Neural processing of orientation differences between the eyes' images

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The aim of this study was to explore the neural mechanisms underlying visual processing of brief stimuli that were either the same in the two eyes or differed in orientation between the two eyes. To examine the neural mechanisms, I measured event-related potentials (ERPs) to 200-ms sine-wave gratings differing in orientation between the eyes from 0° to 90°. The gratings were either both of high contrast or both of low contrast. They elicited typical ERPs at occipital electrodes, with a first major component (P100) 100 ms after stimulus onset and a second major component (N170) 170 ms after stimulus onset. Global electrical field strength and focal amplitudes of both components were affected by grating contrast: High-contrast gratings elicited larger amplitudes than low-contrast gratings, confirming that neural responses depend on stimulus salience. P100 amplitude followed a U-shaped function: It was larger when the orientations were the same in the two eyes (yielding binocular fusion), intermediate when the orientations were maximally different between the eyes (leading to binocular rivalry), and smallest for in-between orientation differences. N170 amplitude followed a linear function: It was smallest when the orientations were the same and increased with orientation difference between the eyes. These results suggest that the P100 reflects processes in which the binocular input are offset against each other, and that the N170 reflects binocular rivalry. I argue that the N170 shows the effects of reciprocal inhibition and adaptation—both critical factors in theories of binocular rivalry.

Keywords: dichoptic stimulation, orientation, contrast, binocular rivalry, binocular fusion, stereopsis, ERP, P100, N170, global field power.

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Introduction

One of the intriguing mechanisms in the processing of visual stimuli is how the inputs of our two eyes result in a single coherent percept (e.g., Blake & Wilson, 2011). It is intriguing because slight differences between the two eyes' inputs yield enduring binocular fusion of some compromise between the two inputs and, if the differences are the right sort, depth perception from stereopsis (Wheatstone, 1838), whereas large differences between the two eyes' inputs yield a completely different phenomenon: perception of one and the other's inputs in irregular alternation—binocular rivalry—and no depth perception (Wheatstone, 1838).

Why and how do the processes underlying these fundamental phenomena of binocular vision occur? There is some consensus for binocular fusion and stereoptic depth perception. They occur to avoid confusion about the visual direction of an object (e.g., Duke-Elder & Wybar, 1973) and to inform about the distance of the object from the eyes (Wheatstone, 1838). The processes are effected, at least initially, by binocular cells in the visual cortex having receptive fields in each eye that allow for differences in the location or properties of each of the eye's images (Barlow, Blakemore, & Pettigrew, 1967; Ferster, 1981).

For binocular rivalry, there is no modern consensus on the answer to the why question, with some maintaining that is the outcome when binocular fusion fails (Blake, 1989; O'Shea, 2011; Wheatstone, 1838) and others maintaining that they are epiphenomena of the processes arising from when vision is essentially monocular (Arnold, 2011a, 2011b). There is more consensus on the answer to the how question: Rivalry arises from reciprocal inhibition between, and adaptation within, those sets at different levels of the visual system (Blake & Logothetis, 2002; Klink et al., 2008; Tong, Meng, & Blake, 2006).

Although much is known from functional magnetic resonance imaging (fMRI) about the places in the brain active during binocular rivalry, ranging from lateral geniculate nucleus to frontal lobes (e.g., Sterzer,

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Kleinschmidt, & Rees, 2009) and their interconnections (e.g., Wilcke, O'Shea, & Watts, 2009), little is known about the timing of that activity, leading to the question I address: What is the initial neural processing, within the first 200 ms, of stimuli that give rise to the fundamental phenomena of binocular vision? To answer it, I varied the differences between the eyes' images systematically using orientation as the variable. This is because we already know that doing so yields binocular fusion for orientation differences from 0° to about 20° (e.g., Kertesz & Jones, 1970; O'Shea & Crassini, 1982), stereopsis for orientation differences around vertical from 1° to about 40° (e.g., Blakemore, Fiorentini, & Maffei, 1972), and binocular rivalry for orientation differences around vertical from about 20° to a maximum of 90° (Kitterle & Thomas, 1980; O'Shea, 1998; Schor, 1977; Thomas, 1978; but see Wade, 1974). I also varied the contrast of the stimuli, because we also know that this is a key influence on the experience of rivalry: High-contrast stimuli lead to faster perceptual fluctuations than low-contrast stimuli (Alexander & Bricker, 1952; Hollins, 1980).

To examine the timing of neural processes to stimuli varying in orientation between the eyes and contrast across the eyes, I measured electrophysiological brain responses noninvasively with electrodes on the scalp—electroencephalography (EEG)—from which I derived event-related potentials (ERPs), time-locked to the onset of dichoptically presented stimuli. This procedure allows one to determine typical electrophysiological responses to a specific stimulus category—averaged across many trials—and to compare these responses among categories. Because the temporal resolution of EEG is in the ms range (e.g., Churchland & Sejnowski, 1988), one can determine processing differences among the categories pretty much as they occur in the brain, and one can do so without relying on behavioral responses of the person viewing the stimuli. I took advantage of these properties and presented gratings of different orientations to the two eyes for 200 ms, with a 1000 ms break between presentations. Such a brief stimulus presentation is sufficient to initiate binocular fusion (Julesz & Tyler, 1976), stereopsis (Mitchell & O'Hagan, 1972), and in particular, binocular rivalry (De Belsunce & Sireteanu, 1991; O'Shea & Crassini, 1984; Wolfe, 1983); it also allows for many stimulus presentations in the course of the experiment, which are necessary to determine reliable ERPs.

During stimulus presentation, participants performed a task on binocularly identical digits presented at the gratings' center. The task was unrelated to the gratings' orientations, and the digits were presented out-of-synchrony with the gratings. I used this set-up to make sure that participants looked at the gratings without paying attention to them so as to assess the dichoptic gratings' processing unaffected by cognitive evaluation mechanisms.

To my knowledge there have been only three prior studies exploring the effects of interocular orientation differences on electrophysiological responses. Harter, Conder, and Towle (1980) used a paradigm that is now known as flash suppression (Sheinberg & Logothetis, 1997; Wolfe, 1984): They presented a grating of fixed orientation to one eye and flashed gratings of different orientations to the other eye. They found that at about 110 ms after flash onset, the ERP to these flashes showed a smaller (negative) deflection the smaller the orientation difference is between the flash and the continuous grating.

Tyler and Apkarian (1985) used pattern-reversing (counterphasing) gratings and a narrow-band filter to extract electrophysiological responses in the stimulation frequency and its second harmonic. They too presented one orientation constantly to one eye and gratings of varying orientation to the other eye. For most of the orientations they found that the amplitudes in the two frequencies were similar to the amplitudes elicited with monocular stimulation when just the gratings of varying orientation were presented. However, when the constant grating was vertical and the interocular orientation difference was less than 15°, or when the constant grating was oblique and the interocular orientation difference was less than 20°, they found an amplitude increase. This increase most likely reflects stereopsis because no such amplitude increase was found when the constant grating was horizontal. Interocular orientation differences around the horizontal meridian yield only fusion and not stereopsis (Blakemore et al., 1972; Mitchell & O'Hagan, 1972; O'Shea & Crassini, 1982; Ogle, 1950).

Jakobsson (1985) also used pattern-reversing gratings. His participants always saw a vertical grating through the right eye and gratings of varying orientations through the left eye. Pattern-reversal rates differed slightly between the eyes. He assessed binocular interaction as the ratio between ERP amplitudes for binocular and for monocular stimulation, and found that binocular interaction decreased (the binocular/monocular ratio increased) with increasing interocular orientation difference.

All three prior studies used a grating of the same orientation constantly presented to one eye, and therefore did not control for the effects that adaptation to this stimulus might have exerted on their results. Moreover, none of these studies measured ERPs to simultaneous onset of rival stimuli, that is, to the initiation of fundamental binocular phenomena. I aimed to fill these gaps.

Given that it is sufficient to present dichoptically different stimuli for 150 ms to initiate binocular rivalry (De Belsunce & Sireteanu, 1991; O'Shea & Crassini,

1984; Wolfe, 1983), I expected to find ERP differences between different degrees of interocular orientation differences within the first 200 ms after stimulus onset. Using the ERPs elicited by gratings that were of the same orientation in both eyes (0° interocular orientation difference) as a baseline, three outcomes appeared to be possible:

(a.1) The ERPs to gratings with interocular orientation differences larger than 0° differ from the ERP to gratings with 0° interocular orientation difference, but they do not differ from each other. This would suggest that dichoptically incompatible stimuli are differently processed from dichoptically compatible stimuli in an all-or-none fashion. Early neural responses might be boosted by identical (or similar) inputs to the two eyes leading to binocular summation or facilitation (Apkarian, Nakayama, & Tyler, 1981) or generally reduced by incompatible inputs to the two eyes with these responses being mainly driven by binocular interactions that are not orientation-selective (e.g., Sengpiel, Freeman, & Blakemore, 1995).

(a.2) The ERPs to gratings with interocular orientation differences larger than 0° differ from the ERP to gratings with 0° interocular orientation difference, and they do differ from each other as a function of the degree of interocular orientation difference. This would suggest that early neural responses—besides registering the incompatibility of binocular inputs—are susceptible to the amount of this incompatibility at least for stimuli differing in orientation. This in turn can be a signature of binocular cells that are orientation-selective and therefore lead to orientation tuning (Ringach, 1998; Ringach, Hawken, & Shapley, 1997; Roeber, Wong, & Freeman, 2008) and reciprocal inhibition (Lehky & Blake, 1991). The latter is a common theme in theories of binocular rivalry (Blake & Logothetis, 2002; Klink et al., 2008; Tong et al., 2006) that has been taken as an explanation why we see only one of the stimuli during binocular rivalry.

(a.3) The ERPs to all the interocular orientation differences, including the 0° difference, do not differ from each other. This would suggest that there are no early processing differences independent of attention or that ERPs are not sensitive enough to pick up such differences.

To follow up on the notion that stimulus contrast is critical for the initiation (Liu, Tyler, & Schor, 1992) and the perceptual characteristics (Alexander & Bricker, 1952; Hollins, 1980) of binocular rivalry I used—in separate blocks—gratings of high contrast and gratings of low contrast, but of the same overall luminance. This was to explore if ERP measures susceptible to dichoptically different stimuli are affected by stimulus contrast. Again, three outcomes seem possible:

(b.1) ERPs could show a general decrease in amplitude (or increase in latency) with lower contrast irrespective of interocular orientation differences (e.g., Spekreijse, van der Twell, & Zuidema, 1973).

(b.2) ERPs could be differentially affected by stimulus contrast, for example showing a decrease in amplitude (or increase in latency) with lower contrast that varies with the degree of interocular orientation difference.

(b.3) ERPs could not be affected by stimulus contrast at all.

I found that the first two major ERP components, a posterior positivity at about 100 ms (P100) and a posterior negativity at about 170 ms (N170) after stimulus onset, show differential effects in their global field strength and focal amplitudes to both the manipulation of orientation differences and the manipulation of contrast. Both components were generally affected by stimulus contrast (b.1), showing weaker responses with low-contrast gratings. P100 was affected by interocular orientation difference (a.2): Amplitudes to gratings with no orientation difference (0°) were largest; they declined for gratings with intermediate orientation differences and increased for gratings with larger orientation differences. N170 showed a graded response to different degrees of interocular orientation difference (a.2): N170 amplitude increased as a function of orientation difference.

Methods

Participants

Seventeen participants took part in the study for which they received either course credits or payment (EUR 6 per hour). All participants gave written informed consent prior to the experiment. All had normal or corrected-to-normal vision. I tested visual acuity with the Freiburg Visual Acuity Test (Bach, 1996), defining normal as at least Snellen 6/9 with no difference between the eyes of more than two lines. Participants were selected after they showed normal binocular rivalry in a 10-min test session. Two of the participants did not fulfill the selection criteria for normal binocular rivalry (see below). The data of another participant had to be excluded due to equipment failure during EEG recording. The mean age of the remaining 14 participants (four male, one male left-handed) was 24.1 years (ranging from 19 to 37

years). The study was performed in accordance with the ethical standards laid down in the Declaration of Helsinki.

Apparatus

The experiment was conducted in one of the EEG laboratories at the University of Leipzig. During the experiment participants sat in a sound-attenuated and electrically shielded cabin. Participants viewed stimuli through a mirror stereoscope (Screenscope SA-200-Monitor-Type [Stereo Aids, Albany, WA, Australia]) that was attached to a head and chin rest. Stimuli were displayed on a ViewSonic Graphics Series G90fB, 19″, color monitor (CRT) (ViewSonic Corporation, Walnut, CA, USA) showing 1024 × 768 pixels at 100 Hz. Viewing distance was 57 cm. Participants responded using one button of a four-button response pad.

Stimuli

Stimuli were annulus-shaped patches of achromatic sine-wave gratings (spatial frequency: 3.47 cycles/degree; outer diameter: 1.65° of visual angle; inner diameter: 0.67° of visual angle) of 10 different orientations spaced 18° apart (i.e., 0°, 18°, 36°, 54°, 72°, 90°, 108°, 126°, 144°, and 162° from horizontal). The luminance of the gratings was 7.1 Cd/m^2, with a Michelson contrast of 0.98 for the high-contrast gratings and a Michelson contrast of 0.39 for the low-contrast gratings. Stimuli were presented on a medium gray background (7.1 Cd/m^2).

The gratings were surrounded by three concentric, equally spaced white rings (line thickness: 0.03° of visual angle; diameter of inner ring: 2.50° of visual angle; diameter of outer ring: 3.26° of visual angle). These rings served to lock binocular alignment of the gratings. Red digits (0.5° of visual angle) were superimposed on the gratings' inner disc. The horizontal positions of the stimuli were adjusted to allow each participant to view the two stimuli on corresponding retinal positions with normal relaxed viewing.

Procedure

An experimental session consisted of three parts.

1. Binocular rivalry test session

During the binocular rivalry test, participants viewed a horizontal grating with one eye and a vertical grating with the other eye continuously. Participants pressed one key whenever and for as long as they exclusively saw the horizontal grating and another key whenever and for as long as they exclusively saw the vertical grating. A trial lasted 150 s. There were four trials, two with high contrast stimuli (horizontal to left eye/vertical two right eye and vice versa) and two with low contrast stimuli (horizontal to left eye/vertical two right eye and vice versa). The order of trials was counterbalanced between participants. I defined normal as the distributions of exclusive visibilities from the left and right eyes' being monomodal, showing positive skew, and with similar modes and variabilities (Brascamp, van Ee, Pestman, & van den Berg, 2005; Levelt, 1967). Two participants had more than 60% difference in median duration of exclusive visibility between the eyes for the low-contrast gratings and were excluded from the study.

2. Visual evoked potentials to checkerboard reversals

Participants viewed 5° checkerboards (check size: 0.5° of visual angle) with dark and light checks in two contrast conditions (high contrast checkerboards: Michelson contrast of 0.98; low contrast checkerboards: Michelson contrast of 0.39). In both conditions the background was medium gray (7.1 Cd/m^2). The checkerboards phase-reversed at 2 Hz. For each contrast condition, I continuously presented 6 × 80 reversals in the following order: left eye only, right eye only, both eyes, both eyes, right eye only, left eye only. The order of contrast conditions was counterbalanced between participants. During the reversals participants focused on a stream of red digits (0.5 degrees of visual angle, new digit every 500 ms) presented at the checkerboard's center in order to detect those digits that were the same as the ones two digits ago (2-back task). This task was the same as in the experiment proper and served as training. I defined normal monocular and binocular visual evoked potential (VEP) as the VEPs showing a N75, a P100 (P1), and a N175 (N2) that did not differ markedly between the eyes and that were of similar or larger amplitude or of similar or earlier latency for binocular stimulation (Katsumi, Tanino, & Hirose, 1985; O'Shea, Roeber, & Bach, 2010). All participants met these criteria.

3. Experiment proper

The experiment proper consisted of 12 blocks. In half of them participants were presented with high-contrast grating; in the other half participants were presented with low-contrast gratings. Blocks with high- and low-contrast gratings alternated with the contrast in the first block being counterbalanced across participants.

Each block consisted of 200 trials. In each trial, 1 of the 10 grating orientations was presented to the left eye

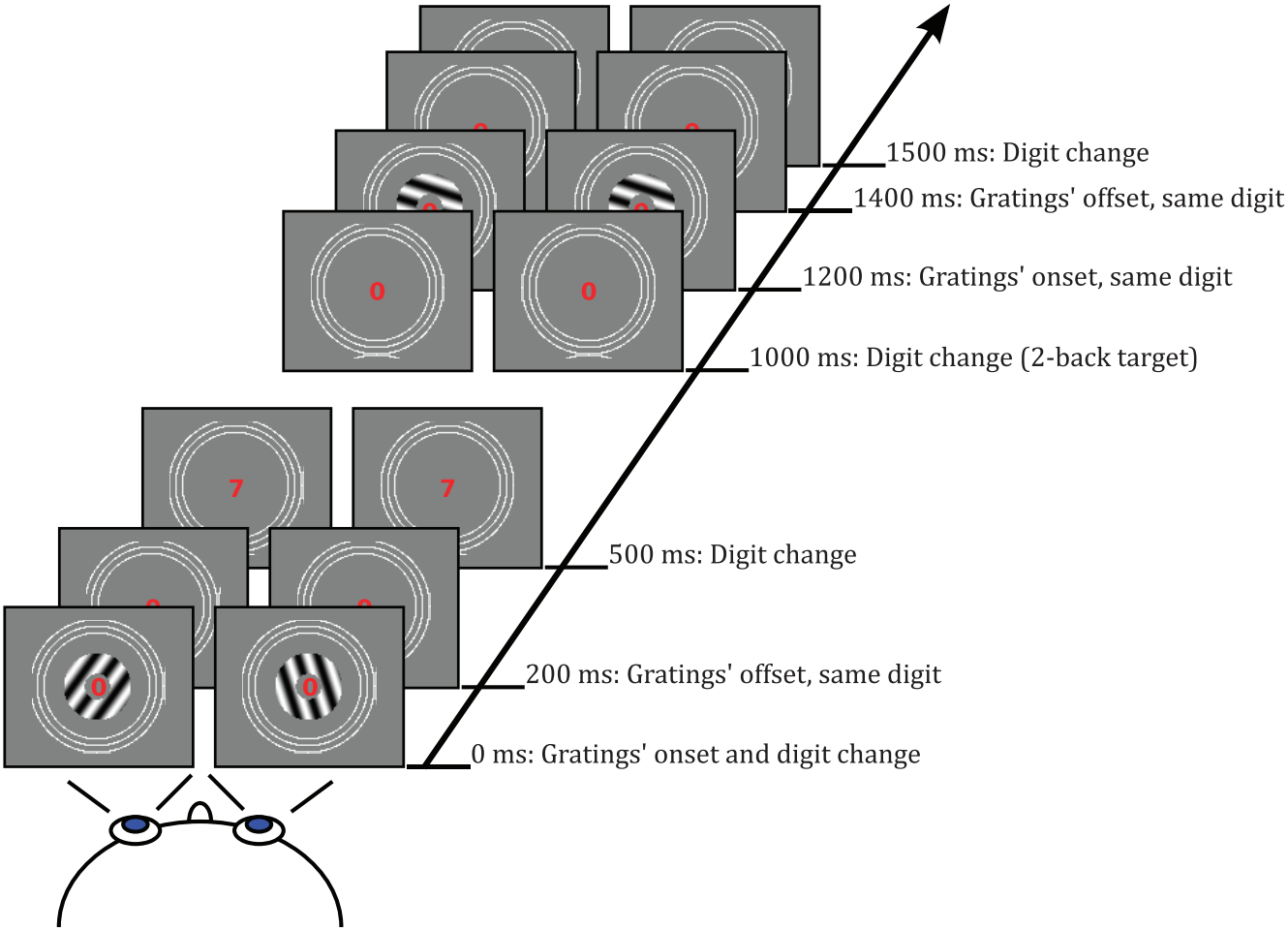

Figure 1. Schematic presentation of example stimuli presented to the left and right eye in the high-contrast condition as a function of time. Gratings were displayed for 200 ms, followed by an interstimulus interval of 1000 ms. Digits in the stimuli's center changed every 500 ms. Note that in this example, 1000 ms the digit changed to "0," which is the same digit that was presented two digits ago (at 0 ms). It thus is a 2-back target requiring a key press from the participant.

and 1 of 10 to the right eye, allowing for 100 different combinations with orientation differences between the eyes varying from 0° to 90°. Each of the combinations was shown twice per block in randomized order. Figure 1 shows a schematic presentation of example stimuli used in the experiment. Presentation of a pair of gratings lasted for 200 ms, followed by an interstimulus interval of 1000 ms in which only the fusion rings were shown.

Simultaneously, I presented a constant, randomized stream of digits (same digits to both eyes) at a rate of 2 Hz at the center of the gratings or fusion rings. Because the gratings were presented in random order, the occasionally occurring simultaneous onsets of gratings and digits were balanced across orientation differences. The digits were of the same luminance and chromaticity in both contrast conditions. We asked participants to concentrate on these digits and press a button as soon as they detected a digit that was the same as the digit two digits ago. Target probability was 10%. The task served to keep the participants alert and to help them to fixate the center of the gratings without paying attention to them. Each block took four minutes to complete. At the end of each block I displayed the percentage of correctly detected 2-back targets and the mean reaction time in this block.

Electrophysiological recordings

Continuous EEG data were collected from 66 active Ag/AgCl electrodes (actiCap) with a BrainAmp system (Brain Products GmbH, Munich, Germany). Four of the electrodes were used to measure horizontal and vertical eye movements (horizontal and vertical electro-oculograms, EOGs). They were attached above and below the right eye and to the outer canthi of both eyes. Another two electrodes were attached to the earlobes to allow for offline re-referencing. The remaining electrodes were mounted in an elastic cap based on the

extended 10–20 system covering the participants' scalps. Electrodes were online referenced to an electrode on position FCz and grounded to an electrode on position AFz. Data were sampled at 500 Hz.

Data analysis

Behavioral data

To ensure that participants paid attention to the 2-back task rather than to the gratings, I determined detection and false alarm rates and calculated sensitivities (d'). I also computed mean reaction times for detected targets. I defined a target as being detected when the participant pressed the key between 150 and 1000 ms after its occurrence. I did the analysis for each contrast condition separately and compared for differences between the conditions with paired t-tests.

Electrophysiological data

In preparation for data analysis, I re-referenced the EEG data offline to the average of all scalp electrodes (average reference) and applied a 0.5–35 Hz bandpass filter (Kaiser windowed sinc FIR filter, 1,857 points). I studied epochs of the data from −100 ms before to 500 ms after stimulus (gratings) onset. Epochs preceding or following a key press within 500 ms were excluded from further analysis, as were epochs with signals exceeding a moving-window, peak-to-peak amplitude of 200 μV at any EEG channel, or of 100 μV at any EOG channel (moving window width: 200 ms, distance between successive windows: 50 ms). I averaged ERPs separately for each interocular orientation difference (0°, 18°, 36°, 54°, 72°, and 90°) and contrast condition (high contrast and low contrast).

For data analysis, I took two approaches: First, I used a global and reference-free measure to take the whole scalp potential field into account—global field power (Lehmann & Skrandies, 1980, 1984; Skrandies, 2005). Global field power is defined as the mean potential difference between all electrodes (spatial standard deviation) at any given time and provides an index of the strength of activity and its fluctuation across time.

I calculated global field power for each participant, separately for all contrast conditions and orientation differences. I used global field power averages across participants to determine component time windows showing local field strength maxima resulting in two time windows: 90 to 110 ms (P100) and 160 to 180 ms (N170). For each time window, I submitted the mean field strength to a repeated-measures ANOVA with the factor's contrast condition (high contrast or low contrast) and orientation difference (0°, 18°, 36°, 54°, 72°, or 90°). When appropriate I applied Greenhouse-Geisser corrections of the degrees of freedom to correct for violations of the assumption of sphericity.

Second, I defined two regions of interest for a more conventional quantification of the centers of gravity of the effects in those two time windows of interest. My regions of interest were clusters of five posterior electrodes (a) at the left hemisphere (P7, PO3, PO7, PO9, and O1), and (b) at the right hemisphere (P8, PO3, PO8, PO10, and O2). I chose these regions because gratings are low-level visual stimuli that are most likely to be processed at early stages of the visual pathway (e.g., Livingstone & Hubel, 1988). These regions include the electrodes that build the bilateral centers of gravity of the potential field in the topographies within both time windows of interest (PO7 and PO8). Note, for completeness and to illustrate the voltage distributions across the scalp, I also present data from two clusters of five anterior electrodes (left hemisphere: AF3, F5, F3, F1, and FC3; right hemisphere: AF4, F6, F4, F2, and FC4) and scalp current density (SCD) maps in the Supplementary Material (Supplementary Figure S2). I performed peak measurements on the grand-average ERPs. I chose these time windows because I expected to see processing differences for interocular orientation differences at the earliest level of cortical visual processing, because these components are affected by visual awareness of changes in orientation (Kaernbach, Schröger, Jacobsen, & Roeber, 1999; Roeber & Schröger, 2004; Roeber, Widmann et al., 2008; Veser, O'Shea, Schröger, Trujillo-Barreto, & Roeber, 2008).

I calculated mean voltages across each time window and region of interest for all contrast conditions and orientation differences separately. For each time window, I submitted the mean voltages to a repeated-measures ANOVA with the factors contrast condition (high contrast and low contrast), orientation difference (0°, 18°, 36°, 54°, 72°, and 90°), and hemisphere (left and right). When appropriate I applied Greenhouse-Geisser corrections of the degrees of freedom to correct for violations of the assumption of sphericity.

Results

Behavioral data

Figure 2 displays boxplots of the sensitivity and reaction time data for the high-contrast condition and for the low-contrast condition. Note that the digits were of the same luminance and chromaticity in both contrast conditions. Participants detected on average (standard error) 39% (2%) of the 2-back targets in the high-contrast condition and 38% (2%) of the targets in the low-contrast condition. False alarm rates were 4%

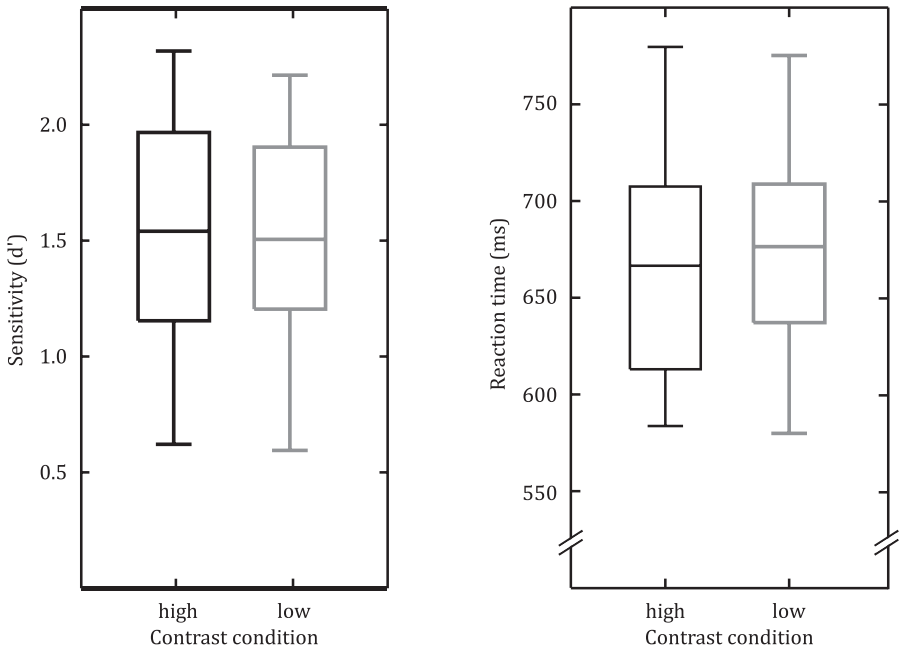

Figure 2. Sensitivity (d′, left panel) and reaction times (right panel) in the 2-back task for the high contrast and the low contrast condition.

(0.7%) in the high-contrast condition and 4% (0.6%) in the low-contrast condition. Sensitivities (high-contrast condition: $d' = 1.55$ [0.12]; low-contrast condition: $d' = 1.54$ [0.11]) showed no significant difference between conditions, $t(15) = 0.23$, $p = 0.82$.

Participants responded in 670 (15) ms to targets in the high-contrast condition and in 675 (14) ms to targets in the low-contrast condition. There was no significant difference in reaction time between conditions, $t(15) = -0.92$, $p = 0.37$. The low sensitivities mean that the participants' task was extremely demanding, leaving little, if any, attention to be given to the gratings. The lack of differences between the contrast conditions means that the task was equivalently demanding in those conditions.

Electrophysiological data

ERPs: Visual inspection

Figure 3 shows the ERPs to gratings with all different types of interocular orientation differences averaged over anterior and over posterior electrodes at the left and right hemisphere for both the high-contrast and the low-contrast condition. ERPs at the anterior electrodes show a slight negative deflection between 100 and 150 ms after stimulus onset and a sustained positive deflection between 200 and 300 ms after stimulus onset. The overall pattern seems to be strikingly similar for all types of interocular orientation differences and across contrast conditions.

All posterior ERPs show a typical cortical pattern to stimulus onset (O'Shea et al., 2010): a positive peak at about 100 ms after stimulus onset—a P100 component, and a negative peak at about 170 ms after stimulus onset—a N170 component, followed by another positive peak between 200 and 300 ms, but with differences in amplitude. In general, deflections appear to be larger in the high-contrast as compared to the low-contrast condition, and on the right hemisphere as compared to the left hemisphere. ERP traces to gratings with a interocular orientation difference (18°, 36°, 54°, 72°, and 90°) sit relatively close together, whereas ERP traces to gratings with no (0°) interocular orientation difference are more positive than the others from about 100 ms after stimulus onset to about 300 ms after stimulus onset.

In the N170 time window for the posterior electrodes, peak amplitudes appear to belong to three clusters, with the smallest amplitude belonging to gratings with no orientation difference, the intermediate amplitudes belonging to gratings with 18° and 36° orientation difference, and the largest amplitudes belonging to gratings with the largest orientation differences (54°, 72°, and 90°).

The anterior ERPs are smaller than the posterior ERPs, but do show some evidence of being modulated by interocular orientation difference and contrast. These modulations presumably reflect the influence of neural generators in the parieto-occipital region of the brain spreading through the volume of the brain. I base this conclusion on scalp current density maps I made of the P100 and N170 time windows for both contrast conditions and for all orientation differences (see Supplementary Material). For each component these maps show very similar current density distributions

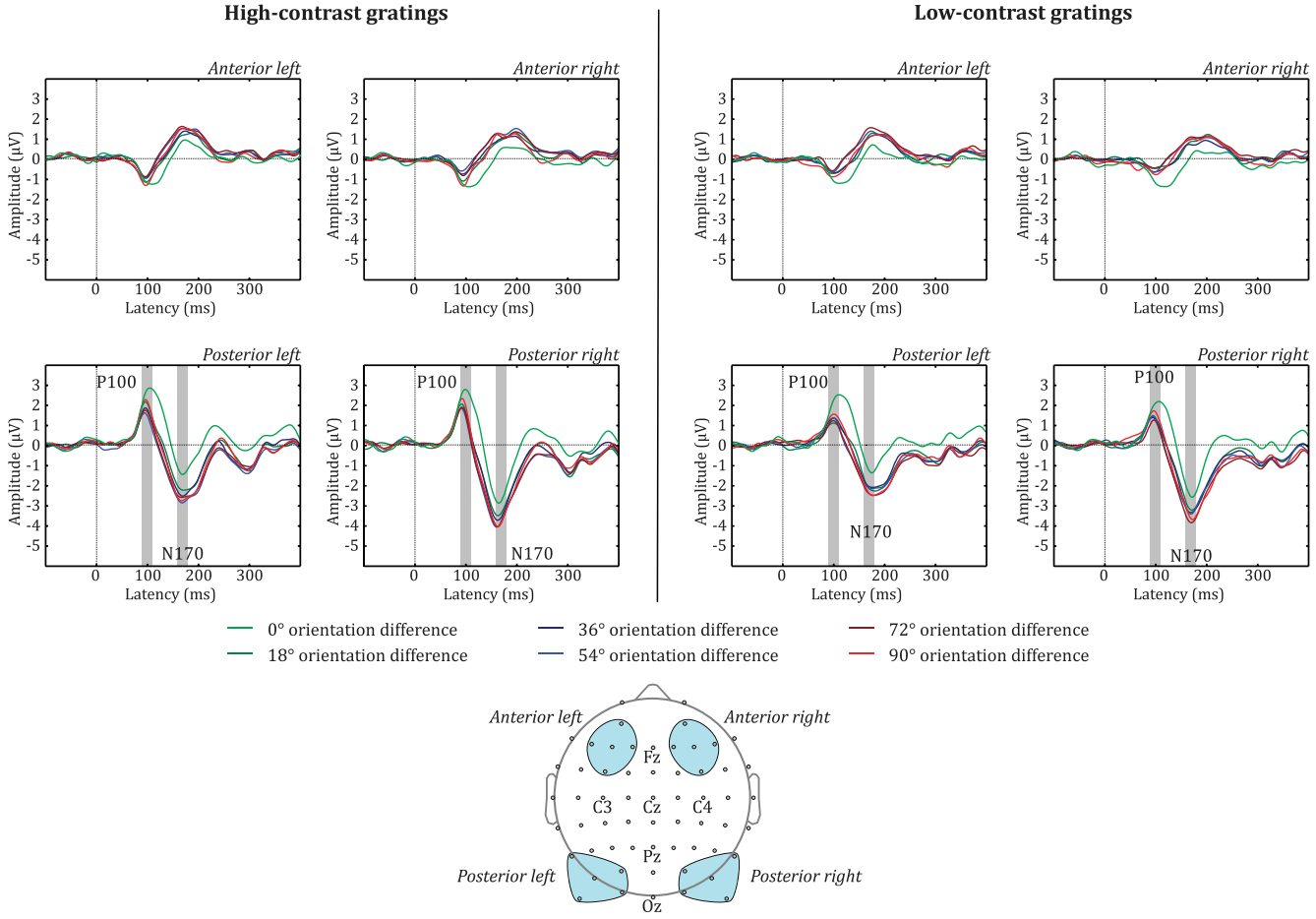

Figure 3. ERPs to gratings with all six levels of dichoptic orientation differences averaged over left anterior (AF3, F5, F3, F1, and FC3), right anterior (AF4, F6, F4, F2, and FC4), left posterior (P7, PO3, PO7, PO9, and O1), and right posterior (P8, PO4, PO8, PO10, and O2) electrodes for high-contrast (left panel) and low-contrast gratings separately. The gray-shaded areas under the posterior ERPs depict the time windows of interest (P100, N170). The schematic heads shows the positions of all recording sites; the blue shaded areas mark the electrodes included in the electrode cluster averages.

across contrast conditions and orientation differences with bilateral parieto-occipital centers of gravity. I do not analyze the anterior electrodes further except as part of the analysis of global field power, next.

Global field power

Figure 4 shows variations in global field power as a function of time for both contrast conditions and for all orientation differences separately and graphs of mean field strength as a function of orientation difference in the two component windows for both high- and low-contrast gratings.

The repeated-measures ANOVA for the P100 time window (90 to 110 ms) showed that the field strength for high-contrast stimuli was larger than for low-contrast stimuli, $F(1, 13) = 36.06$, $p < 0.001$, $\eta = 0.76$. There was also a significant main effect of orientation difference, $F(5, 65) = 6.86$, $p = 0.004$, $\eta = 0.35$, but no significant interaction of these two, $F(5, 65) = 1.06$, $p = 0.38$, $\eta = 0.08$. Mean field strength followed a U-shaped function with increasing orientation differences between the dichoptically presented gratings, $F(1, 13) = 13.74$, $p < 0.003$, $\eta = 0.51$. Excluding the 0° orientation difference yielded the same pattern of results with main effects of contrast condition, $F(1, 13) = 31.05$, $p < 0.001$, $\eta = 0.71$, and orientation difference, $F(4, 52) = 5.52$, $p = 0.007$, $\eta = 0.30$, but no significant interaction of these two, $F(4, 52) = 1.43$, $p = 0.25$, $\eta = 0.10$; a significant quadratic trend for orientation differences, $F(4, 52) = 14.80$, $p = 0.002$, $\eta = 0.53$, but also a significant linear trend for orientation differences, $F(4, 52) = 6.33$, $p = 0.03$, $\eta = 0.38$.

The repeated-measures ANOVA for the N170 time window (160 to 180 ms) showed only that the field strength for high-contrast stimuli was larger than for low-contrast stimuli, $F(1, 13) = 8.18$, $p = 0.01$, $\eta = 0.39$. Neither orientation difference, $F(5, 65) = 3.05$, $p = 0.08$, $\eta = 0.19$, nor the interaction of contrast condition and

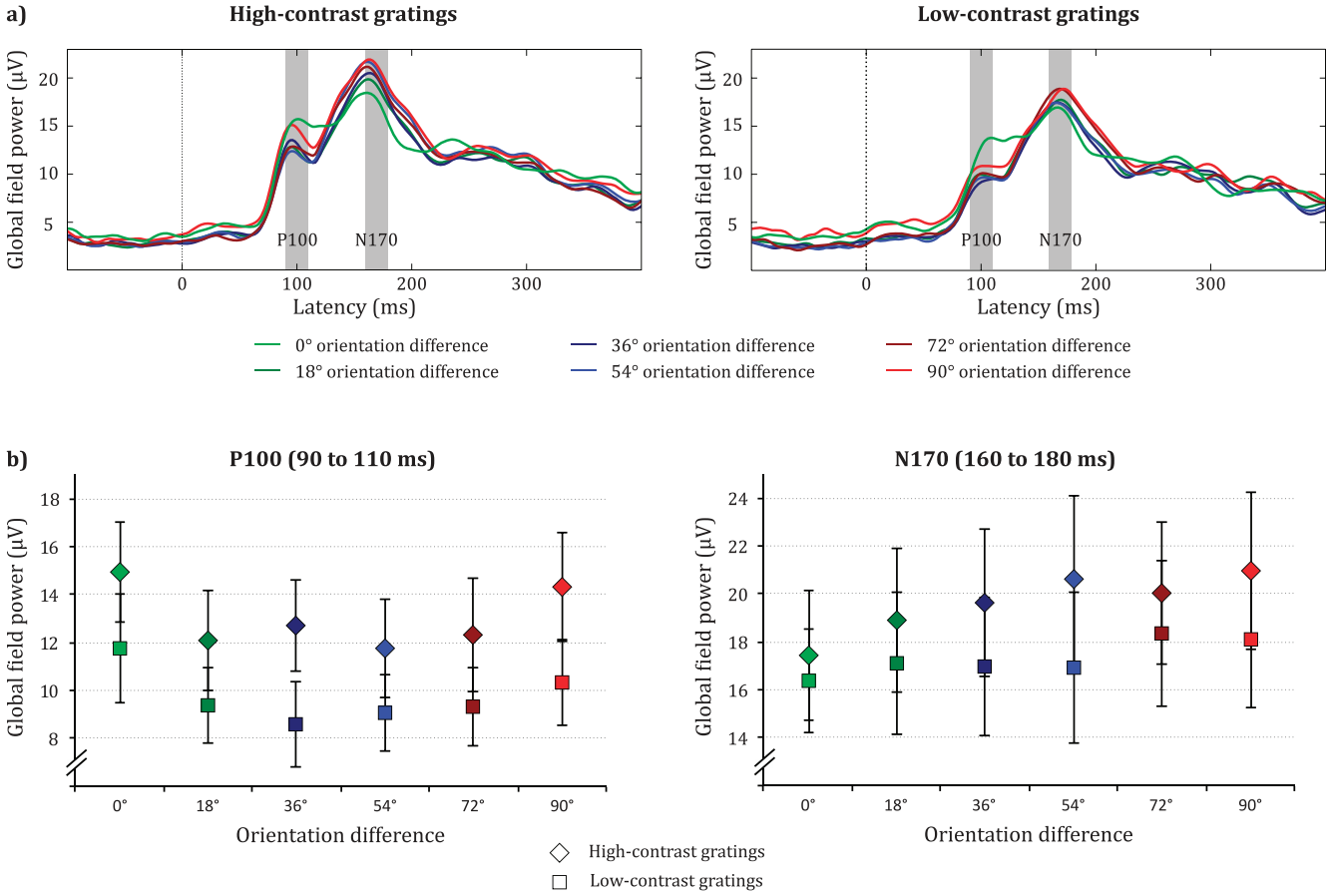

Figure 4. Global field power (a) as a function of time for all orientation differences and for both high-contrast gratings (left) and low-contrast-gratings (right); (b) as a function of orientation difference averaged across the P100 (left) and N170 (right) time windows for high-contrast (diamonds) and low-contrast (squares) gratings.

orientation difference, $F(5, 65) = 1.34$, $p = 0.28$, $\eta = 0.09$, was significant. Excluding the 0° orientation difference from analysis preserved the main effect of contrast condition, $F(1, 13) = 9.37$, $p < 0.01$, $\eta = 0.42$, but also yielded a significant effect of orientation difference, $F(4, 52) = 3.75$, $p = 0.02$, $\eta = 0.22$. For orientation differences larger than 0°, field strength increased as a function of orientation difference as confirmed by a significant linear trend: $F(1, 13) = 13.45$, $p = 0.003$, $\eta = 0.50$. The interaction of contrast condition and orientation difference remained nonsignificant, $F(4, 52) = 1.33$, $p = 0.28$, $\eta = 0.09$.

The global field power results in both the P100 and the N170 time windows are consistent with options a.2 (dependency on the degree of orientation difference) and b.1 (general effect of stimulus contrast independent of orientation difference).

ERP amplitudes: Statistical assessment

Figure 5 shows graphs of the mean P100 and N170 ERP amplitudes (see Figure 3) as a function of interocular orientation difference for both high- and low-contrast gratings, collapsed across the left and right posterior electrode clusters because hemisphere did not significantly affect any of the components (see below).

P100 results

The repeated-measures ANOVA for the P100 time window (90 to 110 ms) with factors of contrast condition, orientation difference, and hemisphere revealed significant main effects of contrast, $F(1, 13) = 7.65$, $p = 0.02$, $\eta = 0.37$, and of orientation difference, $F(5, 65) = 10.52$, $p < 0.001$, $\eta = 0.45$. Neither the main effect of hemisphere nor any of the interactions reached significance, hemisphere: $F(1, 13) = 0.01$, $p = 0.91$, $\eta = 0.001$; contrast condition by orientation difference: $F(5, 65) = 1.60$, $p = 0.20$, $\eta = 0.11$; contrast condition by hemisphere: $F(1, 13) = 0.91$, $p = 0.36$, $\eta = 0.07$; orientation difference by hemisphere: $F(5, 65) = 0.18$, $p = 0.89$, $\eta = 0.01$; contrast conditions by orientation

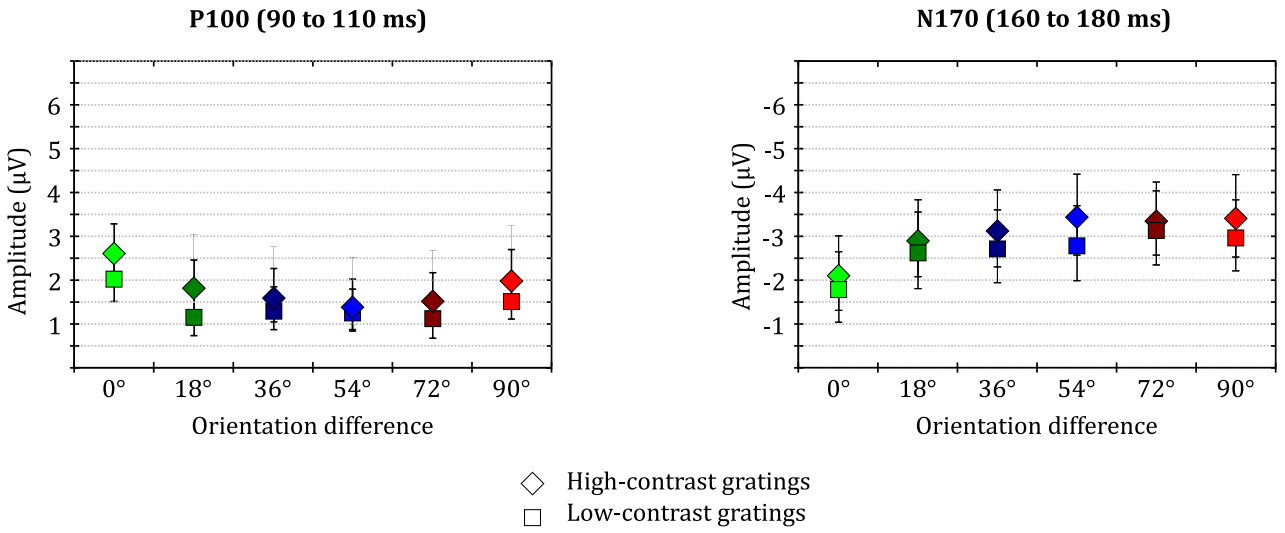

Figure 5. Mean P100 (left) and N170 (right) amplitudes with standard errors as a function of interocular orientation difference for both contrast conditions (high-contrast gratings: diamonds; low-contrast gratings: squares), collapsed across left and right posterior electrodes (see Figure 3). *Note*: N170 amplitudes are negative.

difference by hemisphere: $F(5, 65) = 2.26$, $p = 0.08$, $\eta = 0.15$.

Mean P100 amplitude was larger with high-contrast than with low-contrast gratings. Mean amplitude was more positive when there was no orientation difference than when there was an orientation difference between the dichoptically presented gratings. Including all orientation differences, there were significant linear, $F(1, 13) = 5.58$, $p = 0.001$, $\eta = 0.30$, and quadratic, $F(1, 13) = 28.17$, $p < 0.001$, $\eta = 0.68$, trends of the mean with orientation difference. Excluding the 0° orientation difference from analysis preserved the main effects of contrast condition, $F(1, 13) = 5.76$, $p = 0.032$, $\eta = 0.31$, and orientation difference, $F(4, 52) = 5.50$, $p = 0.005$, $\eta = 0.30$. The linear trend of the mean with orientation difference disappeared when the 0° orientation difference was excluded from analysis, $F(1, 13) = 1.39$, $p = 0.26$, $\eta = 0.1$, whereas the quadratic trend remained, $F(1, 13) = 33.30$, $p < 0.001$, $\eta = 0.72$, and a cubic trend surfaced, $F(1, 13) = 5.12$, $p = 0.04$, $\eta = 0.28$. For orientation differences larger than 0°, mean amplitude varied as a function of orientation difference with the midlevel orientation differences showing the smaller amplitudes.

The P100 amplitude results are consistent with options a.2 (dependency on the degree of orientation difference) and b.1 (general effect of stimulus contrast independent of orientation difference).

N170 results

The repeated-measures ANOVA for the N170 time window (160 to 180 ms) with the factors contrast condition, orientation difference, and hemisphere revealed a significant main effect of orientation difference, $F(5, 65) = 18.15$, $p < 0.001$, $\eta = 0.58$. Neither main effect of contrast condition, $F(1, 13) = 3.56$, $p = 0.09$, $\eta = 0.21$, nor hemisphere, $F(1, 13) = 3.18$, $p = 0.10$, $\eta = 0.20$, nor any of the interactions reached significance, contrast condition by orientation difference: $F(5, 65) = 0.65$, $p = 0.61$, $\eta = 0.05$; contrast condition by hemisphere: $F(1, 13) = 0.11$, $p = 0.75$, $\eta = 0.01$; orientation difference by hemisphere: $F(5, 65) = 1.43$, $p = 0.25$, $\eta = 0.10$; contrast conditions by orientation difference by hemisphere: $F(5, 65) = 0.69$, $p = 0.56$, $\eta = 0.05$.

Mean N170 amplitudes were smaller when there was no orientation difference than when there was an orientation difference between the dichoptically presented gratings. Including all orientation differences, trend analysis yielded a significant linear component, $F(1, 13) = 31.79$, $p < 0.001$, $\eta = 0.71$, and a significant quadratic component, $F(1, 13) = 11.67$, $p = 0.005$, $\eta = 0.47$, of the mean amplitudes with increasing orientation difference. Excluding the 0° orientation difference from analysis preserved the main effect of orientation difference, $F(4, 52) = 6.07$, $p = 0.002$, $\eta = 0.32$. The linear trend also remained when the 0° orientation difference was excluded from analysis, $F(1, 13) = 11.67$, $p = 0.005$, $\eta = 0.47$, whereas the quadratic trend disappeared, $F(1, 13) = 3.31$, $p = 0.09$, $\eta = 0.20$. This shows that the mean N170 amplitude increases with increasing interocular orientation difference.

The pattern of results remains the same if—in order to account for the P100 effect—instead of mean N170 amplitude the mean P100-N170 amplitude difference (peak-to-peak measure) is used with two important exceptions: including all orientation differences yielded a significant main effect of contrast condition, $F(1, 13)$

$= 8.91$, $p = 0.01$, $\eta = 0.41$ and for orientation difference a significant linear trend only, $F(1, 13) = 5.13$, $p = 0.04$, $\eta = 0.28$, but no quadratic component, $F(1, 13) = 1.97$, $p = 0.18$, $\eta = 0.13$. That is the N170 results are consistent with option a.2 (electrophysiological activity varies as a function of orientation difference) and with option b.1 (contrast has a general effect on the electrophysiological activity independent of orientation difference).

One last issue I searched for in my data was whether stereopsis modulated the ERPs. To do this, I compared ERPs for orientations differences up to 36° around the vertical meridian with the same orientation differences around the horizontal meridian. Although the P100 and the N170 emerged in these ERPs, there were no significant differences between the two meridians, possibly because this comparison involved many fewer data than the others. It remains to be learned from other experiments whether stereopsis modulates the two neural signatures.

Discussion

My main aim was to find neural signatures that correlate with or are affected by the degree of dissimilarity between dichoptically presented stimuli and to determine the role they might play for the fundamental phenomena of binocular vision. Using two different approaches, global field power providing a global measurement of the electrical field and focal analysis of the topographic centers of activity, I found two of these signatures, one at 100 ms the other at 170 ms after stimulus onset.

The neural processing of dichoptically presented gratings takes place despite participants' executing an obviously demanding task at the gratings' center as indicated by the rather low detection rates (d'). Importantly, neither d's nor reaction times differed between the two contrast conditions. This means performance was not influenced by the contrast of the task-irrelevant, peripheral stimuli, which in turn suggests that the resources remaining for processing the gratings were the same in both contrast conditions.

The two neural signatures both had a posterior distribution: a positivity at about 100 ms (P100) and a negativity at about 170 ms (N170). Both components commonly occur after discrete visual stimulation (e.g., O'Shea et al., 2010; Spehlmann, 1965).

The P100 has previously been considered to be a merely exogenous, bottom-up component, whose amplitude (and latency) mainly depends on physical stimulus characteristics with stronger stimuli eliciting a larger (or faster) P100, and to some degree on spatial (exogenous) attention (e.g., Heinze et al., 1994; Hopfinger & West, 2006) with spatially cued stimuli eliciting larger P100 than uncued stimuli. However, recent evidence suggests that P100 is also the earliest neural correlate of visual awareness, with identical physical stimulus changes eliciting a larger P100 amplitude when they are perceived as compared to when they are not perceived (Pitts, Nerger, & Davis, 2007; Roeber & Schröger, 2004; Roeber, Widmann et al., 2008; Valle-Inclán, Hackley, de Labra, & Alvarez, 1999; Veser et al., 2008). This indicates a perceptual, top-down influence on P100.

The N170 is also considered to be an exogenously driven component (cf. Luck, 2005). However, it is also affected by top-down mechanisms like endogenous attention (e.g., Haider, Spong, & Lindsley, 1964; Hillyard, Vogel, & Luck, 1998; Luck & Hillyard, 1995): Attended stimuli elicit larger amplitudes than unattended stimuli.

I found that contrast exhibited a general effect on both components: Electrophysiological activity was larger with high-contrast as compared to low-contrast stimuli irrespective of interocular orientation differences. This is consistent with option b.1 (e.g., Spekreijse et al., 1973). It is possible that because both contrasts I used were well above detection threshold, they were not sufficiently different to show differential influences on electrophysiological responses that depended on orientation difference. Alternatively, contrast affected fusion (i.e., at small orientation differences) just as much as it affected rivalry (at large orientation differences). The overall reduction in neural activity with physically weaker stimuli is consistent with both components being exogenously driven.

More importantly, I found that posterior P100 and N170 amplitudes differentiated between binocular compatible and binocular incompatible orientation stimulation. The differentiation as a function of orientation difference (degrees of incompatibility) followed a different pattern for each component. This suggests that there are at least two stages in the processing of binocular input: an early stage (P100), at which the binocular input is offset against each other, and a later stage (N170) at which the binocular input is evaluated.

At the early stage of the initial binocular processing (P100), both global field power and local occipital ERP amplitudes vary with orientation difference providing evidence for option a.2. The variation with orientation difference followed a U-shaped function including a linear component: Activity was largest for gratings with no orientation difference, next largest for gratings of maximally differing orientations, and smallest for intermediate differences in orientation. This pattern of results could arise from:

- An interplay of two neural mechanisms. One mechanism evaluates the compatibility of the binocular input for binocular fusion. It is maximally

activated when both eyes receive identical input, but reduced in activity when the input differs between the eyes—possibly in an all-or-none fashion as assumed in option a.1. (Of course the ability of the experiment to reveal a true all-or-none stimulus dependence is limited by the size of the smallest orientation difference of 18°. It is quite possible that some monotonically decreasing relationship exists between ERP measures and orientation differences between 1° and 17°.) The other mechanism computationally assesses the physical differences in luminance or contrast between the two monocular stimuli on a microlevel (Liu & Schor, 1995), yielding an output for the initiation of the rivalry process. At the microlevel, the larger the orientation difference the more contours of one of the stimuli are overlaid by a different luminance value of the corresponding area in the other stimulus leading to an increase in neural activation. The combination of these two mechanisms results in a pattern as assumed in option a.2.

- An initial involvement of P100 in the differentiation between fusion, stereopsis, and binocular rivalry with stimuli leading to fusion (orientation difference of 0°) eliciting the strongest activation, stimuli potentially leading to stereopsis (orientation differences of 18° and 36°) eliciting the weakest activation, and stimuli potentially leading to binocular rivalry (any orientation difference larger than 18°) eliciting weak activations that increase with orientation difference. The trough of the U-shaped function at 36° and 54° might be explained by these stimuli not reliably leading to either stereopsis or binocular rivalry.

At the later N170 stage, binocular incompatible stimuli elicit a stronger response than binocular compatible stimuli. This might be because they provide a mismatch from what the visual system is usually confronted with (Arnold, 2011b; O'Shea, 2011) and therefore require re-evaluation. This re-evaluation is most likely done by involving more processing resources leading to a stronger neural response. Electrophysiological mismatch responses are usually elicited in a similar latency range and with the same (negative) polarity (e.g., Kimura, Schröger, Czigler, & Ohira, 2011). Critically, I found that the larger the difference, the stronger the response. This suggests that the neural populations generating N170 are orientation-selective and might be involved in orientation tuning. Intriguingly, the latency of N170 coincides with the minimum presentation time of conflicting stimuli to initiate binocular rivalry (De Belsunce & Sireteanu, 1991; O'Shea & Crassini, 1984; Wolfe, 1983), suggesting that the neural mechanisms reflected in N170 are crucial for the initiation of binocular rivalry.

One of these mechanisms may well be reciprocal inhibition, which is not only a prerequisite for orientation tuning (Meese & Holmes, 2007; Roeber, Wong et al., 2008) but also one of the common themes in theories of binocular rivalry (Blake & Logothetis, 2002; Klink et al., 2008; Tong et al., 2006) to explain why one of the conflicting stimuli is suppressed from while the other dominates awareness. The other common theme in theories of binocular rivalry is adaptation. It offers an explanation why perception changes between the conflicting stimuli: Neural populations processing the dominant stimulus adapt, letting neural populations processing the currently suppressed stimulus win the competition for perceptual awareness. A larger N170 component could be a signature of greater adaptation to follow (assuming that more active neural populations adapt faster; see Blakemore & Campbell, 1969; Vautin & Berkley, 1977), leading to a faster perceptual change. Indeed, this is what psychophysical studies find: Larger orientation differences are accompanied by faster perceptual reversal rates (Kitterle & Thomas, 1980; O'Shea, 1998; Schor, 1977; Thomas, 1978). The finding that N170 amplitudes are smaller with low-contrast gratings than with high-contrast gratings further supports this interpretation that a smaller N170 corresponds to less adaptation, which in turn leads to slower perceptual reversals. Again, this is what psychophysical studies find: Low-contrast stimuli are accompanied by slower perceptual reversals (Alexander & Bricker, 1952; Hollins, 1980).

The P100 and N170 results reported here agree with other studies that show perceptual influences on ERP amplitudes earlier than 200 ms after stimulus or probe onset or change (Pitts, Martínez, & Hillyard, 2010; Roeber & Schröger, 2004; Roeber, Widmann et al., 2008; Valle-Inclán et al., 1999). However, all of these studies have in common that they used binocular rivalry as a technique to assess the neural correlates of consciousness. The ERPs in these studies were time-locked to stimulus changes or to probes that occurred during an episode of established binocular rivalry (Roeber & Schröger, 2004; Roeber, Widmann et al., 2008; Valle-Inclán et al., 1999) or to intermittent binocular-rivalry onsets of identical binocular-rivalry stimuli (Pitts et al., 2010). That is, these studies rely on prior binocular rivalry to elicit these early percept-related ERP effects: ERP amplitudes were larger when the ERP-eliciting event occurred on the currently dominant eye or yielded a perceptual change than when it occurred on the suppressed eye or did not yield a perceptual change. The most likely explanation for these perceptual effects is that the neural populations that are responsive to the new stimulus or probe are differentially modulated by the prior binocular-rivalry stimulation.

Here, there was no binocular-rivalry stimulation prior to the ERP-eliciting event and hence binocular rivalry could not have affected the neural populations responsive to the gratings' onsets. Instead binocular

rivalry might have been a perceptual consequence to the gratings' onsets if the orientation difference between the gratings was large enough. Therefore, a critical detail of the current experimental design is that it reveals ERP effects that are related to the first-time processing of binocular input of varying interocular differences, from which we know that they result in different perceptual consequences (binocular fusion, stereopsis, and binocular rivalry). To my knowledge, this study is the first attempt using the high temporal resolution of ERPs to shed light on the neural mechanisms underlying the initiation of these fundamental binocular processes.

Another critical detail of the current experimental design is that attention was not on the gratings. That is, the binocular orientation differences elicited differences in electrophysiological activity independent of attention, suggesting that interocular differences in stimulation can be automatically detected from early on in the visual pathway. An interesting question to ask is whether any of the fundamental binocular processes occur if someone's attention is not on the stimuli. As far as I know, no one has addressed this question for binocular fusion and stereopsis. I expect that fusion and stereopsis do operate independently of attention and probably send signals to recruit attention (such as when an object appears close to one's face). I expect that processing of dichoptic images exceeding the interocular disparities that yield fusion and stereopsis also operate independently of attention for the same reason (Paffen, Hessels, & Van der Stigchel, 2012). In the case of an object very close to one's face, these processes send signals to the parts of the brain controlling vergence eye movements so one can locate the object (Mitchell, 1970). The question of whether rivalry alternations require attention has been addressed recently for binocular rivalry. My own research suggests that rivalry does persist when attention is withdrawn from the rival stimuli (Roeber, Veser, Schröger, & O'Shea, 2011), but others disagree (Brascamp & Blake, 2012; Zhang, Jamison, Engel, He, & He, 2011).

One could argue that the experimental protocol used here does not allow for inferences about the neural substrates of perceptual phenomena of binocular vision such as binocular rivalry because participants did not report on them. Strictly speaking this is true, and empirical evidence is needed to support the inferences I made. It would be useful to know if identical interocular differences in orientation can result on some trials in stereopsis and on others in rivalry. If so, it would then be useful to know whether the ERPs differed for such trials. However, there is ample psychophysical evidence to show that for the orientation differences I used, fusion and stereopsis occur for orientation differences less than 36° (Blakemore et al., 1972; Kertesz & Jones, 1970; Mitchell & O'Hagan, 1972; O'Shea & Crassini, 1982) and rivalry occurs for larger orientation differences (Kitterle & Thomas, 1980; O'Shea, 1998; Schor, 1977; Thomas, 1978). Moreover, the 200-ms displays I used promote sensory (versus motor) fusion and stereopsis at the expense of rivalry for orientation differences less than 36°. Rivalry is the default outcome for larger orientation differences.

Alternative perceptual consequences with the stimulation I used are dichoptic masking (e.g., Campbell & Kulikowski, 1966; Legge, 1979) and false fusion (e.g., Wolfe, 1983). I argue that both are not in contradiction to the functional significance of the P100 and N170 modulations I inferred.

In a typical masking experiment, contrast thresholds for a test stimulus are measured as a certain property of a masking stimulus. Dichoptic masking occurs when the mask is presented to one eye and the test stimulus to the other. Dichoptic masks of contrasts comparable to the ones used here lead to threshold elevations (Baker & Meese, 2007; Legge, 1979). Although threshold elevations occur when mask and test stimulus differ in orientation (cross-orientation masking), they decline with an increase in orientation between the mask and the test stimulus (Foley, 1994; Ross & Speed, 1991). This is consistent with the N170 result. Indeed, there is circumstantial evidence that a common inhibitory mechanism underlies binocular masking and binocular rivalry (Baker & Graf, 2009; see also Brown, Candy, & Norcia, 1999; Sengpiel, Freeman, Bonhoeffer, & Blakemore, 2001). Furthermore, Sengpiel and Blakemore (1994) found evidence for dichoptic cross-orientation inhibition in the cat's visual cortex. Because dichoptic-masking stimuli are usually only briefly presented, whereas binocular-rivalry stimuli are presented for longer periods, it might well be that dichoptic masking is a precursor of binocular rivalry (Baker & Graf, 2009). It needs to be noted, however, that the experimental manipulations and behavioral measures to assess dichoptic masking and binocular rivalry differ substantially.

Presenting each eye with a grating of a different orientation for less than 150 ms leads to the perception of a plaid—that is to false fusion—instead of binocular rivalry (Wolfe, 1983). I presented the gratings for 200 ms, long enough to initiate binocular rivalry—at least for stimuli that maximally differed in orientation as they were used previously (De Belsunce & Sireteanu, 1991; O'Shea & Crassini, 1984; Wolfe, 1983). I argue that the N170 with a peak latency of about 170 ms belongs to the neural substrate underlying the initiation of binocular rivalry: one of the stimuli gaining perceptual dominance while the other is suppressed. It might well be that P100 is part of the neural substrate establishing false fusion. It is important to note that

observers are able to discriminate falsely fused plaids from physically presented plaids despite their perceptual similarity (e.g., Blake, Yang, & Westendorf, 1991; Paffen et al., 2012). This indicates that even with brief stimulus presentations, there must be neural mechanisms in place that allow for such successful discrimination. The same neural mechanisms are likely to be active also for longer stimulus presentations and the precursors of the mechanisms if not the mechanisms that initiate binocular rivalry.

In conclusion, by using simple visual stimuli that differed only in the visually fundamental dimension of orientation, I showed that electrophysiological activity varies depending on interocular differences as early as 100 ms after stimulus onset even when the orientations were not attended. The initial processing of such stimuli involves two stages. At the first stage the binocular input is preferentially processed when it is compatible (leading to binocular fusion) or maximally different (leading to binocular rivalry) and less so for intermediate binocular differences. At the second stage incompatible binocular input is differentially processed as signified by the larger responses that linearly vary as a function of orientation difference. This differential processing needs 170 ms to get going and might reflect reciprocal inhibition and be a precursor of adaption, both of which are crucial in the initiation and maintenance of binocular rivalry.

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