Endogenous attention selection during binocular rivalry at early stages of visual processing

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ABSTRACT

Directing attention to one of two superimposing surfaces composed of dot fields rotating in opposing directions facilitates processing of brief translations of the attended surface [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 Cognition and Neuroscience, 10*(1), 137–151]. Here we used ERP recordings to investigate the mechanisms of endogenous attentional selection of such competing dot surfaces under conditions of dichoptic viewing (one surface to each eye) and monocular viewing (both surfaces to one eye). Under dichoptic conditions, which induced binocular rivalry, translations of the attended surface presented to one eye elicited enhanced visual P1 and N1 ERP components relative to translations of the unattended surface presented to the other eye. In comparison, during monocular viewing the attended surface translations elicited a significantly larger N1 component in the absence of any P1 modulation. These results indicate that processing of the attended surface is biased at an earlier level in extrastriate visual cortex under conditions of inter-ocular versus intra-ocular competition.

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1. Introduction

During binocular rivalry dissimilar stimuli presented to the separate eyes are seen to alternate spontaneously between one ocular image and the other. These fluctuations in dominance and suppression are unpredictable in duration, but it is possible to bias the dominance of one rival image over the other by boosting the strength of its attributes such as contrast, luminosity, degree of motion, or contour density (Blake & Logothetis, 2002; Silver & Logothetis, 2007) or by blurring the other image (Arnold, Grove, & Wallis, 2007). Apart from explicit changes in the physical features of a stimulus, the role of top-down attention in biasing stimulus dominance has been debated for the past century. Helmholtz (1925) was the first proponent of attentional modulation of rivalry and showed that by mentally counting the contours on a rivalrous target (i.e., by focusing attention on it) he could induce sustained dominance of that stimulus. In recent years considerable evidence for the attentional control of rivalry has accrued (reviewed in Tong, Meng, & Blake, 2006). Ooi and He (1999) showed that voluntary attention directed to a dominant stimulus in one eye made it less likely to be suppressed by a perturbing event presented to the other eye. Mitchell, Stoner, and Reynolds (2004) found that exogenous attentional capture by one of two superimposed rotating non-rivalrous dot surfaces could bias dominance in favor of the selected surface during subsequent periods of rivalry. Chong and Blake (2006) obtained similar results using rivalrous gratings instead of dot patterns and showed that endogenous attention could also bias initial dominance during rivalry. Corroborating Helmholtz's initial findings, Chong, Tadin, and Blake (2005) found that endogenous attention indeed prolonged dominance durations during rivalry, but only when attention was deployed to the features of a rivalrous stimulus. Mere attentional engagement or spatial attention to the location of the rivalrous stimulus was insufficient to bias dominance durations. Hancock and Andrews (2007) also found evidence that involuntary as well as voluntary attention can select a rivalrous grating to be perceptually dominant. Their findings suggest competition during binocular rivalry may be an example of a more general attentional mechanism within the visual system.

Although attentional control of binocular rivalry has been established in psychophysical investigations, little is known of its neural bases. Neurophysiological investigations of attention and binocular rivalry have suggested that the two processes may involve common mechanisms (Stoner, Mitchell, Fallah, & Reynolds, 2005). Competitive stimulus selections via visual attention (reviewed in Kastner & Pinsk, 2004; Reynolds & Chelazzi, 2004) and binocular rivalry (reviewed in Blake & Logothetis, 2002; Moutoussis, Keliris, Kourtzi, & Logothetis, 2005; Tong et al., 2006) are

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both resolved at multiple stages of processing in the visual cortex with progressively greater selectivity observed in higher cortical areas such as V4, MT and IT. Although evidence from human fMRI studies of binocular rivalry suggests that eye-based competitive selection may occur as early as area V1 (Buchert et al., 2002; Lee, Blake, & Heeger, 2005; Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001) or even LGN (Haynes, Deichmann, & Rees, 2005; Wunderlich, Schneider, & Kastner, 2005), stimulus feature competition occurring in higher areas is an integral part of rivalry resolution that correlates more closely with perceptual state (Haynes & Rees, 2005; Leopold & Logothetis, 1996; Sheinberg & Logothetis, 1997). Transcranial magnetic stimulation (TMS) of areas V1/V2 has been shown to induce perceptual state changes during rivalry (Pearson, Tadin, & Blake, 2007), but the authors did not consider their results to be incompatible with involvement of higher cortical areas that govern selection of the rivalrous stimuli via attention. These results together support emerging models of neural processing in binocular rivalry that involve a hierarchy of processing stages (Blake & Logothetis, 2002; Freeman, 2005; Lee, Blake, & Heeger, 2007; Tong et al., 2006; Wilson, 2003).

The time course of inter-ocular competition during rivalry has been studied by means of scalp-recorded event related potentials (ERPs). ERPs allow for observations of precise temporal modulations in visual processing and reportedly have sufficient spatial resolution to distinguish neural generators in striate and extrastriate cortical areas (Di Russo, Martinez, & Hillyard, 2003; Martinez et al., 1999, 2001; Noesselt et al., 2002). Previous investigations of binocular rivalry using ERPs found early modulations beginning at around 100 ms (Roeber & Schröger, 2004; Valle-Inclan et al., 1999), but the neural generators of these effects were not determined. Other EEG and MEG studies of rivalry have demonstrated effects such as greater amplitudes of scalp potentials or fields and greater synchrony between sensors elicited when a stimulus is perceptually dominant vs. when it is suppressed (Brown & Norcia, 1997; Cobb, Morton, & Ettlinger, 1967; Kaernbach, Schroger, Jacobsen, & Roeber, 1999; Lansing, 1964; Srinivasan & Petrovic, 2006; Srinivasan, Russell, Edelman, & Tononi, 1999).

In the present study we investigated the neural basis of attentional allocation to one of two rivalrous stimulus arrays using ERP recordings together with source localization of the underlying neural generators. We employed a paradigm wherein subjects viewed superimposed rotating dot surfaces, which was introduced by Valdes-Sosa, Bobes, Rodriguez, and Pinilla (1998) to investigate surface-based attentional selection in the absence of spatial cues. In this study we compared the neural bases of endogenous attentional selection of these competing dot surfaces under conditions of dichoptic viewing (with binocular rivalry) versus conditions of monocular viewing.

2. Methods

2.1. Task and stimuli

Thirteen right-handed healthy adults (7 males and 6 females, mean age 22 years) participated in the study after giving informed consent. Each participant had normal or corrected-to-normal vision.

Stimuli were displayed on a CRT monitor at 57 cm viewing distance in a darkened room. Subjects rested their heads on a chin-rest and viewed stimuli through a mirror stereoscope. Binocular alignment was ensured before starting the experiment by requiring the subjects to align two dichoptically presented nonius bars. During the experiment subjects fixated on a high-contrast central white annulus having inner and outer radii of 0.1° and 0.5° of visual angle (va), respectively, which was presented to both eyes and perceived as a single annulus through the stereoscope on a dark background. The luminances of the white and dark regions were 24.2 and 0.05 cd/m², respectively. Surrounding the fixation annulus were two overlapping counter-rotating circular random dot patterns (diameter: 4.3° va), one green and one red. These rotating patterns created the perceptual impression of two transparent rigid surfaces sliding across each other (Valdes-Sosa et al., 1998). To induce rivalry the two dot surfaces were presented dichoptically (i.e., one in each

eye) on half the experimental trials. On the remaining trials the two surfaces were presented monocularly (i.e., both surfaces to one eye). Dichoptic and monocular trials were presented in separate runs. Surface rotation direction in either eye was balanced across all trials. Surface rotation speed was 40°/s. Dot density of each dot field was 3.3 dots per square degree of visual angle, and each dot subtended 0.1° of visual angle. Red dot intensity was 5.1 cd/m², while equiluminance of green dots was established independently for every subject prior to the experiment via heterochromatic flicker fusion (Khoe, Mitchell, Reynolds, & Hillyard, 2005).

Stimulus events consisted of brief (100 ms) translations of one of the surfaces in either the upward or downward direction. Dots translated at a speed of 4° va/s. Only a subset of the dots (60%) translated coherently in order to encourage attending to the complete ensemble instead of focusing on individual dots. Interstimulus intervals (ISIs) between successive translations had a uniform distribution ranging from 400 to 700 ms (SOA 500 to 800 ms). The dot set involved in each event was randomly selected.

Each run was of 15 s duration with the first and last 500 ms devoid of dot translations. Four blocks of 20 runs each constituted the full experiment, with 10 s rest break after each run and several minutes of rest between blocks. Dichoptic and monocular runs were presented in counter-balanced order. Prior to each run a red or green color cue flashed on the screen for 3 s to instruct subjects to direct attention to the surface with the cued color. Attended color was randomly selected on each run and counter-balanced across all runs. During runs subjects performed a translation direction discrimination task on the attended surface and were instructed to respond with a button press every time they detected a target translation in the downward direction. Equally probable translations of the unattended surface were to be ignored. Target occurrence probability was 20% for both the attended and the unattended dot surfaces. The translations in the upward direction (80%) required no button press response and were designated as standards. A schematic of the experimental design for both dichoptic and monocular runs is shown in Fig. 1.

Speed and accuracy were both emphasized in the behavioral task, and correct responses were scored within a 200–800 ms period after translation onset. Correct responses to targets were categorized as 'hits' while responses to non-target upward translations were classified as 'false alarms'. The hit and false alarm rates were used to derive the sensitivity estimate d' (MacMillan & Creelman, 1991). Before the experimental recording sessions subjects practiced on the task for about 30 min and achieved a target discrimination sensitivity of $d' \geqslant 1.0$.

2.2. Electrophysiological recordings and data analysis

The electroencephalogram (EEG) was recorded from 64 electrode sites using a modified 10–20 system montage (Di Russo et al., 2003). Horizontal and vertical electro-oculograms (EOGs) were recorded by means of electrodes at the left and right external canthi and an electrode below the left eye, respectively. All electrodes were referenced to the right mastoid electrode during recording. Electrode impedances were kept below 5 kΩ.

The EEG was digitized at 250 Hz with an amplifier band pass of 0.1–80 Hz and gain of 10,000. Prior to signal averaging automated artifact rejection was performed to discard trials with eye movements, blinks or amplifier blocking. For each subject and condition ERPs were averaged time-locked to standard translations of both the attended and unattended surfaces (i.e., to non-target translations that had no associated erroneous button presses). The averages were digitally low-pass filtered with a Gaussian finite impulse function (3 dB attenuation at 46 Hz) to remove high frequency noise produced by muscle activity and external electrical sources. The filtered averages were digitally re-referenced to the average of the left and right mastoids. ERPs from all subjects were pooled to create grand-average waveforms. Attention effects were assessed by comparing the ERPs to attended standards vs. unattended standards, separately for both dichoptic and monocular viewing conditions. ERPs to the attended and unattended targets were also compared in each viewing conditions. Scalp topography maps and source localization analyses (see below) were based on attentional difference waves formed by subtracting the averaged unattended from the averaged attended waveforms for each viewing condition:

Dichoptic difference wave = Dichoptic Attended ERPs − Dichoptic Unattended ERPs.

Monocular difference wave = Monocular Attended ERPs − Monocular Unattended ERPs.

To quantify the significance of the attention effects, the prominent visual ERP components, P1 and N1 were measured as mean voltage amplitudes across 12 posterior electrode sites (6 in each hemisphere) where these components were largest. Mean amplitudes of the P1 (over 112–144 ms) and N1 (over 188–228 ms) components were tested for significance with respect to a 100 ms pre-stimulus baseline using t-tests. The time windows for the P1 and N1 components were centered around the peak latency of each component as measured in the grand-average waveform. Attention effects on the later P2 (240–280 ms), and the P300 (424–492 ms) component elicited by targets were also similarly characterized over 12 central electrode sites.

Scalp distributions of the P1, N1 and P2 components in the attentional difference waves were compared under the two viewing conditions after normalizing their amplitudes prior to ANOVA according to the method described by McCarthy
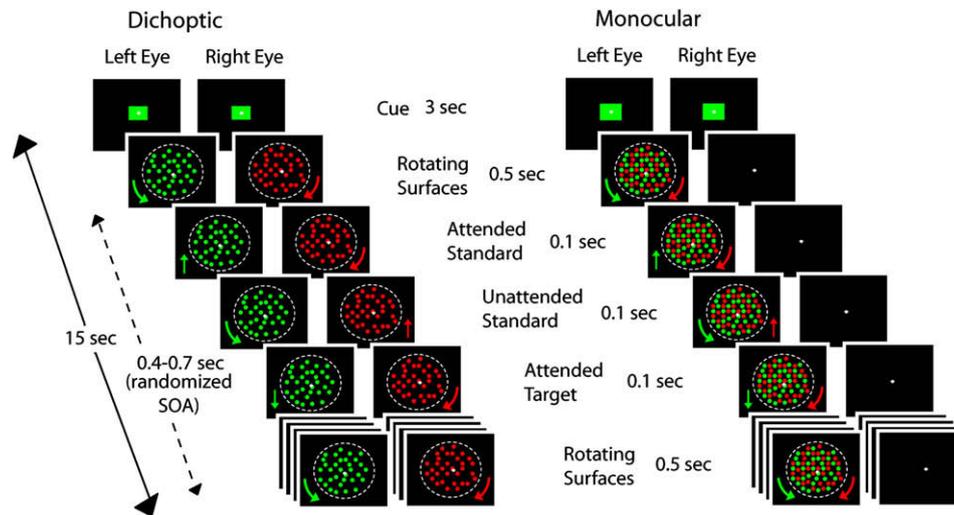
Fig. 1. Overview of the experimental design. Sample stimulus presentations in the dichoptic viewing condition are shown on the left, and in monocular viewing on the right. Target and standard translations of the attended and unattended dot surfaces are denoted. Time proceeds from top to bottom.

and Wood (1985). For the posteriorly distributed P1 and N1 components comparisons were made over 22 occipital electrode sites (9 in each hemisphere and 4 along the midline). For the P2 component comparisons were made over 40 electrodes spanning frontal, central, parietal and occipital sites (16 in each hemisphere and 8 midline). Differences in scalp distribution were reflected in significant stimulus condition (dichoptic/monocular) by electrode interactions.

2.3. Modeling of ERP sources

Source localization was carried out to estimate the intracranial generators of each ERP component in the grand-averaged attentional difference waves. Source locations were estimated both by dipole modeling (Brain Electrical Source Analysis: BESA 2000, version 5) and by distributed linear inverse solutions based on a Local Auto-Regressive Average (LAURA, Grave de Peralta, Gonzalez Andino, Lantz, Michel, & Landis, 2001). The BESA algorithm estimates the location and the orientation of multiple equivalent dipolar sources by calculating the scalp distribution that would be obtained for a given dipole model (forward solution) and comparing it to the actual scalp-recorded ERP distribution (Scherg, 1990). The algorithm interactively adjusts (fits) the location and orientation of the dipole sources in order to minimize the relative variance (RV) between the model and the observed spatio-temporal ERP distribution. This analysis used the three-dimensional coordinates of each electrode site as recorded by a spatial digitizer. Symmetrical pairs of dipoles were fit sequentially to the components of interest within the same time intervals as those used for statistical testing. For example, dipole pairs to the N1 ERP component were fit after dipoles had been fit to the P1 component in the waveform. Dipole pairs were constrained to be mirror-symmetrical with respect to location but were free to vary in orientation.

LAURA (Grave de Peralta et al., 2001) 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. LAURA makes no a priori assumptions regarding the number of sources or their locations and can deal with multiple simultaneously active sources (Michel et al., 2001). LAURA analyses were implemented using CARTOOL software by D. Brunet (http://brainmapping.unige.ch/cartool.php) to provide a visualization of the current source distributions underlying each component.

To estimate the anatomical brain regions giving rise to the component modulations, the current source distributions computed by LAURA and the locations of BESA source dipoles were transformed into the standardized coordinate system of Talairach and Tournoux (1988) and projected onto a structural brain image supplied by MRIcro (Rorden & Brett, 2000) using AFNI (Analysis of Functional NeuroImaging: Cox, 1996) software.

3. Results

3.1. Behavioral results

The hit rates, sensitivity estimates (d') and reaction times for detecting the target translations are given in Table 1. Performance under monocular viewing was significantly better than in dichop-

Table 1
Behavioral performance (d' scores and reaction times (RT)) for detecting the target translations on the attended dot surface in the dichoptic and monocular viewing conditions ($n = 13$)

Stimulus	Hit rate (%)	SEM hit rate (%)	d'	SEM d'	Mean RT (ms)	SEM RT (ms)
Dichoptic	60.3	2.9	1.69	0.13	475	13
Monocular	68.1	2.9	1.99	0.14	471	11

tic viewing: for hit rates ($F(1, 12) = 17.73$, $p < .002$) and for d' ($F(1, 12) = 9.16$, $p < .02$). However, no difference in reaction times was found between the two conditions ($F(1, 12) = 0.53$, $p = $ n.s.). The eye to which the attended surface was projected did not affect either hit rate or d' ($F(1, 12) = 0.002$, $p = $ n.s.), nor did the color of the attended dot surface ($F(1, 12) = 0.04$, $p = $ n.s.).

3.2. ERP results

Since no behavioral differences were found based on eye of origin or color of stimulus, ERPs were collapsed across these factors. ERPs to the attended and unattended standard translations in the dichoptic and monocular viewing conditions are shown in Fig. 2A and B, respectively. ERPs to unattended stimuli over occipital sites showed greatly reduced amplitudes in both viewing conditions; none of the measured components (P1, N1, P2) was significantly greater than baseline in the unattended waveforms. Under dichoptic viewing ERPs elicited by attended translations showed significant P1 (peaking at 130 ms; $t(12) = 2.74$, $p < .02$) and N1 (peaking at 210 ms; $t(12) = 4.60$, $p < .0005$) components. Attention effects on the P1 and N1 components seen in the dichoptic attentional difference wave (calculated as described in Section 2) are listed in Table 2. A hemispheric difference was found in the P1 interval with the attention effect being larger over the right hemisphere ($F(1, 12) = 4.99$, $p < .05$). The N1 component did not show any significant hemispheric asymmetry. As shown in Table 2, an attention effect was also obtained for the later P2 component that had a broad distribution over fronto-central electrode sites.

During monocular viewing the ERP elicited by the attended stimuli showed a significant N1 component ($t(12) = 4.30$, $p < .0009$), but in contrast to the dichoptic viewing condition, no significant P1 was elicited ($t(12) = 1.19$, $p = $ n.s.). The attentional difference wave during monocular viewing thus did not show
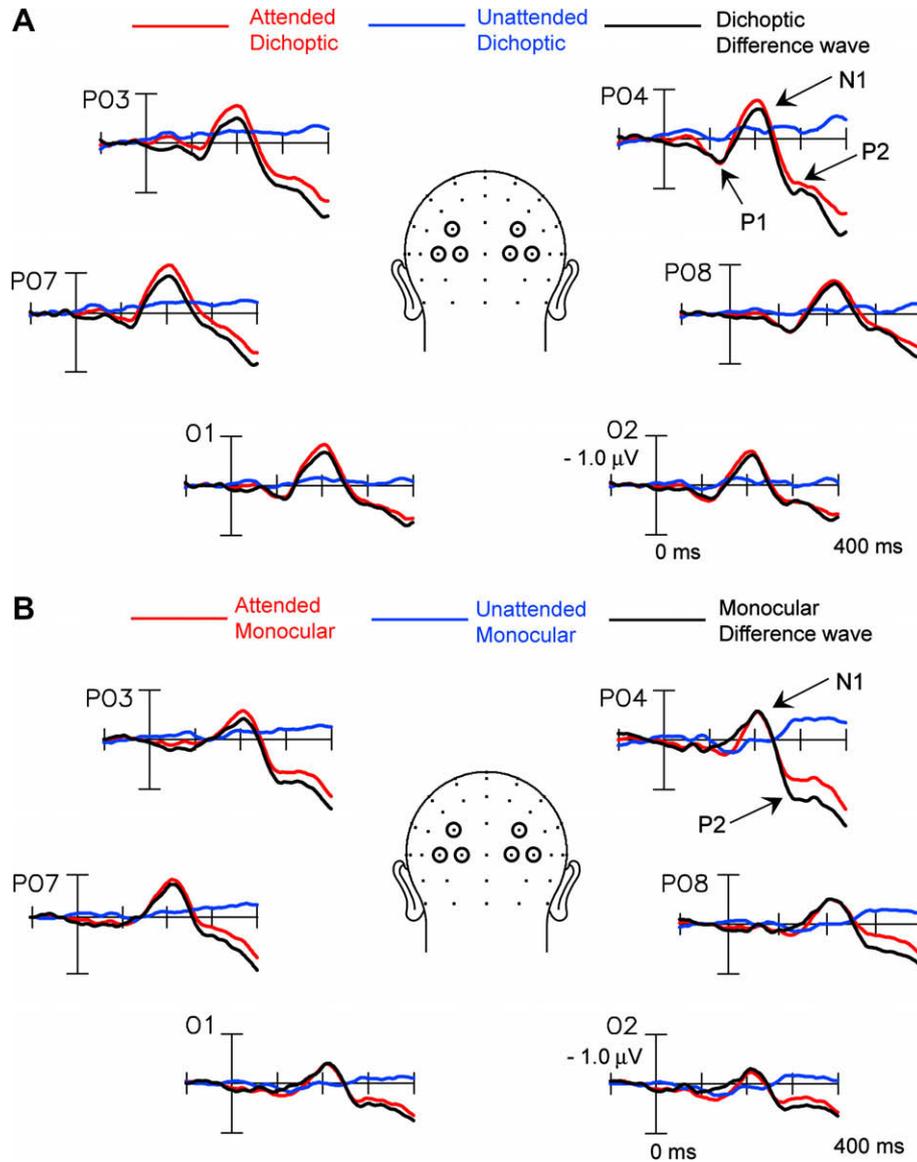
Fig. 2. Grand-average ERPs (n = 13) associated with endogenous attention to one of two superimposed dot surfaces under dichoptic (A) and monocular (B) viewing. (A) ERPs elicited under dichoptic viewing by attended and unattended surface translations (standards) and the attend minus unattend attentional difference wave. Recordings are from three pairs of electrodes at parieto-occipital (PO3,4 and PO7,8) and occipital sites (O1,2). (B) ERPs as in (A) under monocular viewing.

any attention effect in the P1 latency range, while the posterior N1 and fronto-central P2 did show significant attention effects (Table 2).

A highly significant P300 component was elicited by attended but not by unattended targets in both dichoptic ($t(12) = 8.49$,

Table 2
Mean amplitudes of ERP components in the dichoptic and monocular attentional difference waves (ERPs to standard translations when attended minus when unattended)

Attention difference wave	Component	Amplitude (μV)	SEM (μV)	t(12)	p<
Dichoptic	P1 (112–144 ms)	0.25	0.05	4.68	.0006
	N1 (188–228 ms)	−0.56	0.14	4.01	.002
	P2 (240–280 ms)	1.56	0.20	7.69	.0001
Monocular	P1 (112–144 ms)	0.05	0.07	0.69	n.s.
	N1 (188–228 ms)	−0.46	0.12	3.80	.003
	P2 (240–280 ms)	1.09	0.20	5.50	.0002

Component amplitudes were measured over scalp sites of maximal amplitude and tested for significance with respect to the 100 ms pre-stimulus baseline.

$p < .0001$) and monocular ($t(12) = 8.09$, $p < .0001$) viewing conditions (waveforms not shown). The amplitude of the target-elicited P300 component did not differ between the two conditions ($F(1, 12) = 1.42$, p = n.s.).

The scalp topographies of the attention effects in the P1, N1 and P2 latency windows were compared between the dichoptic and monocular viewing conditions (Fig. 3). Under dichoptic viewing (Fig. 3A), the attention-related P1 modulation was distributed over lateral occipital electrodes with greater amplitude over the right hemisphere. The enhanced N1 with attention was distributed bilaterally over lateral occipital sites, with a more ventral spread than the P1 effect. During monocular viewing (Fig. 3B) the difference wave distribution within the P1 latency window was no different from noise levels. This scalp distribution significantly differed from that of the dichoptic P1 attention effect ($F(21, 252) = 1.83$, $p < .02$). The topography of the N1 attention effect in the monocular attention difference wave did not differ from that of the dichoptic N1 effect ($F(21, 252) = 0.70$, p = n.s.), nor did the distributions of the P2
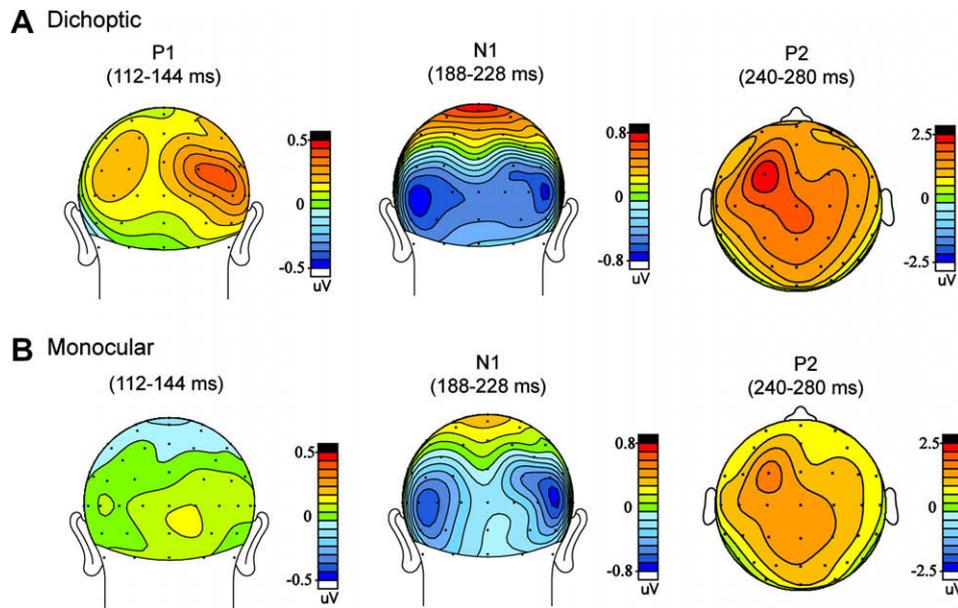
Fig. 3. Topographical maps of ERP amplitudes in the P1, N1 (back view) and P2 (top view) latency windows in the attentional difference waves under (A) dichoptic and (B) monocular viewing.

difference wave component differ between the two conditions ($F(39,468) = 1.07$, p = n.s.).

3.3. Source analysis

Using the BESA algorithm pairs of dipoles were fit to the scalp topographies of the P1 and N1 components in the grand-average dichoptic attentional difference wave and to the N1 component in the monocular attentional difference wave. The P1, N1 and P2 difference wave components were also modeled using a distributed minimum-norm approach (LAURA, Grave de Peralta et al., 2001). The location of the BESA dipoles and the generator sites estimated by LAURA were transformed into the standardized coordi-

nate system of Talairach and Tournoux (1988) and superimposed on the rendered cortical surface of a single individual's brain (Fig. 4). Talairach coordinates of the dipole pairs and an estimate of their goodness of fit as reflected by residual variance is listed in Table 3. In the case of the P2 component a satisfactory dipole model with low residual variance could not be achieved, and hence only the current source maxima as modeled by LAURA are reported.

The dipole pair accounting for the P1 component in the dichoptic attentional difference wave was localized to ventro-lateral extrastriate visual cortex (Fig. 4A). The N1 components in both dichoptic and monocular difference waves were accounted for by dipole pairs in the same general region, about 10 mm more
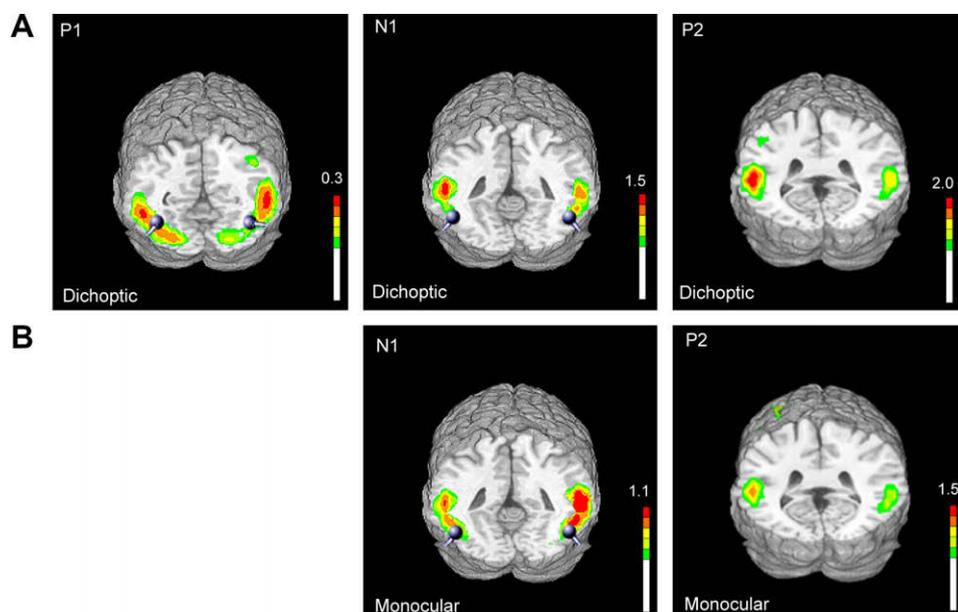
Fig. 4. Estimated sources for the major visual ERP components in the grand-average attention difference waveforms in the (A) dichoptic (P1, N1 and P2 components) and (B) monocular (N1 and P2 components) viewing conditions modeled using LAURA and BESA. Sources and dipoles are projected onto a standard MRI rendered brain in Talairach space. BESA dipole fits are shown in gray. LAURA inverse solutions are represented in units of current source intensity (nA/mm³).

Table 3
Talairach coordinates of BESA dipole pairs that modeled ERP components in the dichoptic and monocular attention difference waves

Attention difference wave	Component	x (mm)	y (mm)	z (mm)	Residual variance (%)
Dichoptic	P1	±36	−58	−9	9
	N1	±41	−67	−6	8
	P2	±51	−35	6	(LAURA only)
Monocular	N1	±49	−70	1	12
	P2	±51	−36	6	(LAURA only)

For the P2 component coordinates of the current source maxima as modeled by LAURA are shown. Percent residual variance not accounted for by the model over the time interval 112–228 ms is shown for each component.

posterior than the P1 dipoles. As seen in Fig. 4, the LAURA estimates of current source intensity for each of these components corresponded well with the BESA source dipoles. For each modeled component, the locations of the maximum current source foci of the LAURA solution were within 10–15 mm of the dipoles fit using BESA. The later P2 components in the dichoptic and monocular difference waves as modeled by LAURA had bilateral sources in the vicinity of the superior temporal gyri.

4. Discussion

This study used ERPs to investigate the neural correlates of endogenous attentional allocation to superimposed rivalrous counter-rotating dot surfaces. When the two surfaces were presented dichoptically (one to each eye), brief translations of the attended surface elicited much larger P1 (112–144 ms), N1 (188–228 ms) and P2 (240–280 ms) components of the ERP than did translations of the unattended surface. On the other hand, during monocular viewing (both surfaces presented to the same eye) the attended surface translations elicited enlarged N1 and P2 components relative to the unattended surface translations, but the P1 was not modulated by attention. These results indicate that attentional selection can bias neural activity at an earlier level of processing when attended and unattended surfaces are presented to the separate eyes.

Behaviorally, subjects were able to attend effectively to one surface under both dichoptic and monocular viewing conditions, although target detection rates were significantly higher during monocular trials. It is likely that target detection was hampered during dichoptic viewing because attention could not completely eliminate the spontaneous rivalry process, which caused the attended surface to be occasionally suppressed from view. Such an assumption is supported by previous research showing that endogenous attentional control of rivalry is relatively weaker than is attentional modulation of other forms of visual competition such as ambiguous figures (Meng & Tong, 2004; van Ee, Noest, Brascamp, & van den Berg, 2006) or even exogenous attentional capture of a rivalrous surface (Chong & Blake, 2006). The small difference in target detection rates (68% vs. 60%) between the two viewing conditions might also be attributed to an overall difference in task difficulty resulting from interference with the attentional selection process by spontaneous rivalry. While a difference in difficulty might possibly affect the ERP attention effects, it seems unlikely that the modest difference in difficulty observed here would engender the substantial difference in attentional modulation of the P1 that was obtained between the dichoptic and monocular conditions.

The earliest effect of attentional selection during dichoptic viewing was found on the P1 component in the 112–144 ms range that was localized to lateral extrastriate visual cortex. In contrast, attentional selection during monocular viewing was not associated with modulation of the P1. This difference between the two view-

ing conditions was due to the presence of a significant P1 component in the ERPs to the attended stimuli under dichoptic viewing but not under monocular viewing. ERPs to the unattended stimuli did not show any significant components under either viewing condition. These results suggest that selective processing of the attended surface begins at an earlier stage (manifested in the P1 component) when the competing surfaces are presented to the separate eyes as opposed to the same eye. It should be cautioned, however, that the presence of P1 modulation only under dichoptic conditions might reflect an interaction between attentional selection and inter-ocular competition rather than an earlier level of selection.

In contrast with the present findings, an earlier ERP investigation of endogenous attention to superimposed rotating dot surfaces (presented under binocular viewing conditions) did in fact observe attentional modulation of the P1 component (Valdes-Sosa et al., 1998). Their differing results might have been due to much longer periods of sustained attention and greater attentional demands in a more difficult task of translation discrimination in all cardinal directions. Another possibility is that binocular viewing, while being perceptually similar to monocular presentation, may activate additional neural populations that are susceptible to attentional modulation in the P1 latency range.

The present results provide further evidence that the visual P1 attention effect is dissociable from attention effects on the N1, which has been demonstrated in previous ERP studies of visual spatial attention (Luck, Heinze, Mangun, & Hillyard, 1990; Luck et al., 1994, reviewed in Hopfinger, Luck, & Hillyard, 2004). The source localization of the P1 component obtained here is consistent with previous studies that localized the generators of the P1 to the lateral extrastriate visual cortex, which includes areas V3, V3a and V4 (Clark, Fan, & Hillyard, 1995; Clark & Hillyard, 1996; Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002; Martinez et al., 1999, 2001). Within these extrastriate cortical regions inhibitory interactions between the eyes implemented in binocular neurons have been found to be very efficient, especially in areas V3 and V4. Dichoptic masking studies suggest that such inhibition builds up incrementally in strength at successively higher areas and is relatively weak in striate cortex itself (Hubel & Wiesel, 1961; Macknik, 2006; Macknik & Martinez-Conde, 2004; Tse, Martinez-Conde, Schlegel, & Macknik, 2005). The present results suggest that attentional allocation may employ these inhibitory circuits to enhance inter-ocular selectivity during dichoptic viewing.

It should be noted, however, that the present results do not entirely rule out the possibility of an earlier attentional selection at the level of striate cortex, as suggested by many fMRI studies of binocular rivalry (Buchert et al., 2002; Lee et al., 2005; Polonsky et al., 2000; Tong & Engel, 2001). If such early selection did occur in primary visual cortex but did not produce an organized ERP field over the scalp (either due to low current strength, poor time-locking, or non-optimal cellular geometry), ERP recordings may fail to register the selection process. The consequences of such an early selection might then only become detectable at higher levels where neural activity was organized in such a way as to produce an enhanced ERP detectable at the surface.

Translations of the attended surface elicited enlarged N1 components (188–228 ms) relative to the unattended translations in both the dichoptic and monocular viewing conditions. The N1 source generators in both viewing conditions were localized to the ventro-lateral extrastriate visual cortex. These results fit well with previous source estimations of the N1 component elicited in association with object-selective attention (Martinez, Ramanathan, Foxe, Javitt, & Hillyard, 2007; Martinez et al., 2006). In several studies of attentional selection, the N1 has been found to be associated with discriminative processing of visual information in the

extrastriate cortex (Hopf, Vogel, Woodman, Heinze, & Luck, 2002; Martinez et al., 2006; Ritter, Simson, & Vaughan, 1988; Vogel & Luck, 2000). The posterior N1 has also been consistently enhanced by attention in previous investigations of attentional selection of superimposed rotating dot surfaces (Khoe et al., 2005; Lopez, Rodriguez, & Valdes-Sosa, 2004; Pinilla, Cobo, Torres, & Valdes-Sosa, 2001; Rodríguez & Valdes-Sosa, 2006; Valdes-Sosa et al., 1998, 2003). Our results are in accord with these findings and provide further evidence that object (surface) selection is manifested in the N1 component generated within specialized regions of visual cortex where objects are represented (Martinez et al., 2007; Murray et al., 2002), not only under binocular viewing but also with dichoptic and monocular viewing.

The later P2 component was found to localize primarily to superior temporal cortex with some activity also present in the inferior parietal lobule. The origins of this component are not well understood, and its exact role in visual selection has remained elusive. Here we found that a robust P2 was elicited by the attended surface under both dichoptic and monocular viewing. Interestingly, the P2 attention effect was found to be somewhat greater under dichoptic viewing. Although a convincing interpretation of this result is not within reach, it could be that dichoptic attentional selection requires greater involvement of higher cortical areas to resolve competition than does monocular selection. Further investigations are required to decipher this effect.

In summary, we found that the earliest influence of attention on inter-ocular competition during rivalry was evident in an amplitude modulation of the P1 component of the visual ERP generated within extrastriate visual areas, followed by attention effects on the N1 and P2 components. In contrast, during monocular viewing only the later N1 and P2 components were modulated by attentional selection of competing surfaces. This is in line with recent evidence (Khoe, Mitchell, Reynolds, & Hillyard, in press) that both the P1 and N1 components are modulated by exogenous attentional cueing of competing dot surfaces during rivalry, but only the N1 is modulated by exogenous cueing of monocularly presented surfaces. It appears from these parallel findings that attentional biasing of rivalrous surfaces affects visual processing in a similar way whether induced via top-down instructions to attend or bottom-up capture of attention. The neural processes that underlie this differential modulation of the P1 component under the two viewing conditions need further investigation using higher resolution recording techniques.

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