Early correlates of visual awareness following orientation and colour rivalry

Sandra Veser [a], Robert P. O'Shea [b], Erich Schröger [a], Nelson J. Trujillo-Barreto [c], Urte Roeber [a,*]

[a] *Institute of Psychology I, Leipzig University, Seeburgstr. 14-20, 04103 Leipzig, Germany*
[b] *Department of Psychology, University of Otago, Dunedin, New Zealand*
[c] *Cuban Neuroscience Center, Havana, Cuba*

ABSTRACT

Binocular rivalry occurs when dissimilar images are presented to corresponding retinal regions of the two eyes: visibility alternates irregularly between the two images, interspersed by brief transitions when parts of both may be visible. We measured event-related potentials (ERPs) following binocular rivalry by changing the stimulus viewed by one eye to be identical to that in the other eye, eliciting binocular fusion. Because of the rivalry, observers either saw the change, when it happened to the visible stimulus, or did not see the change, when it happened to the invisible stimulus. The earliest ERP differences between visible and invisible changes occurred after about 100 ms (P1) when the rivalry was between stimuli differing in orientation, and after about 200 ms (N1) when the rivalry was between stimuli differing in colour. These differences originated from ventro-lateral temporal and prefrontal areas. We conclude that the rivalling stimulus property influences the timing of modulation of correlates of visual awareness in a property-independent cortical network.

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1. Introduction

We view our world through two eyes but we are typically aware of only a single, coherent image. There is good psychophysical (e.g., Blake & Boothroyd, 1985; O'Shea, 1987) and electrophysiological (e.g., Ferster, 1990; Nikara, Bishop, & Pettigrew, 1968) evidence that this arises from a neural process called binocular fusion combining the two eyes' retinal images. Fusion takes place only when the two retinal images are similar. When the two retinal images are dissimilar they compete for perceptual dominance; this is called binocular rivalry (discovered by Porta, 1593; cited by Wade, 1998). During binocular rivalry, one image wins the competition, is dominant, for about a couple of seconds, while the other, losing image is invisible, suppressed. Then the first image becomes suppressed while the other image becomes dominant. These alternations in visibility continue at random for as long as one cares to look. Transitions between visibility of one image and the other can be abrupt, but can also be gradual, in which one image is seen briefly intermixed with the other, a so called patchwork or mosaic, or in which one image might appear to spread out to cover the other.

Visual experience in binocular rivalry is thought to arise from activation, and suppression, of neurons at a succession of stages in the visual system (e.g., Blake & Logothetis, 2002; Freeman, 2005; Leopold & Logothetis, 1996). Our interest in binocular rivalry is to use it as a tool with which to find the neural correlates of visual awareness (Crick & Koch, 1995; Frith, Perry, & Lumer, 1999). Specifically, we used EEG to study the temporal and spatial characteristics of the earliest neural processes correlated with visual awareness following binocular colour and orientation rivalry.

Various techniques have been used to find the time and place of neural correlates of awareness in binocular rivalry in human participants. By neural correlates of awareness, we mean any signs of neural activity that differ between conditions in which participants were aware of a particular stimulus and conditions in which participants were not aware of the same stimulus. Techniques employing this logic include functional magnetic resonance imaging (fMRI) (Lumer, Friston, & Rees, 1998; Polonsky, Blake, Braun, & Heeger, 2000; Tong, Nakayama, Vaughan, & Kanwisher, 1998; Wunderlich, Schneider, & Kastner, 2005), magnetoencephalography (MEG) (e.g., Kobayashi, Kato, & Kuriki 2000; Srinivasan, Russell, Edelman, & Tononi, 1999), and transcranial magnetic stimulation (TMS) (Pearson, Tadin, & Blake, 2007). Results from all of these techniques suggest that awareness in binocular rivalry is mediated by feedforward and feedback influences from as early as the LGN up to networks involving striate and extrastriate visual areas, and parietal and frontal sites.

The technique we use involves event-related potentials (ERPs). This is one of the first electrophysiological techniques to be used with binocular rivalry (e.g., Cobb, Morton, & Ettlinger, 1967; Lansing, 1964; Motokawa, Nakayama, & Kohata, 1956; Pellet, 1966).

* Corresponding author. Fax: +49 341 9735969.
E-mail address: urte@uni-leipzig.de (U. Roeber).

Its excellent temporal resolution combined with a relatively inexpensive apparatus and technology is still unmatched by other techniques. Recently developed Variable Resolution Electromagnetic Tomography (VARETA) (Valdes-Sosa, Marti, Garcia, & Casanova, 1996) has considerably improved the ability to localise ERP sources.

The specific ERP paradigm we use was pioneered by Kaernbach, Schröger, Jacobsen, and Roeber (1999). They showed an observer a left-slanted grating to one eye and a right-slanted grating to the other to induce binocular rivalry. When the observer was seeing one orientation only, one of the gratings was changed to make it identical to that in the other eye, yielding binocular fusion. Kaernbach et al. (1999) measured ERPs following the change. If, because of the binocular rivalry, the observer was seeing the grating that changed, he or she was aware of the stimulus transition. We call this a *percept-incompatible transition*. If, because of the binocular rivalry, the observer was seeing the other grating, he or she was unaware of the stimulus transition (although occasionally observers might have noticed a slight change in the quality of the visible grating). We call this a *percept-compatible transition*.

In Kaernbach et al.'s (1999) study the change in the stimuli was identical for percept-incompatible and percept-compatible transitions. Therefore they had to attribute any differences in ERPs from the two conditions to the differences in visual awareness. They reported the earliest ERP modulation at around 200 ms. Roeber and Schröger (2004) using more sensitive recordings found the first percept-dependent modulation occurring even earlier at around 100 ms. The same latency for correlates of visual awareness has been found in other studies using different experimental approaches such as change blindness, masking, contrast manipulation, and multistable images (de Labra & Valle-Inclan, 2001; Koivisto & Revonsuo, 2003; Koivisto, Revonsuo, & Salminen, 2005; Kornmeier & Bach, 2005, 2006; Pins & ffytche, 2003; Pitts, Nerger, & Davis, 2007; Valle-Inclan, Hackley, de Labra, & Alvarez, 1999). Recently, Roeber, Trujillo-Baretto, Hermann, O'Shea, and Schröger (2008) confirmed the earliest modulation at 100 ms and, using VARETA, located the site of this modulation to a network within the ventro-lateral occipito-temporal cortex.

The previous studies (Kaernbach et al., 1999; Roeber & Schröger, 2004; Roeber et al., 2008) elicited binocular rivalry using stimuli that differed in orientation. We were concerned that conclusions drawn from orientation rivalry are true only for this type of rivalry. Differences in ERPs might have arisen from differences in orientation processing occurring in early visual areas. To test this alternative explanation we decided to modulate awareness using a different form of binocular rivalry: colour rivalry. Desaguiliers (1716) was, as far as we know, the first to observe binocular rivalry when each eye views different colours, although it was described more carefully by Dutour 1760; translated by O'Shea (1999).

More recent studies have shown that colour rivalry can operate independently from orientation rivalry. When images of contours of different orientation and colour are presented to the two eyes a dissociated binding or misbinding can occur (Breese, 1909; Creed, 1935; Hastorf & Myro, 1959; Holmes, Hancock, & Andrews, 2006; Hong & Shevell, 2006). For example, when a red left-slanted grating is presented to one eye and a green right-slanted grating is presented to the other, observers sometimes report seeing a green left-slanted grating or a red right-slanted grating. Results of priming experiments also show that colour and orientation rivalry can be independent. For example, Ikeda and Morotomi (2000, 2002) found that after a brief presentation of stimuli of identical colour to the two eyes observers perceived the other colour during subsequent colour rivalry. Holmes et al. (2006) found a similar priming effect for orientation rivalry after a brief presentation of one of the orientations. Critically, they also showed that when the primer's

orientation was biased towards one of the rival stimuli and the primer's colour was biased towards the other, orientation stimuli tended to rival whereas colour stimuli tended to fuse, consistent with independence of the two forms of rivalry.

Because colour and orientation rivalry differ, it is possible that the earliest neural processes correlated with visual awareness (following orientation or colour rivalry) might also differ. We tested whether colour rivalry yields the same time and place of the earliest neural correlates of visual awareness as found with orientation rivalry.

We also need to ensure that possible effects can be traced back to differences in the correlates of visual awareness due to the type of rivalry; and that they cannot be fully explained by differences in processing of the different stimulus dimensions. To test this, we included for comparison a condition that was perceptually identical to a percept-incompatible transition but involved no rivalry—a *fusion-to-fusion transition*. An example of such a transition in orientation would be from both eyes' viewing red right-slanted gratings to both eyes' viewing red left-slanted gratings. An example of such a transition in colour would be from both eyes' viewing red right-slanted gratings to both eyes' viewing green right-slanted gratings. If the pattern of results from the two stimulus dimensions in fusion-to-fusion transitions were identical to that in percept-incompatible transitions, then we would be forced to say that those patterns were due to dimension-specific processing. Any other results would be consistent with there being something unique about awareness modulated by prior rivalry.

We found that neural activity correlated with awareness (rather than with stimulus dimension) following colour rivalry lagged behind activity following orientation rivalry by about 100 ms, but that both involved overlapping cortical areas.

2. Methods

2.1. Participants

There were 17 participants (3 male, 13 right-handed, mean age 22.2 ± 4.2 years standard deviation), all with normal or corrected-to-normal vision. They received either course credits or payment (6 €/h). Participants were selected after they showed normal binocular rivalry in a 12-min test session. The data of 5 (all female and right-handed) of the 17 participants had to be excluded from further analysis; one due to technical problems, the others because of too many artefacts in the electrophysiological and behavioural data. The study was performed in accordance with the ethical standards laid down in the Declaration of Helsinki (World Medical Association, 2000).

2.2. Apparatus

During the experiment the participant sat in a sound-attenuated and electrically shielded cabin, with his or her head stabilized with a chin rest. The participant viewed stimuli through a mirror stereoscope (Screenscope SA-200-Monitor-Type), and through a window in the cabin, on a monitor (Llyama HM 903 DTA) placed outside the cabin at a viewing distance of 45 cm. The monitor displayed 1024×768 pixels at 100 Hz. Stimuli were exposed, and responses collected, by MatLab programs using Cogent 2000. Participants responded using two buttons of a four-button response pad.

2.3. Stimuli

The stimuli consisted of patches of black/green (CIE $x = .282$, $y = .295$, $Y = 15.9 \text{ cd/m}^2$) or black/red (CIE $x = .616$, $y = .351$, $Y = 17.7 \text{ cd/m}^2$) square-wave gratings windowed with a circular

cosine envelope. The gratings were oriented 45° to the left or right from vertical. The gratings had contrasts of 0.78 and 0.80, respectively. Each stimulus had a diameter of 5.7° of visual angle and a spatial frequency of 1 cycle per degree. There was also a central black fixation cross of 0.4°. Stimuli were presented on a grey background ($10.4\ cd/m^2$). The horizontal positions of the stimuli and their fixation points were adjusted to allow each participant to view the two stimuli on corresponding retinal positions with normal relaxed viewing.

2.4. Procedure

The main manipulated variable of the experiment was the stimulus dimension that changed at a transition: *orientation* vs. *colour*, run in separate blocks. In half the blocks, transitions involved a change of grating orientation (e.g., from left-tilted to right-tilted) but with no change in colour (e.g, always red). In these orientation blocks, participants reported the orientation of the stimulus they currently perceived by holding down one of the two buttons assigned to that orientation. Participants had to release the buttons if they saw any combination of the two orientations. In the remaining blocks, transitions involved a change of grating colour between the two eyes (e.g., from red to green) but with no change in orientation (e.g., always left-tilted). In these colour blocks, participants reported the colour of the stimulus they currently perceived by holding down one of the two buttons assigned to that colour. They had to release the buttons if they saw any combination of the two colours or any different colour (such as yellow).

The experiment consisted of 24 blocks taking around 3 min each. Stimulus dimension that changed (orientation vs. colour) alternated over blocks, as did the colour of the stimuli (red or green) for orientation stimuli, and as did the orientation of the stimuli (tilted to the left or right) for colour stimuli. Block sequence was balanced across participants. Within a block, there were periods of rivalry stimulation occurring randomly among periods of fusion stimulation. In an orientation block, rivalry occurred when each eye viewed different orientations; fusion occurred when each eye viewed the same orientation. Frequency of occurrence of orientations (left-tilted vs. right-tilted) was equal over a block. In a colour block, rivalry occurred when each eye viewed different colours; fusion occurred when each eye viewed the same colour. Frequency of occurrence of colours (red vs. green) was equal over a block.

Periods of rivalry stimulation lasted 6 s plus a random time between 0.2 and 1.0 s. This was to establish rivalry and to allow a few changes in perceptual dominance before a transition. Moreover, a stimulus transition following rivalry occurred only if the participant had pressed one key for 0.3–0.6 s. Periods of fusion stimulation were shorter because there were no perceptual switches during the stimulation; they lasted 2 s plus a random time between 0.1 and 0.5 s (see Fig. 1a for a typical trial sequence during an orientation block and Fig. 1d for a typical trial sequence during a colour block). The differences in the temporal jitter between periods of rivalry and fusion were to match the same differences in previous experiments with the same paradigm (see Kaernbach et al., 1999; Roeber et al., 2008).

2.5. Electrophysiological recordings

We recorded EEG continuously with 128 Ag/AgCl active electrodes mounted in an elastic cap radially equidistant from Cz according to the ABC electrode layout (http://www.biosemi.com/headcap.html). Additionally, we attached two active electrodes to the earlobes. The horizontal and vertical electrooculograms (EOGs) were recorded to monitor eye movements. EEG and EOG were sampled at 512 Hz and amplified by BioSemi Active-Two amplifiers (http://www.biosemi.com). The data were offline re-referenced to the linked earlobes. A low pass filter of 35 Hz (Blackman window sinc FIR filter, filter order = 700) was applied to the data before analyses.

3. Results

For analysis, we classified four different events: transitions from rivalry to fusion were divided into percept-incompatible transitions and percept-compatible transitions depending on the prevailing percept at the moment of the stimulus transition as indicated by the observer's button press. We depict these transitions for orientation rivalry in Fig. 1b and c and for colour rivalry in Fig. 1e and f. Furthermore there were fusion-to-fusion transitions (from one fusion stimulation to the other fusion stimulation) and rivalry-to-rivalry transitions (in which the rival stimuli swapped between the eyes). We excluded from further analysis trials with a button press within 200 ms after the stimulus transitions and trials when the observer released the button after a percept-compatible transition. All event classifications and initial data processing as described below were done for both sorts of blocks separately, unless stated otherwise.

3.1. Behavioural data

For each condition, we normalised each participant's rivalry dominance durations by dividing each one by that participant's mean duration. Then we pooled all normalised durations into a frequency distribution. Fig. 2 shows that the distributions for orientation rivalry and for colour rivalry followed the classical gamma shape (Fox & Herrmann, 1967; Levelt, 1967). Mean dominance duration was longer for orientation rivalry (mean of 1.93 ± 0.60 s) than for colour rivalry (1.62 ± 0.50 s), $t(14) = 3.26$, $p < .05$.

To evaluate the processing speed of transitions in orientation and transitions in colour, we calculated mean reaction times (RTs) for percept-incompatible transitions and fusion-to-fusion transitions for each participant, and then conducted a two factor, repeated-measured analysis of variance (ANOVA). We analysed RTs only from correct responses; there were so few errors (fewer than 1%) that it was impossible to conduct any analysis of them. We found that mean RTs were longer for orientation (fusion-to-fusion transition: 0.565 ± 0.103 s; incompatible transition: 0.633 ± 0.104 s) than for colour (fusion-to-fusion transition: 0.549 ± 0.125 s; incompatible transition: 0.584 ± 0.110 s), $F(1,11) = 5.77$; $p < .035$, $\eta^2 = .34$. We also found a main effect of type of transition with percept-incompatible transitions yielding slower responses than fusion-to-fusion transitions, $F(1,11) = 21.83$; $p < .001$, $\eta^2 = .67$. This is consistent with binocular summation (Blake & Fox, 1973): percept-incompatible transitions involved a change to the stimulus in one eye whereas fusion-to-fusion transitions involved the same changes to the stimuli of both eyes. The interaction was not significant.

3.2. ERP data

We averaged ERPs separately for the different event classes in a 1000-ms window time-locked to the stimulus transitions, including a 200 ms pre-stimulus-transition baseline. Prior to averaging, we rejected any epochs containing a signal change of more than 120 µV at any electrode by using an automatic peak-to-peak voltage artefact detection method. After event classification and artefact rejection, for each participant we could include 43 (±13) percept-compatible, 54 (±10) percept-incompatible, 23 (±3) fusion-to-fusion, and 25 (±3) rival-to-rival transitions for orientation stimuli, and we could include 44 (±7) percept-compatible, 48 (±10) percept-incompatible, 24 (±3) fusion-to-fusion, and 25 (±7)
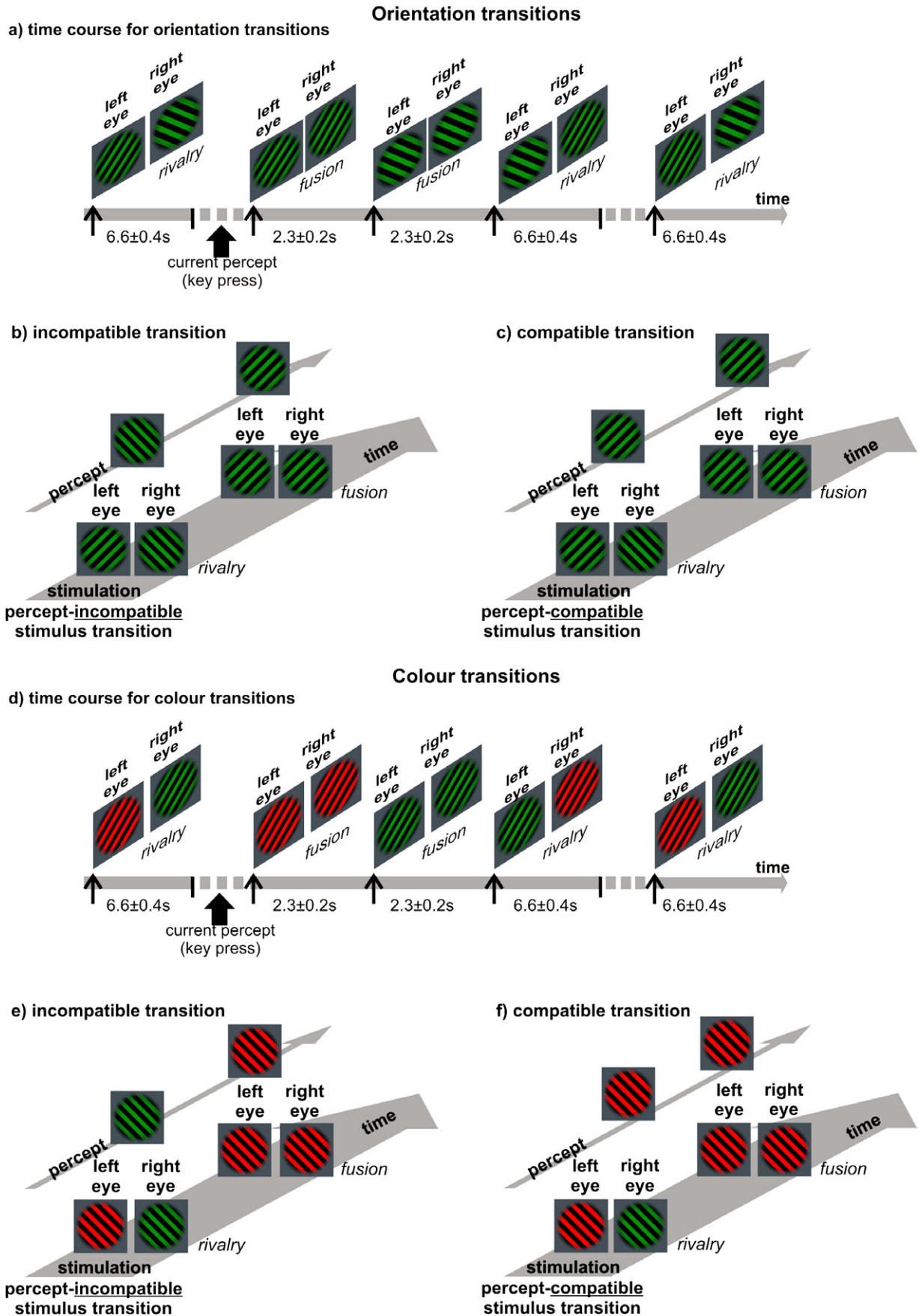
Fig. 1. Experimental design: examples of the time course of rivalry and fusion stimulation during (a) orientation transitions and (d) colour transitions. (b) A transition from rivalry to fusion when the fused orientation stimuli are incompatible with an observer's perception. (c) A transition from rivalry to fusion when the fused orientation stimuli are compatible with an observer's perception. (e and f) The equivalent events for colour transitions.
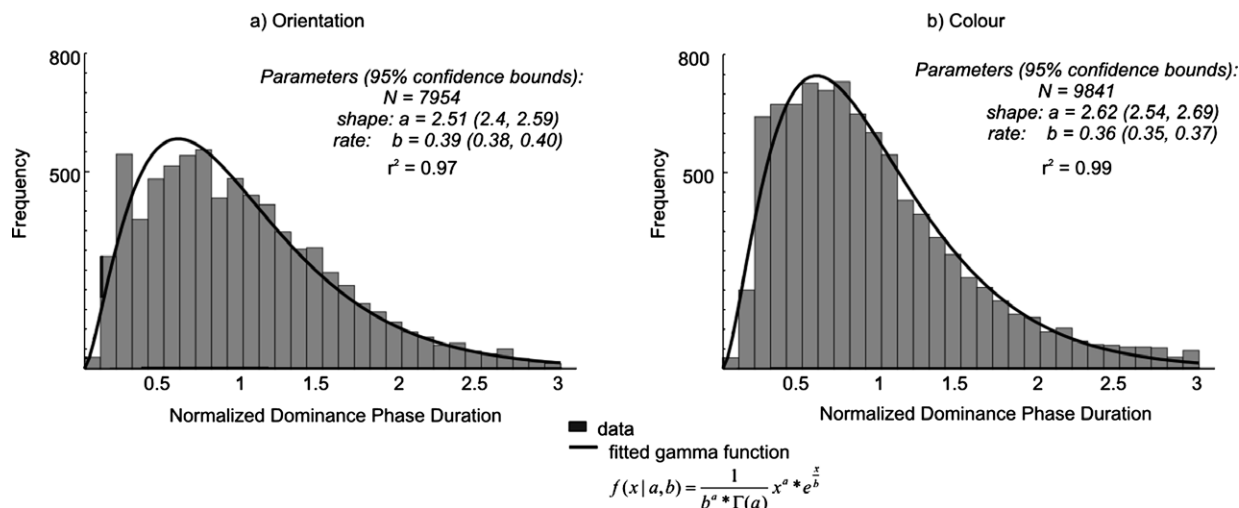
a) Orientation

b) Colour

Parameters (95% confidence bounds):
N = 7954
shape: a = 2.51 (2.4, 2.59)
rate: b = 0.39 (0.38, 0.40)
r² = 0.97

Parameters (95% confidence bounds):
N = 9841
shape: a = 2.62 (2.54, 2.69)
rate: b = 0.36 (0.35, 0.37)
r² = 0.99

■ data
— fitted gamma function

$$f(x\,|\,a,b) = \frac{1}{b^a * \Gamma(a)} x^a * e^{\frac{x}{b}}$$

Fig. 2. Distributions of the normalised dominance durations (a) during orientation rivalry and (b) during colour rivalry. The grey bars represent the empirical frequencies, the black solid lines the fitted gamma distributions with the formula and parameters given in the figure. N denotes the number of dominance durations accumulated over the 12 participants for each sort of rivalry.

rivalry-to-rivalry transitions for colour stimuli. Fig. 3 displays all four ERPs at frontal, central, parietal, and occipital regions (as cluster averages including 6 electrodes each) of the left and right hemisphere. It shows orientation stimuli on the left side and colour stimuli on the right side. To be consistent with convention, we show positive deflections (P) going below the Y-axis and negative deflections (N) going above (e.g., Luck, 2005; p. 10).

Using visual inspection of the grand average ERPs, we determined the peak windows of the P1 and N1 components at posterior electrodes: P1 for both orientation and colour from 100 to 120 ms; N1 for orientation from 150 to 180 ms, and N1 for colour from 195 to 225 ms. For statistical analyses, we grouped four electrode clusters of 6 electrodes each for occipital and parietal regions of the left and right hemisphere (refer to Fig. 3). For all subsequent analyses, we used amplitudes averaged within these time windows and pooled over the electrodes of each cluster. We show major components (P1, N1, P3b) as letters in Fig. 3.

All orientation transitions (Fig. 3, left side) except for percept-compatible transitions elicited a significant P1 around 100 ms at occipital and parietal sites. That is, when our stimulation changed in orientation in either one or both eyes, ERP amplitude in the P1 time window was larger when the change occurred with awareness (percept-incompatible transitions, fusion-to-fusion transitions, and rivalry-to-rivalry transitions) than when the change occurred without awareness (percept-compatible transitions). As well, all transitions elicited an N1 around 160 ms that was most pronounced at occipital and parietal sites.

Of colour transitions (Fig. 3, right side) only fusion-to-fusion transitions elicited a significant P1. That is, for changes of colour in one eye (rivalry to fusion) P1 was absent when the change occurred with awareness (percept-incompatible transitions) as well as when it occurred without awareness (percept-compatible transitions). All transitions elicited an N1 around 200 ms at occipital and parietal sites. These were pronounced for fusion-to-fusion transitions and for percept-incompatible transitions (with awareness) and less distinct for percept-compatible transitions (without awareness).

In the ERPs to both orientation and colour transitions we also found a positive deflection starting at about 300 ms and peaking at about 400 ms after the stimulus transition, which was most pronounced at parietal sites (marked as P3b at the parietal electrodes in Fig. 3). P3b is associated with the detection of task-relevant events (Polich, 2007), such as pressing the key to respond to the

transition. In this study, we are interested in the earliest difference in the stream of visual processing correlated with awareness, so we do not elaborate further on P3b effects.

To compare the crucial conditions differing in awareness, we compared ERPs from percept-incompatible transitions (awareness of the stimulus change) with percept-compatible transitions (no awareness of the stimulus change) for the two types of rivalry. In Table 1, we give the results of three-way, repeated measures ANOVAs on mean amplitude for the first component showing an amplitude difference between percept-incompatible and percept-compatible transitions for each sort of rivalry (i.e., P1 for orientation rivalry and N1 colour rivalry).

Following orientation rivalry, we found a main effect of transition on P1 amplitude (Table 1): the ERP amplitude in the P1 time window was larger when the change occurred with awareness (percept-incompatible transitions) than when the change occurred without awareness (percept-compatible transitions) in both regions (occipital and parietal). This then is the earliest neural activity correlated with awareness following orientation rivalry. This finding is consistent with previous studies using orientation rivalry (Roeber & Schröger, 2004; Roeber et al., 2008).

Following colour rivalry, we found a main effect of region and an interaction of transitions and region on N1 amplitude (Table 1). Planned t-tests for both occipital and parietal regions showed a higher N1 amplitude for percept-incompatible transitions than for percept-compatible transitions at occipital electrodes, $t(11) = -2.40$; $p < .05$, but not at parietal electrodes, $t(11) = -0.76$, $p > .1$ The occipital activity is the earliest neural activity correlated with awareness following colour rivalry.

In order to ensure that the effects of type of rivalry we report above are differences in awareness rather than differences in the processing of the stimulus dimensions, we also separately analysed P1 and N1 amplitudes of the fusion-to-fusion transitions for both dimensions. We conducted stimulus dimension (orientation vs. colour) × hemisphere (left vs. right) × region (occipital vs. parietal) ANOVAs. The analysis of P1 amplitudes yielded no main effects or interactions: the processing of unambiguous colour and orientation transitions does not differ at P1. This suggests that the absence of P1 following colour rivalry is from rivalry processing rather than from differences in processing of the two stimulus dimensions.

The analysis of N1 amplitudes yielded significant stimulus dimension by region, $F(1, 11) = 10.58$, $p < .001$, and stimulus dimension by hemisphere, $F(1, 11) = 6.24$, $p < .05$, interactions. Col-
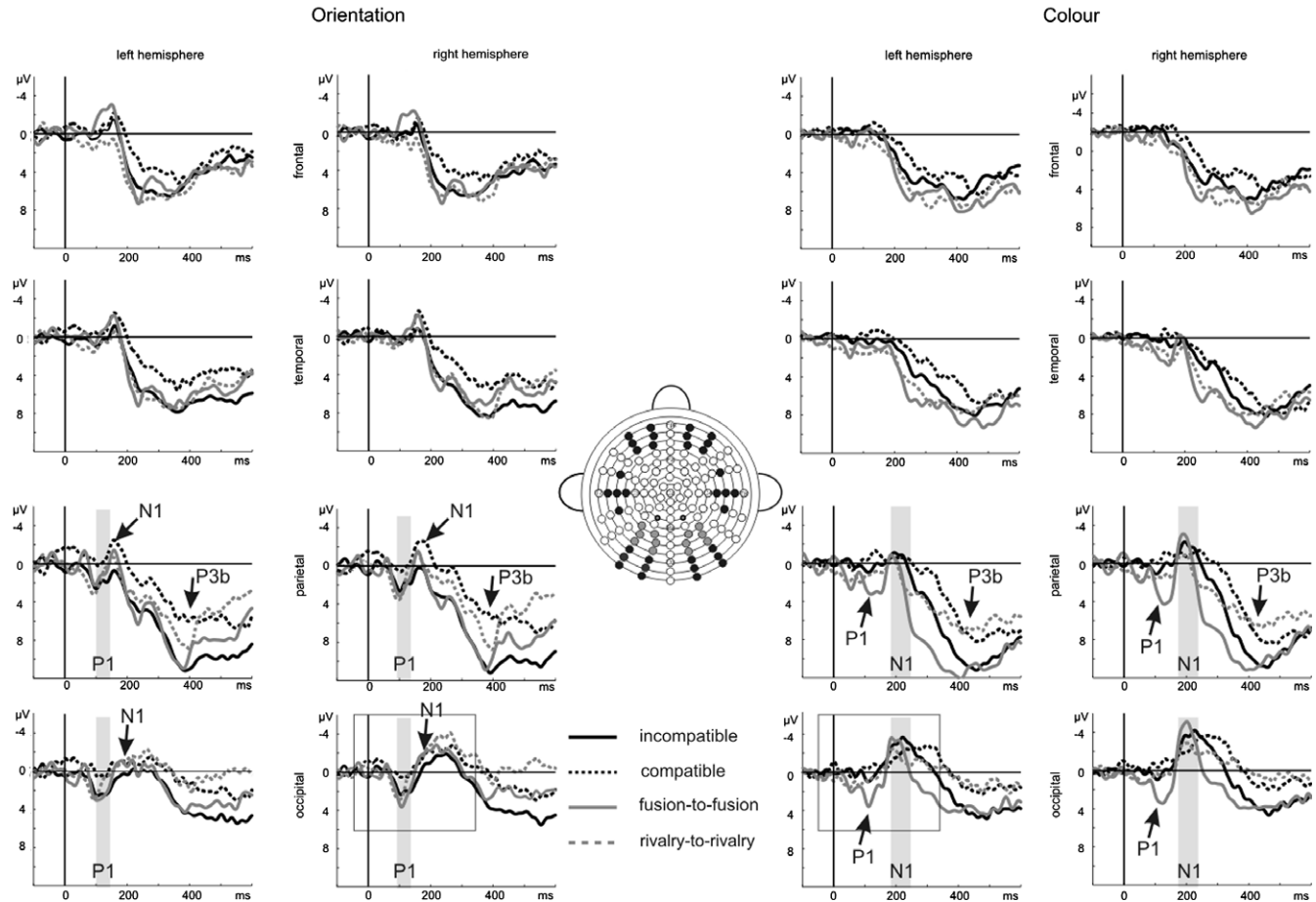
Fig. 3. Electrophysiological data: we show ERPs to orientation transitions on the left side of the figure and ERPs to colour transitions on the right side. Each diagram represents ERPs averaged across six electrodes from frontal, temporal, parietal, and occipital sites of the left and right hemisphere, respectively. We marked the electrodes included in the respective regional means in the schematic head. ERPs from rivalry-to-fusion transitions (black lines) were classified dependent on the observer's prevailing percept at the moment of the change into percept-incompatible transitions (black solid lines) and percept-compatible transitions (black dashed lines). ERPs to transitions with a stimulus change on both eyes (grey lines) occurred either from fusion-to-fusion transitions (solid grey lines) or from rivalry-to-rivalry transitions (dashed grey lines). Note, we show the ERPs to rivalry-to-rivalry transitions for completeness only; they do not appear in any of the analyses. The ERP components P1, N1, and P3b are highlighted (light-grey shades or arrows) where they are most pronounced (P1 and N1 at occipital and parietal clusters, P3b at parietal clusters). The light-grey shades also mark the time windows we used to analyse the first ERP difference between percept-incompatible and percept-compatible transitions: P1 following orientation rivalry and N1 following colour rivalry, respectively. The grey-bordered rectangles at the right occipital diagrams indicate the latency-by-amplitude window that we use to magnify the relevant early part of the ERP traces in Fig. 4.

Table 1

Results of separate repeated measures ANOVAs including the factors of transition (percept-incompatible vs. percept-compatible), of hemisphere (left vs. right), and of region (occipital vs. parietal) for the earliest difference in ERP between orientation transitions (P1: 100–120 ms) and colour transitions (N1: 195–225 ms)

		Orientation P1 (100–120 ms)	Colour N1 (195–225 ms)
Transition	$F(1,11)$	**9.01**[*]	1.89
	η^2	**.47**	.15
Hemisphere	$F(1,11)$	0.00	2.14
	η^2	.00	.16
Region	$F(1,11)$	0.16	**6.55**[*]
	η^2	.014	**.37**
Transition × hemisphere	$F(1,11)$	0.02	0.24
	η^2	.00	.02
Transition × region	$F(1,11)$	0.10	**5.21**[*]
	η^2	.01	**.32**
Hemisphere × region	$F(1,11)$	1.61	0.64
	η^2	.13	.06
Transition × hemisphere × region	$F(1,11)$	1.31	3.37
	η^2	.11	.24

We highlighted significant main effects and interactions by using boldface.
[*] $p < .05$.

our transitions elicited larger N1 amplitudes than orientation transitions at occipital sites; this difference diminished at parietal sites. The difference in N1 amplitude between the two stimulus dimensions was more pronounced in the right than in the left hemisphere.

To find the neural correlate of the slower RTs to orientation transitions than to colour transitions, we first looked for the earliest deflection of the ERP. This was the opposite of the RTs for the incompatible transitions (earlier for orientation, P1, than for colour, N1) and there was no difference in the P1s for fusion-to-fusion transitions. We were forced to conclude that it must be the amplitude of the N1 that reflects the processing speed of the two stimulus dimensions because it is the first component to show a difference in the same order as the RTs. That is, RTs to colour transitions were faster than to orientation transitions, and N1 amplitudes to colour transitions were larger than to orientation transitions.

3.3. Source analysis

For the P1 from orientation transitions and for the N1 from colour transitions we used Variable Resolution Electromagnetic

Tomography (VARETA) to estimate the generators of the electro-physiological activity (Gruber, Trujillo-Barreto, Giabbiconi, Val-des-Sosa, & Müller, 2006; Roeber et al., 2008; Valdes-Sosa et al., 1996). VARETA is based on a discrete spline distributed inverse model, which estimates the spatially smoothest intracranial primary current density (PCD) distribution in source space that generates the measured EEG data.

We constructed statistical parametric maps (SPMs) based on a voxel-by-voxel Hotelling T^2 test against zero to localise the sources of the ERP components. Activation threshold correction was calculated by means of Random Field Theory (Worsley, Marrett, Neelin, & Evans, 1996) to account for spatial dependencies between voxels. We provide the details of this analysis and the SPMs of the solutions for percept-incompatible, percept-compatible, and fusion-to-fusion transitions for both stimulus dimensions in Supplementary material (Supplementary Fig. 1 and Supplementary Table 1).

On the top of Fig. 4 we show an enlarged version of the critical ERPs from the right-hemisphere occipital electrodes. On bottom of Fig. 4 we depict SPMs of the contrast in PCD between percept-incompatible and percept-compatible transitions for P1 in orientation rivalry and for N1 in colour rivalry. These SPMs were based on repeated-measures ANOVAs. Following orientation rivalry (P1 difference), the SPM shows significant differences in source activation in temporal regions of both hemispheres but more pronounced in the right, and significant differences in the right prefrontal cortex. Following colour rivalry (N1 difference) the SPM shows a similar picture but with the addition of significant differences in source activation in occipital cortex. Again, differences are more pronounced in the right hemisphere.

The critical comparison is that between the two SPMs showing the differences in cortical activation for orientation and colour correlated with awareness. From simply looking at them they appear intriguingly similar, despite deriving from different types of rivalry (orientation vs. colour) and from different times after onset of binocular fusion (100 ms for orientation and 200 ms for colour).

To quantify the similarity of two distributions we note that (1) more than 50% of the significantly activated tissue in one type of rivalry is also significantly activated in the other type of rivalry (66% of the tissue showing a significant difference in activation following orientation rivalry also show also a significant difference in activation following colour rivalry; and 56% vice versa); (2) the centres of gravity for both types of rivalry are located in conjointly activated cortical tissue; (3) the Euclidean distance between these centres of gravity is smaller than the expected Euclidean distance between randomly located centres of gravity. To do this last sort of analysis, we showed that the obtained Euclidean distance is on the left side ($p < .05$) of a probability distribution that we constructed by randomly drawing 10^4 pairs of voxels out of all voxels included in SPM estimation by VARETA and calculating the Euclidean distance between the members of each pair (see Schröger, 1998, and Schröger, Rauh, & Schubö, 1993, who describe the use of Minkowski distances in order to determine the similarity or dissimilarity between discrete variables in detail).

The overlap in the cortical areas showing a significant difference correlated with awareness suggests that similar activity in a similar cortical network occurs following the two types of rivalry. This network is mainly located in lateral temporal cortex, spreading into occipital and prefrontal areas.
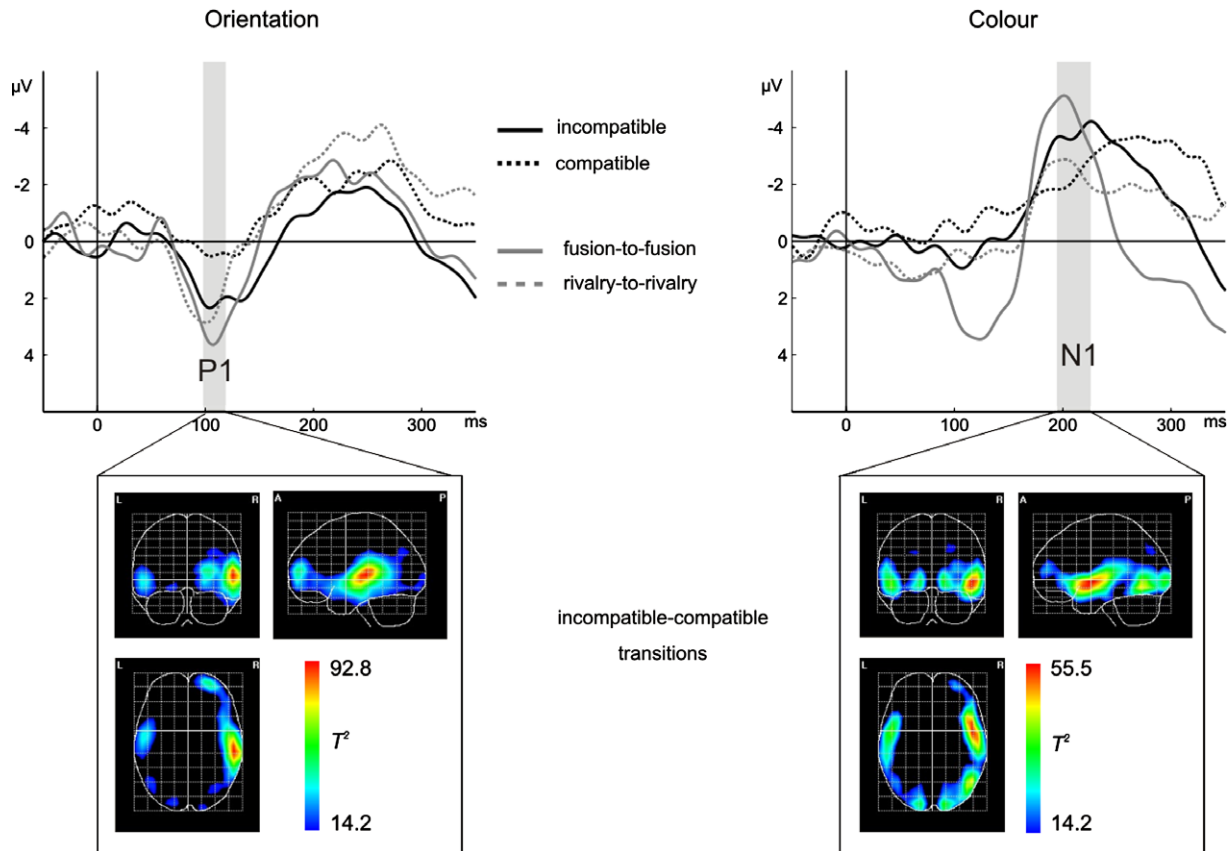

Fig. 4. ERPs traces at the occipital right cluster magnified in the relevant early time window for orientation transitions (top left) and for colour transitions (top right). ERPs to the different transitions are of the same colour and line-style as in Fig. 3. Percept-incompatible (solid black lines) and percept-compatible transitions (dashed black lines) show the earliest difference at about 100 ms (P1) for orientation and at about 200 ms (N1) for colour. The grey shades mark the time windows we used to analyse these first ERP differences. Below the ERPs we show the difference in primary current density (PCD) distributions for the first percept-dependent ERP modulation for orientation (P1; bottom left) and for colour (N1; bottom right). The SPMs represent the difference in activation between percept-incompatible and percept-compatible transitions. They are shown as maximum intensity projections. The "hotter" colours correspond to higher probability values (thresholded to $T^2 > 14.2$, which corresponds to $p < .01$).

4. Discussion

We set out to determine whether time and place of neural correlates of awareness in the visual processing stream are dependent on type of binocular rivalry: orientation and colour. We used the paradigm of Kaernbach et al. (1999) allowing us to compare brain activity to two identical stimulus transitions that differ only in visual awareness via binocular rivalry, namely percept-incompatible and percept-compatible transitions. Our results show that the neural correlates of visual awareness have a shorter latency following orientation rivalry (at about 100 ms) than following colour rivalry (at about 200 ms). Despite this difference in time, the places in the brain underlying these percept-dependent modulations in ERP are similar for both stimulus dimensions with a focus of activity in the lateral temporal cortex of the right hemisphere. In the following discussion, we elaborate on differences in the rivalry phase durations for the two sorts of rivalry. Then we differentiate between dimension-correlated processing, reflecting the detection of a stimulus transition, and awareness-correlated processing, reflecting the difference between being aware of a stimulus transition and being unaware of it.

4.1. Psychophysical differences between the two sorts of rivalry

Psychophysically, orientation rivalry differs from colour rivalry. For example, rival stimuli differing in both orientation and colour can yield percepts combining one eye's orientation with the other eye's colour (Breese, 1909; Creed, 1935; Hastorf & Myro, 1959). For another example, priming with orientation yields different rivalry from priming with colour (Holmes et al., 2006; Ikeda & Morotomi, 2000, 2002). Our behavioural data also point to differences. Dominance phase durations lasted longer during orientation rivalry than during colour rivalry. This observation agrees with the finding of others that colour stimuli are more likely to fuse whereas orientation stimuli are more likely to rival (de Weert & Wade, 1988; Holmes et al., 2006).

4.2. Dimension-related processing

Our RT data are consistent with slower processing of orientation than of colour (Clifford, Arnold, & Pearson, 2003; Moutoussis & Zeki, 1997). This is true whether the change in the stimuli was from rivalry to fusion or from fusion to fusion. The magnitude of the RT difference (between 20 and 50 ms) agrees with other reports of a temporal advantage in perceiving colour over perceiving orientation (e.g., Shikata et al., 2001).

When we look at EPRs to orientation and colour fusion-to-fusion transitions (seen most clearly in Fig. 4), we find further support for our behavioural results. A change to the orientation of identical stimuli viewed by the two eyes yielded a P1. A change to the colour of identical stimuli viewed by the two eyes also yielded a P1 of about the same amplitude as the orientation P1. Moreover, in both cases P1 was followed by an N1 that differed in amplitude between orientation and colour transitions: N1 amplitude for colour changes was larger than for orientation changes—with a right hemisphere and occipital focus of that difference. One process that N1 reflects is the processing speed of different kind of stimuli (Hopf, Vogel, Woodman, Heinze, & Luck, 2002; Vogel & Luck, 2000). This difference in amplitude underscores our behavioural results: when it comes to discriminating between two features of the stimuli we used in our experiment colour is favoured over orientation.

We propose that the N1 amplitudes and RTs depend on qualitative differences between the two types of stimuli that are unrelated to rivalry. For example, the orientation changes involved one stimulus changing into its left–right mirror image, a difficult change to distinguish (e.g., Attneave & Olson, 1967; Over, 1967; Rudel & Teuber, 1963), whereas the colour changes involved one stimulus changing to its opposite, such as red to green, a much easier change to distinguish (Beaudot & Mullen, 2001; Cattell, 1886).

4.3. Awareness-correlated processing

4.3.1. When does awareness-correlated activity start to happen?

We found the earliest neural activity correlated with awareness after 100 ms as a positive shift following a change from orientation rivalry to binocular fusion, and after 200 ms as a negative shift following a change from colour rivalry to binocular fusion. There is increasing evidence from different experimental paradigms for neural correlates of visual awareness to occur as early as 100 ms as a positive shift (Kornmeier & Bach, 2005, 2006; Pitts et al., 2007; Roeber & Schröger, 2004; Roeber et al., 2008; Valle-Inclan et al., 1999), to occur around 200 ms as a negative shift (Koivisto, Revonsuo, & Lehtonen, 2006), and to occur as late as 270 ms as a positive shift (Del Cul, Baillet, & Dehaene, 2007). Our results, both for timing and for polarity, sit squarely within this temporal range. Differences between different studies might be from differences in procedures, paradigms, tasks, and definitions of awareness.

Of more importance are studies that failed to find an effect correlated with awareness around 100 ms. One of these appears to be the original study that inspired our research (Kaernbach et al., 1999). Although there is a striking N1 effect in that study, examination of the ERPs in the figure shows a P1 effect too for which they did not test. We retrieved the data from that study and analysed the P1 amplitudes. We found that the P1 effect is statistically significant, consistent with what we have found here.

Other studies using different paradigms have explicitly looked for a P1 effect and failed to find it (Koivisto et al., 2008, 2006; Wilenius & Revonsuo, 2007). There are at least two possible reasons. First, the P1 is correlated with the salience of a stimulus (e.g., Regan, 1989). Contrast and stimulus duration are major components of salience. Koivisto et al. (2006), Wilenius and Revonsuo (2007), and Koivisto et al. (2008) all used near-threshold, low-salience stimuli. Second, the P1 might depend on level of processing within the visual system. Our current findings are consistent with this: we found a P1 effect following orientation rivalry, but not following colour rivalry. Colour is fully processed at a higher level (V4; Bartels and Zeki) than orientation (V1/V2; Bartels & Zeki, 2000; Hubel & Wiesel, 1965; Leopold & Logothetis, 1996). Koivisto et al. (2006) and Wilenius and Revonsuo (2007) used complex stimuli likely to be processed at a higher level of the visual system than V1.

One aspect of our results deserves further comment. We failed to find a N1 effect following orientation rivalry. If anything, the ERPs go in the opposite direction, with greater negative deflections to percept-compatible transitions than to percept-incompatible transitions. But we do not think this is evidence against a N1 component in other awareness-related tasks. It is quite possible that the greater positive deflections from the earlier percept-incompatible transitions did not give brain electrical activity a chance to subside sufficiently to show a later N1 effect.

Before we leave this section, we should comment on when awareness, rather than when activity correlated with or preceding awareness, happens. Our research, and the research of others we cite, allows us to specify only the latter. To specify the former will require converging operations from electrophysiology research, from brain-imaging studies, and from some sort of psychological research akin to mental chronometry (e.g., Donders, 1868/1969; Meyer, Osman, Irwin, & Yantis, 1988; Posner, 2005). Our best guess is that awareness actually happens some time after 100 ms, maybe closer to the N1 time range, around 200 ms. This is because the P1 time range is within that traditionally identified as reflecting

simple sensory processing (Hillyard & Kutas, 1983). But just as we have no real reason from our own research to place the time after 100 ms, equally we have no real reason not to place it around 100 ms, just where we find the earliest ERP activity correlated with awareness.

4.3.2. Where does early awareness-correlated activity happen?

We suppose each stimulus feature is processed by its own specialised brain area (Tootell, Dale, Sereno, & Malach, 1996; Zeki et al., 1991) and then all features are bound together into a coherent percept. Any change in a specific feature (such as in colour) should affect only that feature's specific processing stage and stages beyond. Orientation information reaches its specialised processing stage (V1/V2; Bartels & Zeki, 2000; Hubel & Wiesel, 1965; Leopold & Logothetis, 1996) earlier than colour information reaches its specialised processing stage (V4; Bartels & Zeki, 2000). Although this is in the same order as our ERP results, it is several orders of magnitude too fast. For example, Schmolesky et al. (1998) and Schroeder, Mehta, and Givre (1998) report that it takes only 20 ms for ERPs to be generated in the highest visual areas of the brain. Foxe and Simpson (2002) have shown that initial flow of activation elicited by visual stimulation reaches the frontal cortex within about 80 ms. Instead, we assume that recurrent feedback mechanisms play a crucial role in enhancing the neural activity to those signals that eventually reach our awareness (Hochstein & Ahissar, 2002; Lamme, 2003; Supèr, Spekreijse, & Lamme, 2001). Roeber et al. (2008) presented movies of source activation in percept-incompatible and percept-compatible transitions with frames 20 ms apart that reveal activity surging back and forth among occipital, temporal, and parietal sites that may reflect such feedback.

Of critical importance are the differences in source activation correlated with awareness. To assess these differences, we first reconstructed the sources in the brain underlying the ERP components (see Supplementary Fig. 1). These revealed the usual networks. For P1 following orientation rivalry, we found a rather widespread network of activity in the posterior part of the cortex, the visual brain, mainly propagating from ventro-lateral occipito-temporal and temporal areas. Such a broad network for P1 is in accordance with reports from other studies (Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002; Foxe & Simpson, 2002), including our previous work with the same paradigm but different orientation stimuli (Roeber et al., 2008). For N1 colour rivalry, a similar network of posterior brain areas was active but with slight shifts in the key nodes of activity and with additional amplification of activity in parietal cortex. This also corroborates findings from other ERP source localisation studies (Del Cul et al., 2007; Di Russo et al., 2002; Foxe & Simpson, 2002).

There were critical differences in source activation correlated with awareness. At P1 latency they arose strongly in the temporal lobe of the right hemisphere, but also in right prefrontal regions. At N1 latency, the same differences between transitions in colour arose in similar brain regions, extending more into the lateral occipito-temporal cortex. These findings suggest that even though earliest neural correlates of visual awareness can vary in the time of their onsets depending on the stimulus attribute that needs to get through to perception, the brain areas mediating that access are largely common for the two types of rivalry we used here.

From our results we cannot conclude if this common set of awareness-correlated brain areas is continuously active and affects orientation processing earlier than colour processing or if it gets activated afresh for each specialised feature processing. The results support, however, the assumption that the ventral visual pathway is a key figure for conscious visual perception (Goodale & Milner, 2004; Pins & ffytche, 2003). They also provide further evidence for a right over left hemisphere advantage when it comes to processing for visual awareness (Fink, Marshall, Weiss, & Zilles,

2001; Macaluso & Frith, 2000). Goodale and Milner (2004) have proposed that this reflects a reduction of spatial processing capacity in the left hemisphere because of its specialisation for language. Others also have reported right over left hemisphere dominances for simple discrimination tasks in the fusiform cortex (Dupont et al., 1998), for shape information in the anterior temporal cortex (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991) and for object recognition in the lateral occipital cortex (Vanni, Revonsuo, Saarinen, & Hari, 1996).

The frontal activity we found following both sorts of rivalry agrees with a fronto-parietal network of activity underlying perceptual alternations during binocular rivalry found with different techniques (Lumer et al., 1998; Srinivasan & Petrovic, 2006).

5. Conclusion

We have two main conclusions: First, the timing of the earliest neural correlates of visual awareness following binocular rivalry depends on the stimulus attributes that rival: earlier for orientation than for colour. Second, the cortical structures underlying these correlates remain roughly the same despite the differences in time. This suggests that visual awareness following rivalry is mediated by a network involving right ventro-lateral temporal areas and frontal trajectories.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.visres.2008.07.024.

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