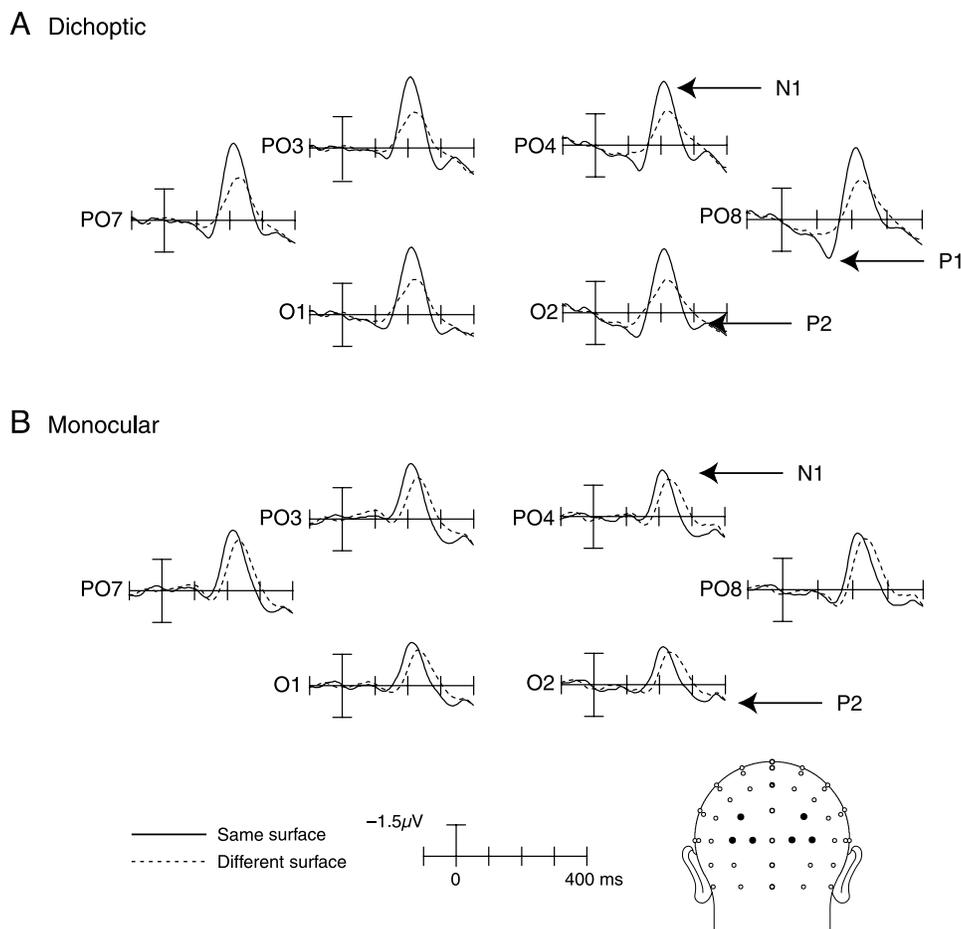

Figure 3. Grand average ERPs at posterior electrode locations elicited by T2 for same (cued) and different (uncued) surfaces under dichoptic (A) and monocular viewing (B) conditions.
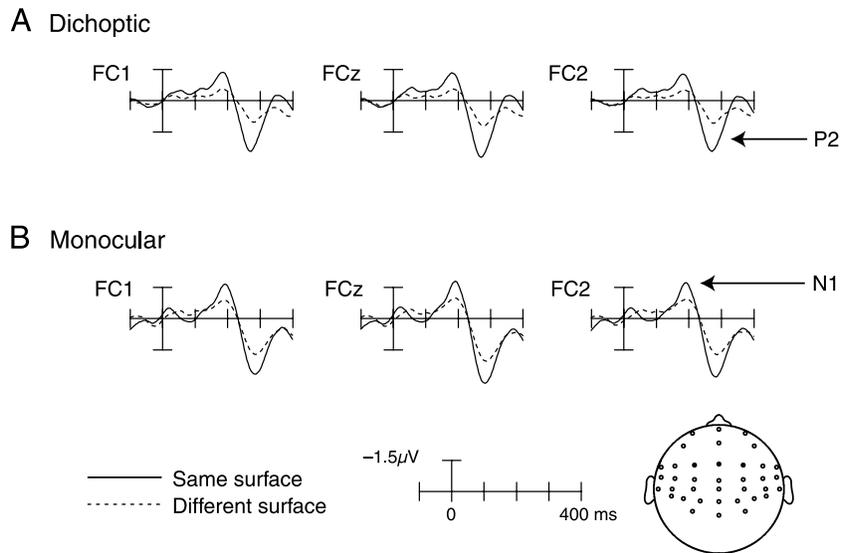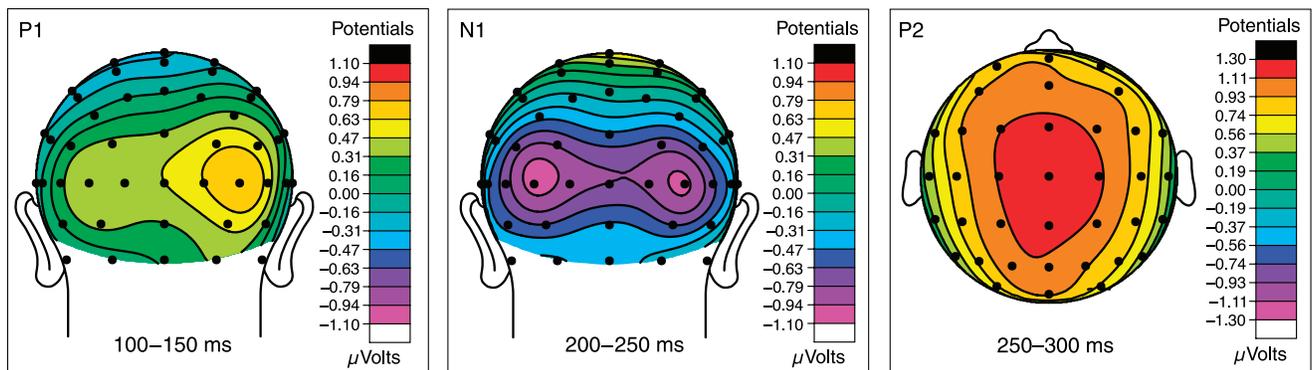
Figure 4. Grand average ERPs at anterior electrode locations elicited by T2 of the same (cued) and different (uncued) surface under dichoptic (A) and monocular viewing (B).
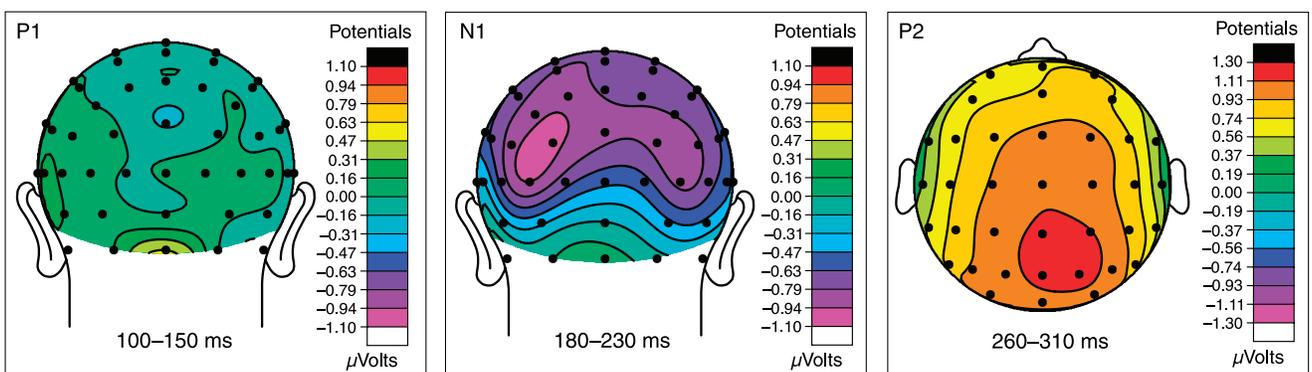

Figure 5. Scalp topographies of the P1, N1, and P2 attentional difference wave during dichoptic (A) and monocular viewing (B). Difference waves were calculated as mean amplitudes over indicated latency ranges for components when elicited by T2 of the cued surface minus when elicited by T2 of the uncued surface.

peak latency of the N1 to the cued surface T2 occurred earlier than the uncued surface T2 during monocular viewing (211 vs. 224 ms). In contrast, there were no significant differences between peak N1 latencies to the cued versus uncued T2's during dichoptic viewing (213 vs. 210 ms).

Scalp topography of attention effect

For dichoptic viewing (100–150 ms), the scalp distribution of the P1 attentional difference wave, that is, the amplitude difference between the P1 elicited by T2 of the cued versus the uncued surface, was focused over lateral occipital sites with a non-significant right hemispheric bias (Figure 5A). In contrast, this P1 difference was at noise levels in the monocular condition (Figure 5B). The N1 attentional difference had a bilateral occipital distribution in dichoptic viewing, whereas it had a more dorsal occipitoparietal distribution in monocular viewing ($F(1, 13) = 31.29$, $p = 0.0001$). The P2 attentional difference was broadly distributed over central and parietal sites, with a more central distribution for the dichoptic compared to the monocular condition ($F(1, 13) = 5.18$, $p = 0.04$).

Discussion

The present study investigated the interaction between surface-selective cueing of attention and binocular rivalry. Consistent with the findings of Mitchell et al. (2004), a brief translation of one of two superimposed surfaces resulted in a marked impairment in judging a subsequent translation of the other (uncued) surface during both monocular and dichoptic viewing. As in the Mitchell et al. study, the magnitude of the impairment was significantly different between viewing conditions, with greater relative impairment when subjects had to judge the second translation under dichoptic viewing. In association with these perceptual cueing effects, we observed cue-related modulations of the P1, N1, and P2 components of the visual ERPs elicited by the second translation, T2. The magnitude and time course for the ERP cueing effects differed significantly between monocular and dichoptic viewing conditions.

During dichoptic viewing, the occipital P1 component (110–160 ms) evoked by T2 was enhanced for translations of the cued surface relative to the uncued surface. In contrast, this early cueing effect on the P1 was not observed with monocular viewing. The occipital N1 component (170–220 ms) also exhibited a larger cue-related amplitude modulation during dichoptic viewing relative to monocular viewing, as did the centro-parietally distributed P2 component (250–300 ms). These complementary behavioral and ERP data suggest that interocular selection, made possible during dichoptic viewing, occurred at a processing stage earlier than during monocular surface selection. Given the only difference between viewing conditions was whether the surface images were presented dichoptically or monocularly following the cueing translation, the earlier P1 modulation can be singly ascribed to an interocular selection mechanism. Further, the larger N1 and P2 attentional modulations observed during dichoptic viewing can be attributed to presenting competing disparate images to each eye. Presumably, the enhanced early selection made possible during dichoptic presentation is fed forward to higher stages of processing.

The P1 and N1 attention effects observed in the current study have occipital scalp distributions similar to those seen in spatial attention studies that used briefly flashed stimuli (Di Russo, Martínez, & Hillyard, 2003). In those studies, the attention-related P1/N1 modulations were localized by dipole modeling to ventral and lateral extrastriate occipital cortex. Previous studies using motion-onset stimuli, as in the present experiment, identified N1 generators in ventral–lateral occipital–temporal cortex including areas MT/V5 and V3/V3A (Heinrich, 2007; Probst, Plendl, Paulus, Wist, & Scherg, 1993; Rodríguez & Valdés-Sosa, 2006; Schellart, Trindade, Reits, Verbunt, & Spekreijse, 2004). The present data suggests that the P1 observed here indexes interocular selection during dichoptic viewing that occurs at an earlier level of extrastriate cortex. It is conceivable, however, that the early cue-related P1 modulation might reflect interocular selection occurring at an even earlier level—possibly in primary visual cortex—if such a selection did not produce an organized ERP field recordable on the scalp until activity reached a higher extrastriate stage. The broad scalp topography of the P2 makes it difficult to localize, but it appears to reflect a later stage of surface selection that is modulated by attention. While these ERP localizations based on surface recordings always have a degree of uncertainty, the precise timing information available in the ERP does allow us to conclude that an earlier level of selection is engaged when the competing surfaces are presented to the separate eyes rather than to the same eye.

Related studies

EEG and MEG studies have established a linkage between the neural activity and the periods of dominance and suppression that occur during rivalry. The general finding is that the amplitude of neural activity is attenuated for stimuli presented to the suppressed eye (Brown & Norcia, 1997; Cobb, Morton, & Ettlinger, 1967; de Labra & Valle-Inclán, 2001; Kaernbach, Schröger, Jacobsen, & Roeber, 1999; Lansing, 1964; Srinivasan, Russell, Edelman, & Tononi, 1999; Srinivasan & Petrovic, 2006; Valle-Inclán,

Hackley, de Labra, & Alvarez, 1999). Of particular interest, Roeber and Schröger (2004) observed a reduction in the amplitudes of the P1 and N1 elicited by suppressed stimuli during binocular rivalry. Their findings provide evidence consistent with the view that interocular competition is initially resolved at the level of extrastriate occipital cortex. Tse, Martinez-Conde, Schlegel, and Macknik (2005) observed increased BOLD modulations associated with dichoptic masking at successively higher extrastriate visual areas ascending the visual pathway. They proposed that extrastriate occipital areas contain the necessary cortical inhibitory circuitry to produce interocular suppressive effects. Consistent with these findings, we obtained evidence that neural activity elicited in association with rivalrous surface selection occurred in early extrastriate occipital areas and was maintained in higher areas.

ERP studies of selective attention to superimposed surfaces have presented identical surface images to the two eyes under normal binocular viewing conditions (Khoe et al., 2005; López et al., 2004; Pinilla, Cobo, Torres, & Valdés-Sosa, 2001; Valdés-Sosa, Bobes, Rodríguez, & Pinilla, 1998). Under sustained endogenous cueing conditions, both P1 and N1 amplitudes were found to be larger in response to translation of the attended surface versus the unattended surface (Valdés-Sosa et al., 1998). However, in experiments where attention was cued endogenously or exogenously on a trial-by-trial basis, only the N1 component was consistently modulated. These earlier studies provide evidence that the N1 modulation reflects surface-based selective attention.

The current finding that the P1 component is modulated by surface selection under conditions of rivalry support the idea that surface-based cueing can influence selection mechanisms initiated during rivalry. Moreover, such mechanisms are elicited at an earlier level of processing than those involved in surface selection alone. A similar result was recently obtained by Mishra and Hillyard (in press) in a study where selective attention was cued endogenously to one of two surfaces defined by overlapping patterns of dots; the P1 was larger to the attended surface under conditions of dichoptic viewing but not in monocular viewing. ERP studies of other types of bistable stimuli that do not elicit interocular competition, such as Necker cubes, have reported early P1 modulations (~115 ms) associated with perceptual switching; the P1 modulation may reflect feedback signals to lower visual areas that bias perception between perceptual possibilities (Kornmeier & Bach, 2005; Pitts, Nerger, & Davis, 2007). In contrast, the present results indicate that surface selection is initiated at a higher level of processing indexed by an amplitude increase and latency decrease of an N1 component (180–230 ms) having a occipitoparietal scalp distribution. A similar effect upon peak latencies was evident in the N1 modulation produced by cueing under monocular viewing in a prior study (i.e., Khoe et al., 2005).

The role of feedback in binocular rivalry

In the hybrid model of binocular rivalry, it is proposed that excitatory feedback from pattern selective neurons may selectively activate neurons with monocular preferences that are directly involved in interocular competition (Tong et al., 2006; Wilson, 2003). This hybrid model is consistent with the time course of behavioral impairments observed previously using the current paradigm (Mitchell et al., 2004). Mitchell and colleagues varied the timing of the second translation relative to the cueing translation to examine the time course of the cueing effect in monocular and dichoptic viewing. With monocular viewing, the cue led to an immediate impairment in judging the translation of the uncued surface, which lasted several hundred milliseconds. In dichoptic viewing, the cueing effect was much weaker at first, but grew in strength over several hundred milliseconds of dichoptic viewing, ultimately giving a larger and longer lasting impairment than in monocular viewing. Assuming that surface cueing modulates later stages of processing associated with surface encoding under both viewing conditions, the hybrid model would predict that dichoptic viewing of the competing surfaces allows for interocular competition to take place at earlier stages of processing that are biased to favor the cued surface via feedback. However, some delay—that is, the time between the first and second translation—would be necessary for surface-based selection at later stages to bias the ongoing lower-level interocular competition so as to favor the eye whose bottom up input image matches the features of the cued surface. Once the balance of interocular competition is tipped in favor of the eye containing the cued surface, the subsequent rivalry-related modulations maintain the selection of the cued surface at later stages, resulting in larger and longer lasting cueing effects such as were observed by Mitchell et al.

Our current findings are consistent with the interaction of late and early levels of processing proposed in the hybrid model. In particular, the P1 modulation under dichoptic viewing may reflect top-down attentional modulations of monocular neurons driven by the eye that viewed the cued surface during rivalrous viewing conditions. This P1 modulation likely reflects ocular selection at the level of early extrastriate occipital cortex, although as noted above selection may have occurred earlier in primary visual cortex but may not have generated an organized ERP field until it reached extrastriate cortex. This early ocular selection is fed forward and possibly amplified at higher levels of visual processing as reflected in the N1 and P2 components. During monocular viewing, attention only acts to bias surface selection at a later processing stage as indexed by the modulations of these later components. The present findings shed light on the interplay between different stages of processing in selecting information that reaches visual awareness during rivalry and attention.

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