WHEN the two eyes of an observer are exposed to conflicting stimuli, they enter into binocular rivalry and the two possible percepts will alternate in dominance. We investigated neural activity and its time course following binocular rivalry by measuring human event-related brain potentials to transitions from rivalrous to non-rivalrous stimulation. When these changes did not entail a change in conscious perception they elicited a markedly attenuated N1 component and a delayed and attenuated P3 peak as compared to percept-incompatible changes and non-rivalrous control conditions. These results suggest that in humans binocular rivalry is resolved at latest in extrastriate visual areas. *NeuroReport* 10:713–716 © 1999 Lippincott Williams & Wilkins.

Key words: Binocular rivalry; Event-related brain potentials; Consciousness; ERPs; Visual perception

Effects of consciousness on human brain waves following binocular rivalry

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Introduction

Extensive behavioral research has revealed the main perceptual parameters of binocular rivalry [1,2] and has established it as a classical bistable consciousness phenomenon [3]. Single-cell recordings in monkeys specified the involvement of visual areas [4–6]. It has been shown that binocular rivalry does not reflect a fatigue of the suppressed ocular channel but rather a rivalry of perceptual representations for visual awareness [3], and that it is modulated by Gestalt principles [7,8]. The involvement of frontal and parietal areas in the selection of perceptual representation during binocular rivalry has been demonstrated with functional magnetic resonance imaging [9]. Whereas this indicates that rivalry is not an input-driven and automatic process, at least some cells in the primary visual cortex of monkeys are already sensitive to the percept more than to the stimulus [5]. The percentage of perception-modulated neurons during continuous rivalrous stimulation increases from 20% in the monkey primary visual cortex to 30–40% in higher cortical areas [4]. While these percentages are still quite low, it should be considered that cortical activity is strongly dependent on stimulus change or the novelty of a stimulus. It might be that during physical changes of the stimulus much more brain activity is devoted to this stimulus and that this activity is modulated by perception to a much higher degree. Since ERPs are especially sensitive to stimulus change and since they constitute a widely accepted tool to study the brain's cognitive functioning [10] we utilized the recording of ERPs elicited by

physical changes of rivalrous stimuli in order to unravel the neural processing underlying binocular rivalry in humans. Moreover, recent work suggests that temporal mechanisms such as oscillation and synchronization are involved when binocularly rival stimuli compete for awareness [6,11,12]. The temporal dynamics of the processing of rivalrous stimulation in humans can only be investigated with electrophysiological methods that feature high temporal resolution, such as the recording of human ERPs.

We studied changes from incongruent (rival) to congruent stimulation (see Fig. 1, label i/c) which requires the stimulus of one eye to be changed. Depending on the prevailing percept reported by the observer this change could concern the eye that was dominating or the suppressed eye (see Fig. 2). We were interested in whether there would be differences in ERP components for these two situations. The aim of this study was two-fold. On the one hand, it should be determined whether or not there is a difference in the exogenous ERP components for physically identical changes contingent on the prevailing conscious percept. On the other hand, we wanted to test the hypothesis that the endogenous
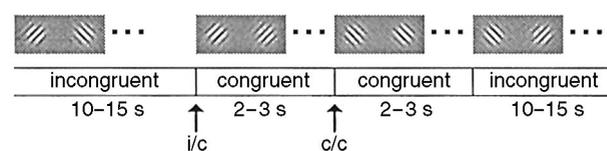

FIG. 1. Time course of incongruent (rival) and congruent stimulation. Labels i/c and c/c refer to ERP-relevant stimulus changes, see Fig. 2.
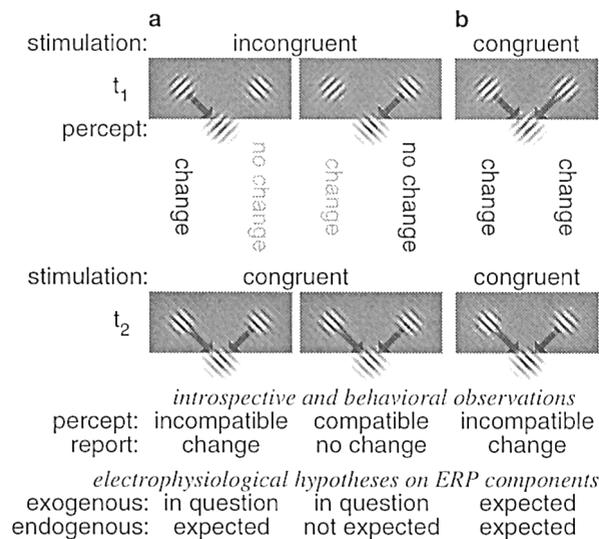
FIG. 2. Events used for ERP recordings. (**a**) Changes from incongruent (rival) to congruent stimulation (see Fig. 1, label i/c) required the stimulus of one eye to be changed. Depending on the prevailing percept reported by the observer this change could concern the eye that was dominating (left-hand column) or the suppressed eye (right-hand column). Whereas in the former case this led to a new, incompatible percept and hence to a change of the observer's report, in the latter case the prevailing percept was compatible to the new stimulation and hence no reaction was necessary. (**b**) As a control condition, we recorded ERPs to congruent/congruent changes, i.e. changes where the identical stimuli to both eyes were both changed (see Fig. 1, label c/c).

P3 component is elicited by incompatible changes but not by compatible changes.

Materials and Methods

Ten students (four male) with normal or corrected-to-normal vision participated in this study. Observers gave informed consent after the nature of the study was explained to them. Dichoptical presentations of orthogonal gratings oriented to the upper left or upper right were presented to the participants (see schematic samples in Fig. 1 and Fig. 2). Dichoptical presentation was achieved using wireless LCD shutter glasses that let every second image pass to a different eye (dynamic range 1:100). The screen refresh rate was 100 Hz. The stimulus was flickered with 16.6 Hz (40 ms stimulus, 20 ms medium gray screen) to minimize after-effects following stimulus changes. The stimuli were generated on a computer screen 1.10 m in front of the observer. The gratings were computed as Gabor wavelets, i.e. a sinusoidal profile with a Gaussian envelope on a medium gray background ($\sigma = 1.5$ cm, phenomenal diameter = 6 cm (3.1 deg), spatial frequency = 1.4 cycles/cm (2.6 cycles/deg)). During 20 sessions of 2 min each the observer viewed gratings with 45° and 135° orientation. Periods of incongruent stimulation lasted 10–15 s and were followed by one or two periods of congruent stimulation lasting 2–3 s (see Fig. 1).

The task of the subjects was to report the dominat-

ing view by depressing one of two keys with the same finger. Observers passed two sessions of 1 h each before the EEG recording session. By this means observers showing normal stereopsis leading to regular binocular rivalry were selected. At the same time, the observers could train themselves to press the report key in a quick and reliable fashion. Percentage of correct responses during congruent stimulation and the ratio of the mean phase durations for the left and the right eye during rivalrous stimulation were determined for each observer. Six observers met the criterion of a minimum percentage of correct key press of 75% (perfect performance corresponded to 90%, considering that in half of the cases the observer was pressing an incompatible key and needed some reaction time to switch to the correct key) and of the ratio of left to right eye phase durations, being close to one ($\pm 10\%$).

In the ERP recording session observers were seated in a comfortable chair in an electrically and acoustically attenuated booth. The stimuli and the task of the observers were exactly the same as in the training sessions. EEG was measured with Ag/AgCl electrodes from 25 scalp locations of the extended 10-20 system [13] (FP1, FPZ, FP2, F7, F3, FZ, F4, F8, FC5, FC6, T7, C3, CZ, C4, T8, CP5, CP6, P7, P3, PZ, P4, P8, O1, OZ, and O2) and from the left and right mastoids (LM, RM). The horizontal and vertical EOG was monitored with bipolar pairs of electrodes placed at the outer canthi of the left and the right eye and from above and below the right eye, respectively. The reference electrode was placed at the nose. EEG and EOG were digitized at 500 Hz (bandpass 0.05–100 Hz) in continuous mode. The data were then filtered offline with finite-impulse response filters (FIR, bandpass 0.2–20 Hz, 2001 points). Epochs were calculated off-line and were of 1000 ms duration (including a 100 ms pre-stimulus baseline). Average rejection was performed based on a standard deviation criterion with a sliding window of 200 ms (VEOG: 40 µV, HEOG, FZ, LM: 30 µV). This led to an average rejection rate of 23% of all epochs. ERPs were averaged separately for the different stimulus types. ERPs were low-pass filtered at 10 Hz (FIR, 201 points) in order to suppress the 16 Hz response due to the flickering stimulation. One of the six remaining observers had to be excluded from further analysis due to technical artefacts.

We recorded ERPs to changes from incongruent (rival) to congruent stimulation (Fig. 2a). These events were then classified into two different classes, depending on the percept reported at the moment of this change. On the one hand, the change could be incompatible with the report of the observer, i.e. the observer reported that stimulus to be dominant that was going to be changed (left-hand column of Fig.

2a). In this case the new unambiguous stimulus elicited a different percept and lead to a change of the response key. On the other hand, the change could be compatible with the report of the observer, i.e. following to the observer's report the change concerned the suppressed eye (right-hand column of Fig. 2a). This category of changes did not elicit a change in the perceived orientation of the gratings. As the reported percept was compatible with the new congruent stimulation, there was no need to change the response key. Most observers reported, however, that while they did not perceive a change of orientation they did occasionally notice a kind of salience increase. As a control condition we recorded ERPs to congruent/congruent changes, i.e. where the stimuli to both eyes were changed such that there was congruent stimulation before and after the change (Fig. 2b). The hypotheses concerning the ERPs to be expected in these different conditions are depicted in Fig. 2.

Results and Discussion

In order to assure that we replicated the classical binocular rivalry phenomenon we determined the distributions of the phase durations during rivalrous stimulation. Figure 3 shows the distribution pooled over the remaining six observers, after having divided the phase durations by the mean phase duration of the respective observer. For bistable phenomena, the distribution of these normalized phase durations is expected to follow a γ function [2]. We fitted a γ function (solid line: exponent 3.35, $\chi^2 = 23.1$, $k-1 = 22$) to the distribution with the exclusion of the first three bins which are obviously not following the γ function. The congruence of the
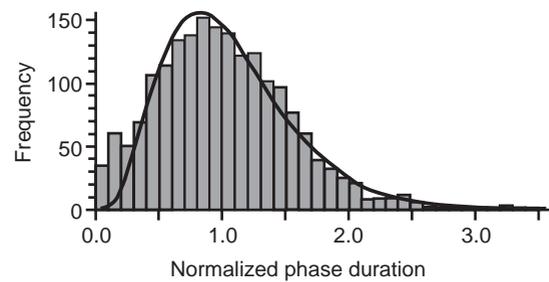

FIG. 3. Distribution of normalized phase durations during rivalrous stimulation pooled over six observers ($n = 1888$). The phase durations were divided by the mean phase duration of the respective observer. This distribution is typically approximated by a γ function (solid line).

empirical distribution and the γ function indicates that the subjects reported perceptual dominance as they were supposed to.

Figure 4 shows the grand-average ERPs elicited by incongruent/congruent changes (solid lines), classified into compatible (thin line) and incompatible (thick line) changes. The dotted line shows the ERPs elicited by the control condition (congruent/congruent). The latter show a marked negativity peaking at 240 ms with a characteristic occipital distribution. This represents the exogenous visual N1 component as is to be expected by any change of the visual stimulation. The comparably late timing is partly due to the stereo presentation (20 ms cycle) and to the low contrast of the stimuli. The positivity peaking at 400 ms and largest over PZ represents a P3 component that is related to the detection of a task-relevant change.

The ERPs for the incongruent/congruent changes differ markedly depending on the perceptual state of the observer as reported by the key press at the moment of the change. Incompatible changes elicit
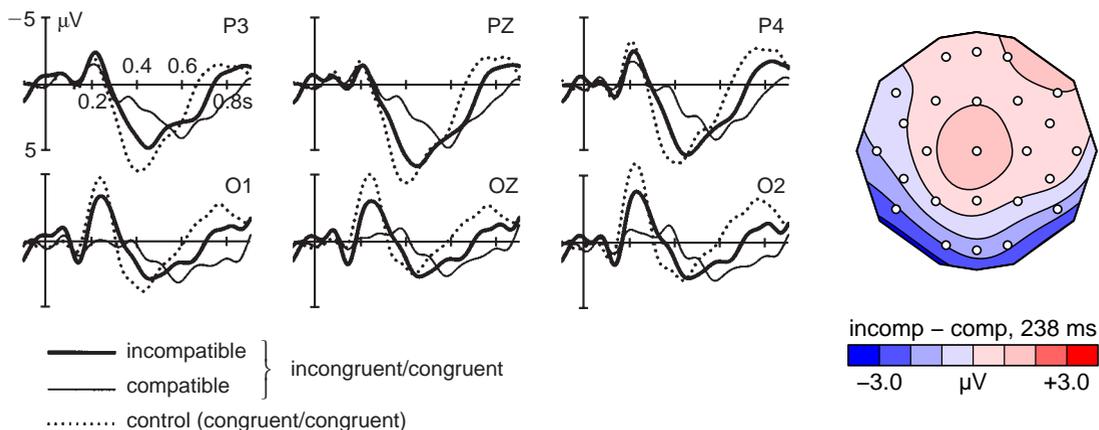

FIG. 4. ERPs recorded for incongruent/congruent and for congruent/congruent changes (left panel). Potential map for the incompatible minus compatible ERP difference waves 238 ms after stimulus onset (right panel). The thick line represents the ERPs to changes that lead to incompatible percepts and hence to a change of percept and of the report of the observer. They show a N1 negativity (OZ around 240 ms) and a P3 positivity (PZ around 400 ms) just as with the control condition (dotted line), whereas the ERPs to compatible changes (thin line) lack an occipitally distributed N1 component and reveal an attenuated and delayed P3 component. The observed differences reflect the introspective observation that compatible changes do not elicit a change of the prevailing percept while incompatible changes do. The occipital distribution visible in the difference potential map of the incompatible minus compatible subtraction wave also supports the view that the N1 is modulated by the percept at the moment of the change.

curves very similar to congruent/congruent changes. There is again a marked negativity peaking at 246 ms with approximately the same distribution. For the following ANOVA, the N1 was measured as the mean of the 220–260 ms interval relative to the onset of the congruent stimulus, at O1, OZ and O2. The ANOVA including the within-observers factors compatibility (levels: compatible vs incompatible) and lead (levels: O1, OZ, O2) yielded a main effect of compatibility ($F(1,4) = 14.83$, $p < 0.02$) indicating enhanced negativity in N1 with incompatible as compared to compatible changes. The main factor lead and the interaction were not significant. Thus for the same physical change the N1 strongly depends on the perception at the moment of the change. The potential map (Fig. 4), spline-interpolated on a 2000 points mesh, of the incompatible minus compatible subtraction wave at its peak in the N1 window (238 ms) reveals an occipitally distributed activity as is typical for an N1 component. Hence it can be assumed that the N1 component elicited by the stimulus change is modulated by the perceptual state of the observer. It should be noted that the above results are not an artifact of the flickering presentation of the stimulus. The latter is known to have no influence on the distribution of the phase durations during rivalrous stimulation and to prevent the subject from detecting a change in the suppressed eye [3]. Any artificial effects of the flickering on the ERPs surviving the low pass filtering would be present in all of the measured ERPs and would thus not show up on the potential map.

Contrary to our expectations, there is a positivity in the curves for compatible incongruent/congruent changes that compares to the P3 component found in the other two ERPs. It is, however, markedly smaller and later. An ANOVA comparing the mean of the 300–500 ms interval at lead PZ yielded a main effect of compatibility ($F(1,4) = 15.4$, $p < 0.02$) indicating an enhanced positivity elicited by incompatible as compared to compatible changes. The latencies were determined in the 300–700 ms range. An ANOVA yielded a main effect of compatibility ($F(1,4) = 13.09$, $p < 0.03$) showing that the latency of the positivity was markedly later for compatible changes. This positivity probably represents a P3 component elicited by the task-irrelevant change in salience of the stimulus that was reported by the observers.

Conclusion

The present study demonstrates that the N1 and the P3 elicited by changes from rivalrous to non-rivalrous binocular stimulation depend on whether the stimulus is compatible or incompatible with the predominant percept; that is, these brain waves go with the percept rather than with the objective physical stimulation. This supports the hypothesis that binocular rivalry merely reflects cognitive–central and not peripheral–physiological processing [3,7–9]. Since the visual N1 is generated in extrastriate visual cortex [14] it may be concluded that binocular rivalry in humans is resolved in these areas at the latest [15]. Top-down modulations of the exogenous N1 have also been found in other contexts such as selective attention [16,17]. In the present study, the ERP method proved to be a highly sensitive tool for the investigation of perceptually multistable phenomena: while during continuous rivalrous stimulation about one-third of the active neurons in monkeys was modulated by perception [4,5], our results suggest that with physical changes of rivalrous stimuli even a higher number of neurons in the human brain is sensitive to perception at this early processing stage.

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