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Fluctuations in Conscious Perception and Neural Activity: a  
Binocular Rivalry Study

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**ABSTRACT**

During binocular rivalry visual awareness alternates spontaneously between two different images presented to the two eyes. Because the percept fluctuates between conflicting interpretations of identical sensory input, this well studied perceptual illusion allows a dissociation of neural activity related to physical stimulus properties from that related to conscious perception. Though it seems widely accepted that both high- and low-level neural stimulus representations contribute to perceptual dynamics during rivalry, their relative contributions, and how they vary over time, are only beginning to be understood. Indeed, it was recently shown that initially stabilizing contributions of both, eye- and stimulus-based processes, decline in parallel during a dominance phase in rivalry, eventually favouring a perceptual switch (Bartels & Logothetis, 2010). Such a co-varying change is indicative of direct interactions between image- and eye-of-origin representations that may be dependent on the amount of neural substrate involved and the complexity of stimuli processed. We here intended to test this hypothesis directly, presenting rivaling pictures of a house and a face either upright or upside down, and revealed a reduced coupling of low- and higher-level dynamics for the latter, where high-level involvement and feedback to early processing stages may be reduced. Additionally, taking into account several lines of evidence pointing towards a critical role of ‘spontaneous’ activity in cortical processing, we were curious as to whether the phase of neural oscillations biases perceptual dynamics during binocular rivalry. In particular, we hypothesized that EEG phase allows a ‘prediction’ of perceptual reversals on a trial-by-trial basis. While presenting strong support for our first hypothesis, revealing a significant effect of stimulus inversion on the time-varying contributions of eye- and percept-related processes during rivalry, the results of the EEG analysis turned out to be ambiguous and do not convincingly support our second hypothesis.

## I. INTRODUCTION

*Whilst part of what we perceive comes through our senses from the object before us, another part (and it may be the larger part) always comes (...) out of our own head.*

–William James (1890)

### A. Fluctuations in conscious perception

When two incompatible images are presented to corresponding retinal locations of the two eyes, you may experience a perceptual illusion called binocular rivalry, in which each monocular image dominates conscious awareness for a few seconds at a time while the other is perceptually suppressed and invisible (Blake & Logothetis, 2002; Helmholtz, 1911; Levelt, 1966; Tong, Meng, & Blake, 2006; Wheatstone, 1883). Fluctuations in dominance and suppression during binocular rivalry are characterized by their stochastic, dynamical fashion, in that successive periods of dominance (emerging in a wave-like manner over space) of either the left- or right-eye stimulus are unpredictable in their exact duration; however, in contrast to the alternation process itself, the distribution of dominance phases for a given percept is ‘predictable’ and can typically be approximated by a gamma-distribution (c.f. Leopold & Logothetis, 1999). Certainly fascinating in its own right, what makes binocular rivalry and related ‘multistable’ phenomena particularly interesting is the fact that conscious perception fluctuates spontaneously between two mutually exclusive interpretations of the same physical stimulus, allowing a dissociation of neural activity related to sensory stimulation from that related to visual awareness. While early theories favoured a model of reciprocal inhibition between monocular neurons in the primary visual cortex (V1) (Blake, 1989), it now seems established that rivalry most likely reflects the outcome of competitive neural interactions at multiple levels of cortical processing, involving both eye- and stimulus-based processes (Blake & Logothetis, 2002; Freeman, 2005; Sterzer, Kleinschmidt, & Rees, 2009; Tong et al., 2006; Wilson, 2003).

Given the combined contribution of low-level ‘eye-based’ and higher-level ‘stimulus-based’ processes, it should be of special interest how or whether their relative contributions vary over time, since it is this variation that possibly accounts for perceptual fluctuations. Indeed, by means of a novel paradigm, Bartels and Logothetis (2010) recently demonstrated that initially stabilizing contributions of both, high-level processes and those related to the eye-of-origin, decline in parallel over time and to the

same extent, respectively. Whereas early in a dominance phase it was primarily the stabilizing contribution of the eye-of-origin, after long dominance it was mainly the destabilizing influence of the stimulus that determined the percept. Such a co-varying change might be interpreted in terms of feedback from higher-level stimulus representations, affecting the strength of the eye-of-origin contribution to dominance (c.f. Bartels & Logothetis, 2010). While being consistent with current theories on the neural bases of binocular rivalry and multistable perception in general (Sterzer et al., 2009), this interpretation also corresponds to several psychophysical studies demonstrating perceptual influences on low-level eye-based processing stages (Gilroy & Blake, 2005; Tsuchiya & Koch, 2005; van Boxtel, Tsuchiya, & Koch, 2010; Watson, Pearson, & Clifford, 2004).

Interestingly, however, Bartels and Logothetis (2010) further found that rivalry between simple gratings (as opposed to more complex flower stimuli) led to a slightly reduced co-variation between eye- and percept-related contributions, suggesting that their coupling may be dependent upon stimulus complexity. Similarly, prior studies showed that stimulus complexity can influence rivalry dynamics in several aspects, such as rate and coherence of perceptual alternations, suppression depth, or its susceptibility to attentional modulation (Alais & Melcher, 2007; Alais, van Boxtel, Parker, & van Ee, 2010; Knapen, Kanai, Brascamp, van Boxtel, & van Ee, 2007; Nguyen, Freeman, & Alais, 2003; Rogers, Rogers, & Tootle, 1977; van Boxtel, Alais, & van Ee, 2008). However, because different subjects were tested, and considering the fact that flower and grating stimuli were not matched in their low-level visual features, it remained unclear whether the small difference was indeed due to the difference in high-level stimulus content (Bartels & Logothetis, 2010).

In the first part of the present study we therefore sought to rule out these alternative explanations and showed the same two images of a house and of a face, presented either upright or upside down (i.e. inverted), to the same human subjects. Houses and human faces belong to object categories our species is very familiar with and that are both processed in high-order object-related regions of the ventral visual stream (Aguirre, Zarahn, & D'Esposito, 1998; Epstein & Kanwisher, 1998; Grill-Spector & Malach, 2004; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Kanwisher, McDermott, & Chun, 1997; Levy, Hasson, Avidan, Hendler, & Malach, 2001). Clearly, however, we do not have much expertise with such objects viewed upside down. Indeed, since Yin's classical study (1969) has revealed that the decrement in recognition performance is disproportionate for inverted faces relative to other usually 'mono-oriented' objects, a

large body of experimental work documented a robust “face-inversion effect” (FIE), at both the behavioural and neural level (Aguirre, Singh, & D’Esposito, 1999; Gilaie-Dotan, Gelbard-Sagiv, & Malach; Hancock, Bruce, & Burton, 2000; Kanwisher & Yovel, 2006; Rossion & Gauthier, 2002; Yovel & Kanwisher, 2005), and even in another species (Dahl, Wallraven, Bulthoff, & Logothetis, 2009). Thus, faces and other mono-oriented objects, though the latter presumably to a lesser extent, are apparently processed differently when viewed upside down (Epstein, Higgins, Parker, Aguirre, & Cooperman, 2006; Reed, Stone, Bozova, & Tanaka, 2003; Rossion & Gauthier, 2002; Yin, 1969).

Consistently, rivalry between inverted but not upright faces was shown to exhibit low-level rivalry characteristics, such as shallow suppression depth and less coherent perceptual alternations, possibly due to a reduced level of competitive feedback from higher levels of processing (Alais & Melcher, 2007). Similarly, upright faces have an advantage over inverted faces in breaking suppression (Jiang, Costello, & He, 2007; Zhou, Zhang, Liu, Yang, & Qu, 2010), suggesting that inverted faces do not achieve the same cortical representation as upright faces (at least when invisible), perhaps reducing the amount of feedback from object-related representations to the early processing stages.

We here hypothesise that inverting rivaling face/house stimuli from their canonical upright orientation will reduce competitive interactions between higher-level stimulus representations and the amount of feedback from these areas respectively, possibly apparent in a reduced co-variation of eye- and image-based contributions during binocular rivalry. Adopting the rivalry paradigm recently introduced by Bartels and Logothetis (2010), we first induced dominance in a flash suppression setting (Wolfe, 1984) and then interrupted the rivalry display 0.3 s or 3.0 s after dichoptic stimulation onset by a brief, binocularly presented ‘interruption pattern’, concurrent with an optional eye-swap (Fig.2a). As in the original study, this procedure allowed us to obtain a time-resolved measure of the perceptual stability instilled by processes related to the stimulus plus those related to the eye-of-origin (no eye-swap condition), and differentiate it from that instilled by the stimulus minus eye-based processes (eye-swap condition). This yielded four experiments for each of the two stimuli pairs.

## **B. Fluctuations in neural activity**

In the neurosciences it was, and still is, common to study neural activity related to certain experimental events. This approach of investigating evoked activity certainly is highly informative and valuable for a better understanding of brain function, though it largely

dismisses the fact that the brain – representing just about 2% of the total body weight in humans while accounting for approximately 20% of the total energy consumed – is never at rest, rather constantly active, and devoting most of its energy consumption to ‘ongoing’ or ‘spontaneous’ activity (e.g. Raichle, 2010). Indeed, while the largest part of the brain’s energy demand (up to 80%) is devoted to signalling associated with the input and output of neurons, favouring the use of energy-efficient neural codes and wiring patterns (Attwell & Laughlin, 2001), the brain’s total energy consumption seems relatively little affected by task performance or evoked activity, as it is usually measured in experimental conditions (Buzsaki, Kaila, & Raichle, 2007; Sokoloff, Mangold, Wechsler, Kenney, & Kety, 1955). However, it would be hard to conceive why natural selection should have favoured the evolution of an organ as costly as the brain that devotes most of its energy consumption on superfluous activity or the production of pure ‘noise’, and it thus might not come as a surprise that recent evidence points towards important functions of ongoing activity in neural processing. For example, the brain’s intrinsic activity was shown to be far from being random, exhibiting patterns that closely resemble those of neural activity evoked by sensory stimulation (Kenet, Bibitchkov, Tsodyks, Grinvald, & Arieli, 2003; Tsodyks, Kenet, Grinvald, & Arieli, 1999). There is good evidence that spontaneous activity could reflect a continuous top-down signal that interacts with incoming input, linked to the underlying connectivity of the cortical network, which in turn is shaped by the statistics of naturally occurring stimuli (Ringach, 2009). Such a view seems consistent with that of the brain being a ‘foretelling device’, whose predictive power emerges from its spontaneous activity that is ‘calibrated’ by the statistical features of the environment, and allowing it to ‘predict’ most effectively the consequences of external ‘perturbations’ or inputs (Buzsaki, 2006).

No matter what the exact functions are, if there are any at all: the finding that spontaneous activity significantly contributes to the inter-trial variability in the response of single neurons (Arieli, Sterkin, Grinvald, & Aertsen, 1996), but also to the variability in both, perceptual (Busch, Dubois, & VanRullen, 2009; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009; Super, van der Togt, Spekreijse, & Lamme, 2003) and behavioural performance (Fox, Snyder, Vincent, & Raichle, 2007), questions the view of intrinsic activity as simply being random “noise”, traditionally eliminated or considerably attenuated by extensive data averaging.

A prominent feature of ongoing activity that apparently experiences a resurgence of interest are neural oscillations (Buzsaki & Draguhn, 2004): rhythmic patterns of activity that may be observed in the intracellular voltage, individual spike trains, and/or in the

local field potentials and their volume conducted manifestations in the scalp electroencephalogram (EEG) (Koepsell, Wang, Hirsch, & Sommer, 2010; Whittingstall & Logothetis, 2009). Neural oscillations are a ubiquitous feature of neural systems, evolutionarily highly conserved, and proposed to play a significant role in the encoding of sensory information, learning and memory formation, multisensory integration, or selective attention and working memory (Buzsaki & Draguhn, 2004; Laurent, 2002; Moser, Kropff, & Moser, 2008; Sejnowski & Paulsen, 2006; Wang, 2010). Furthermore, neural oscillations are thought to be related to sub-second fluctuations in neuronal excitability, reflecting a rhythmic shifting of neuronal ensembles between high and low excitability states (Bishop, 1933; Lakatos et al., 2005; Schroeder & Lakatos, 2009; Schroeder, Lakatos, Kajikawa, Partan, & Puce, 2008). In this sense each oscillation has both an “ideal” and a “worst” phase for the processing of incoming stimuli, resulting in an amplification and suppression of inputs respectively (e.g. Lakatos et al., 2005). Such fluctuations in cortical excitability seem to be consistent with the idea of a discrete processing mode, framing perception into discrete epochs or a sequence of perceptual “snapshots” (e.g. VanRullen & Koch, 2003).

It might be of special interest to the current study that two recent studies very convincingly demonstrated an influence of oscillatory activity on human perception. Both studies showed that perceptual performance, i.e. the detection of a near-threshold visual stimulus that was shown for 6 and 12 ms respectively, is tied to the phase of 5-10 Hz oscillations of the human EEG, preceding stimulus onset (Busch, Dubois, & VanRullen, 2009; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009). An important follow-up study not only confirmed this correlation between EEG phase and detection of light flashes presented at perceptual threshold, but further revealed evidence that this periodic sampling applies primarily to attended, and not unattended stimuli (Busch & Vanrullen, 2010).

Though the first EEG-recordings in humans were made over 80 years ago by Hans Berger (1929) the exact neural processes underlying the measured signal, a deeper understanding of which is essential for reasonable interpretations, are far from being understood. Moreover, since decades of EEG research focusing on peaks in event-related potentials (ERPs), obtained by extensive averaging of the EEG-signal time-locked to some experimental event, arguments regarding their exact neural underpinnings are still controversial (Makeig, Debener, Onton, & Delorme, 2004; Sauseng et al., 2007). While certainly informative in many circumstances, this kind of signal analysis largely dismisses information that is potentially contained in pre-stimulus phase of ongoing



oscillations. Evidence for significant phase effects on perceptual performance in humans, together with electrophysiological work indicating that neural oscillations reflect a rhythmic shifting in the excitability of a neural ensemble (e.g. Schroeder & Lakatos, 2009), prompted us to hypothesize that oscillatory phase might be related to fluctuations in conscious perception during binocular rivalry. Adopting the flash suppression paradigm (c.f. Bartels & Logothetis, 2010) already used in the psychophysics-part of this work, we were curious as to whether phase distributions – possibly obtained over those fronto-parietal areas repeatedly shown to be activated by perceptual switches (Kanai, Bahrami, & Rees, 2010; Kleinschmidt, Büchel, Zeki, & Frackowiak, 1998; Lumer, Friston, & Rees, 1998; Sterzer & Kleinschmidt, 2007) – differ between trials in which subjects subsequently experienced a perceptual switch (‘switch-trials’) and those instances in which a current percept did not change during the presentation of the brief mask (‘no-switch trials’).

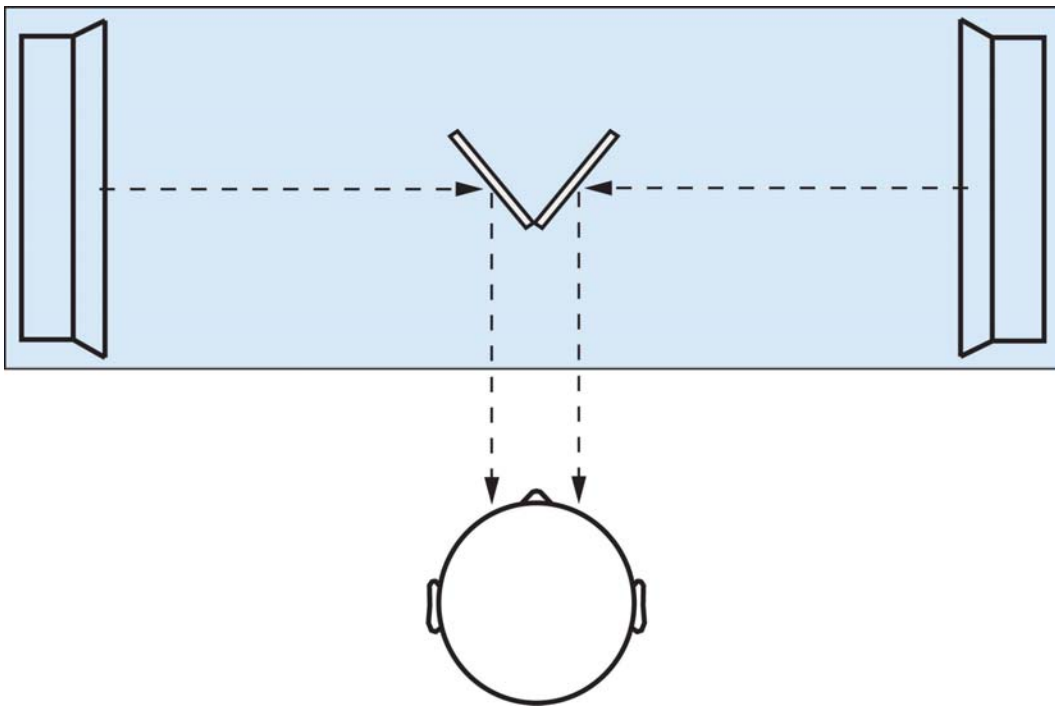
## II. MATERIALS AND METHODS

### A. General Methods

Two independent experiments were conducted, both using a slightly modified versions of the flash-suppression paradigm (Fig. 2 & 6) originally introduced by Bartels and Logothetis (2010). All participants had normal or corrected to normal vision and, in each of the two experiments, all but one subject (the author) were naïve with regard to the purpose of the study. Subjects were given both verbal and visual instructions and performed several training trials in order to ensure proper behavioural performance during data collection. Experiments were approved by the joint ethics committee of the Max-Planck Institute and the University Clinic Tübingen.

Stimuli were generated using the COGENT 1.27 toolbox (John Romaya, Wellcome Department of Imaging Neuroscience, University College London, [www.vislab.ucl.ac.uk/CogentGraphics.html](http://www.vislab.ucl.ac.uk/CogentGraphics.html)) on a Windows PC running MATLAB 2007a (Mathworks, Inc.). They were presented on independently linearized monitors (resolution 1024x768, 85 Hz) that faced each other and were viewed through a set of silver-coated mirrors in a black-shielded setup, installed at the Max-Planck Institute for Biological Cybernetics (Fig. 1). Stimuli for the first experiment – studying the effect of stimulus-inversion on the time-varying contributions of eye- and image-based processes – consisted of circularly cropped images of a house and a face (tinted red and green),

presented foveally and either upright or upside-down. Stimuli were matched in luminance ( $2.5 \text{ cd/m}^2$ ) and RMS contrast ( $1.32 \pm 15\%$  S.D., Michelson:  $\sim 100\%$ ) and were superimposed on an isoluminant gray circular annulus ( $3^\circ$  diameter, CIE chromaticity:  $x: 0.262, y: 0.291$ ) containing a thin black concentric circle ( $1^\circ$  diameter,  $0.04^\circ$  thickness,  $0.0 \text{ cd/m}^2$ ) with centrifugal crosshairs (extending to  $3^\circ$ ), presented on otherwise black screens.



**Figure 1. Schematic illustration of the stereo-setup used in both the psychophysical and the EEG experiment.** Stimuli were displayed on two monitors facing each other, projected onto a pair of angled mirrors, and finally viewed by an observer sitting in front of a black-shielded setup. The mirror stereoscope was originally invented by Sir Charles Wheatstone (1883), and allows the simultaneous presentation of separate images to the two eyes.

For the EEG-experiment the same setup was adopted, but black/white oriented gratings ( $\pm 45 \text{ deg}$ ,  $5 \text{ cpd}$ ) were presented instead of house/face stimuli. An interrupting pattern, as well as a pre-trial mask ( $0.75 \text{ deg}$  diameter), consisted of white noise with  $3.75 \text{ cd/m}^2$  ( $=150\%$ ) luminance and  $100\%$  contrast, and were randomly selected from 10 pre-calculated white noise patterns for each presentation. On- and offsets of stimuli happened instantaneously (from one frame to the next), and subjects were asked to report the perceived image (house or face) or orientation of gratings (left or right), respectively (c.f. Bartels & Logothetis, 2010).

## **B. The effect of stimulus inversion on rivalry dynamics**

### *1. Subjects*

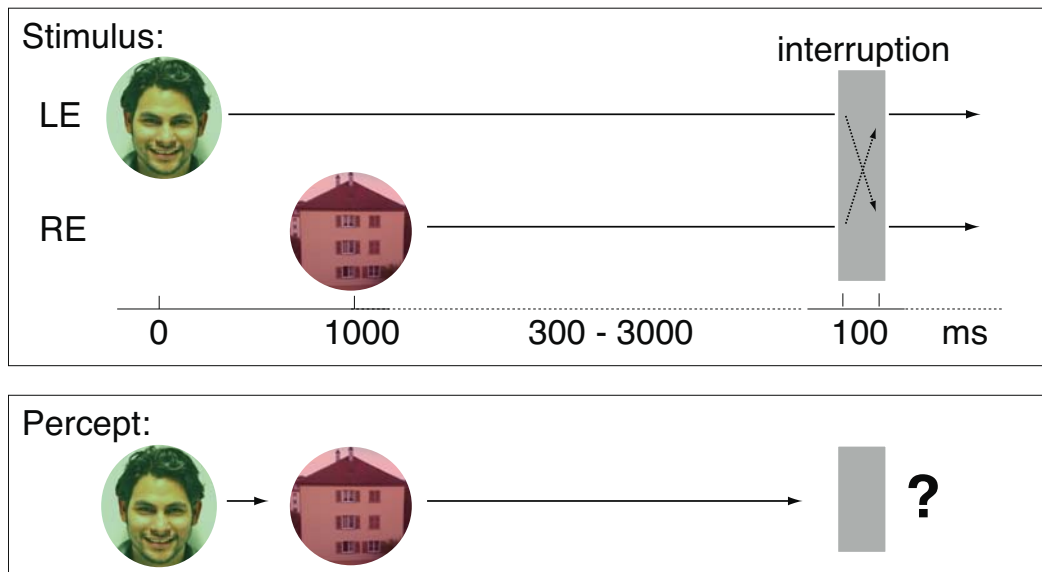
In the psychophysical experiment eleven subjects, aged 23-37 years (6 female), performed in all conditions of the experiment.

### *2. Stimuli and procedure*

Subjects were accustomed to the rivalry paradigm prior to data collection and the contrast of the house/face images was adjusted for each participant individually, in order to reduce extensive piecemeal rivalry and the percentage of ‘failed’ trials, respectively. Experimental blocks consisted of 16 trials each of which began with a 3 s binocular mask (white noise, same properties as the interruption pattern), followed by a gray background for 2 s. Then the image of either the house or the face was presented to one eye (now dominant) for 1000 ms, followed by the presentation of the second stimulus to the other eye for 300 or 3000 ms (this stimulus now being dominant; flash suppression (Wolfe, 1984)) and of a binocularly presented interrupting pattern for 100 ms (Fig. 2). Such brief interruptions favouring neither eye nor percept can, but do not need to, result in a perceptual switch and are thus thought to constitute a test for perceptual stability (Bartels & Logothetis, 2010; Blake & Fox, 1974; Kanai, Moradi, Shimojo, & Verstraten, 2005). After the mask both images were shown for another 1500 ms, either presented in the same position as before, or exchanged between the two eyes (‘eye swap’).

Subjects were asked to report the image – house or face – dominantly perceived immediately after the interruption pattern by pressing one of two key buttons. For subjects to respond, it was sufficient if one of the two pictures was clearly dominant, also when a small part of the percept was mixed. However, participants were instructed *not* to press any button as to indicate a failed trial if: (a) dominance induction by flash suppression failed, (b) *any* spontaneous perceptual alternation or *any* piecemeal percept occurred prior to the interruption, (c) neither the face nor the house was dominant following the interruption.

Trials were balanced for initial dominance side, stimulus side, and post-interruption eye exchange vs. no exchange. Blocks of each, short (300 ms) and long (3000 ms) dominance time before mask onset, were run in counterbalanced order. Each of the eleven subjects performed 4 blocks of each type at a minimum, with both upright and inverted stimuli.



**Figure 2. Illustration of the flash suppression setting used and stimuli presented in the psychophysical experiment.** Perceptual dominance was induced in the 2<sup>nd</sup> eye by stimulating it 1000 ms after the image of either the house or the face was presented to the 1<sup>st</sup> eye ('flash suppression' (Wolfe, 1984)). After 0.3 s or 3.0s a binocular interrupting pattern was presented to both eyes. In half of the trials, stimuli were exchanged between eyes concurrent with the interruption, thus dissociating dominant eye from dominant stimulus. Subjects were asked to report the stimulus perceived immediately after the presentation of the mask.

## C. The effect of oscillatory phase on rivalry dynamics

### 1. Subjects

The behavioural and electrophysiological data of eleven participants were collected in the second part of the study. However, six subjects were excluded from the analysis either because of overly alpha-power in their EEG recordings (c.f. Fig. 7), excessive artifacts in the recorded signal contaminating >50% of the trials, the almost exclusive dominance of one eye, or because of an excessive number of invalid trials due to piecemeal rivalry. Therefore, the data of five subjects – the author and four naïve participants (22-26 years old; 3 females) – were finally considered.

## *2. Stimuli and procedure*

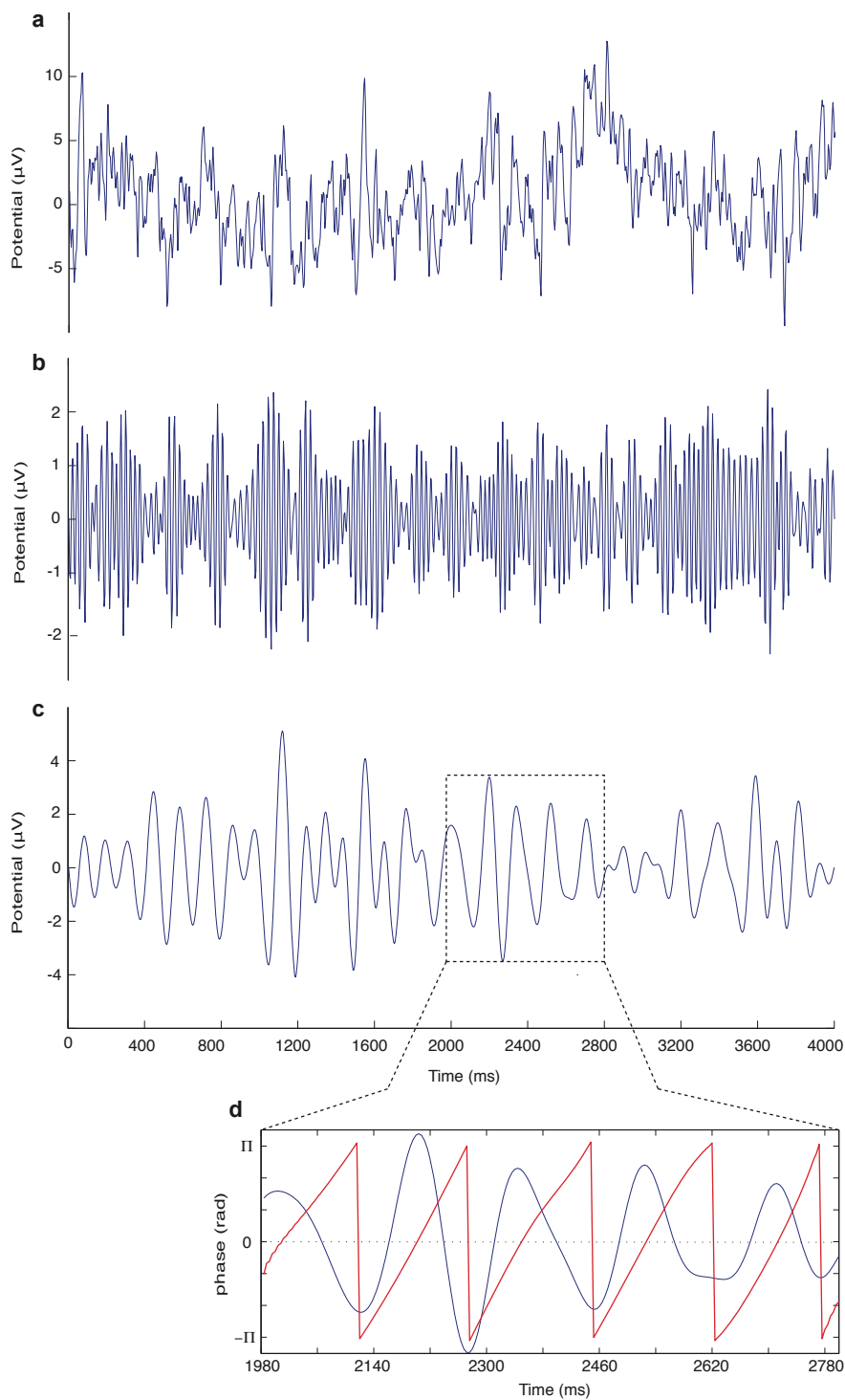
We adopted the rivalry paradigm already introduced in the psychophysics part, however, in order to better control for any biases due to arbitrary preferences of one eye over the other for specific stimulus features, simple sinusoidal gratings were presented instead of coloured images of a house and face (see Fig. 6a for a schematic illustration). Moreover, in the current study, it was always the same stimulus that was shown to a given eye, before and after the binocularly presented interrupting pattern (i.e. there was no eye swap condition).

For each subject then, we determined a time-interval (ranging from 500 to 1200 ms) of binocular stimulus presentation that yielded an approximately equal number of trials in which a subject's percept changed and remained stable over the presentation of the brief mask, respectively. Participants reported the orientation of the grating dominantly perceived immediately after the brief mask, by pressing one of two buttons on an ordinary keyboard. Again, subjects were instructed not to press any key if dominance induction by flash-suppression failed, any perceptual reversals or piecemeal rivalry occurred prior to the interruption, or if neither grating was clearly dominant following the brief mask. Experimental blocks consisted of 16 trials, balanced for initial dominance side, stimulus side, and presented in random order. Depending on the level of fatigue, each of the 5 subjects finally included in the analysis performed 25 blocks at least and 30 at the maximum, corresponding to 400 and 480 trials respectively.

## *3. EEG acquisition and analysis*

Continuous EEG was acquired at a sampling rate of 500 Hz from 64 electrodes with sintered Ag/AgCl sensors mounted in an elastic cap (Vision Recorder, Brain Products, Inc., Munich, Germany). Electrodes were placed according to the international 10–20 system, with a reference electrode at the FCz; an additional 'eye-electrode' (IO) was attached to the outer canthus of the right eye to record the horizontal EOG.

Offline EEG data were down-sampled to 250 Hz, band-pass filtered between 0.5 and 45 Hz and epoched from -2500 before to 1500 ms after onset of the interrupting pattern, using Vision Analyzer (Brain Products). Subsequently, segmented data were converted into a format compatible with the EEGLab software that was used for all further analyses (Delorme & Makeig, 2004).



**Figure 3. The rationale behind the phase analysis.** (a) Shown is the broadband EEG signal (low- and high-cutoff frequency at 0.5 and 45 Hz), recorded at Oz during a whole epoch lasting 4 sec, and before it was band-passed into the traditional EEG bands. Displayed as an example are its (b) gamma (30-45 Hz) and (c) theta (4-10 Hz) components. (d) For each band-limited oscillation, we then extracted the instantaneous phase by calculating the angle of the Hilbert transform (in red) for each trial. The phase of the passband (3-10 Hz) depicted in (c) is shown in radians  $[-\pi, \pi]$ , and in a time-window from 1980 - 2800ms. Note, that the trough of the oscillation is corresponding to  $\pm\pi$  and the peak to  $0^\circ$ .

Artifacts were rejected automatically by excluding epochs in which the signal – acquired on the outer canthus (IO) and above the right eye (FP2) – exceeded a threshold of  $\pm 70$   $\mu\text{V}$ . The remaining data was screened manually for residual artifacts. Four outer channels (FT9, FT10, TP9, TP10) plus the eye-electrode (IO) were excluded, leaving 59 electrodes for analyses.

Phase distributions were calculated for the time-interval between the presentation of the second stimulus (flash suppression) and that of the brief mask, comparing EEG phase between trials in which a subject’s percept changed and was stable, respectively. In order to circumvent possible biases in our data, the number of switch and no-switch trials were matched for each eye-of-presentation/stimulus combination, and subject separately.

In keeping with its traditional classification, EEG data were band-passed into five frequency bands – *delta* (3-4 Hz), *theta* (4-10 Hz), *alpha* (10-15 Hz), *beta* (15-30 Hz) and ‘low’ *gamma* (30-45Hz) – using a linear ‘finite impulse response’ (FIR) filter. For phase-analysis, the angle of the Hilbert transform was calculated for single-trial data, and instantaneous phase  $[-\pi, \pi]$  was extracted in each of the band-limited oscillations (Fig. 3 illustrates the basic rationale behind this procedure). Due to its circular nature, oscillatory phase cannot be analysed with traditional linear statistics, and circular statistics have to be used instead (e.g. Fisher, 1993). To this end we applied the ‘multi-sample test for equal median directions’ (a circular analogue to the Kruskal-Wallis test), using the Matlab implementation provided by Berens (2009).

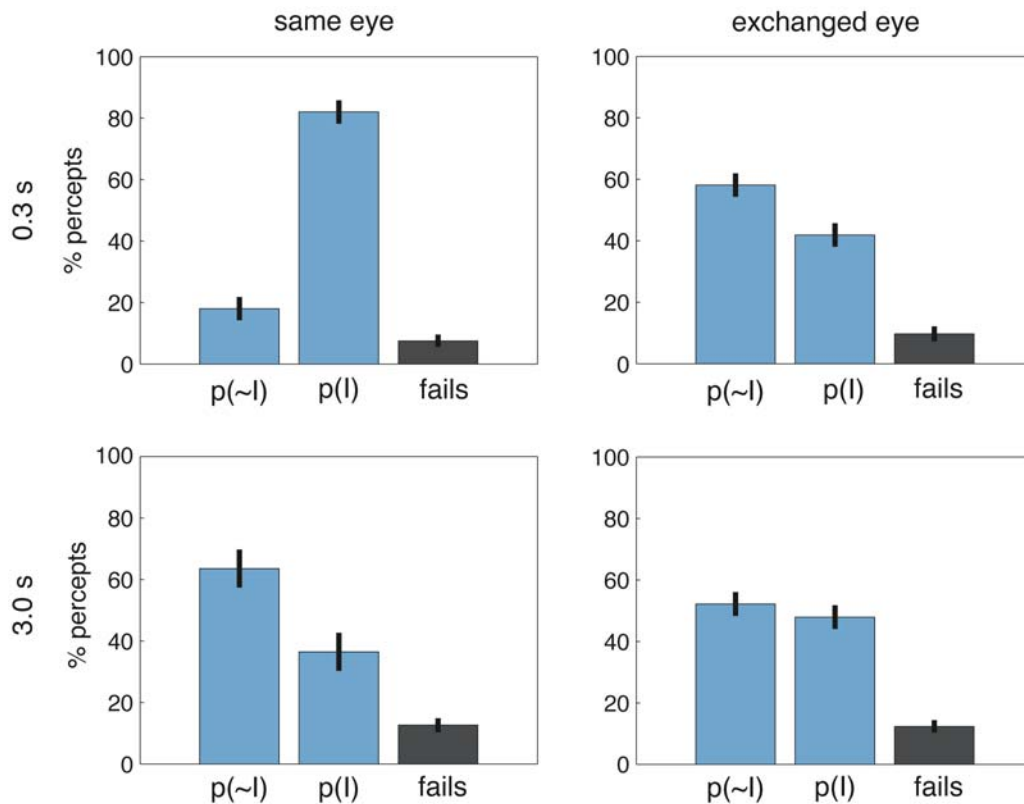
### III. RESULTS

#### A. The effect of stimulus inversion on rivalry dynamics

In keeping with Bartels and Logothetis (2010), we denote the perceived image of the initially dominant stimulus  $I$ , and the initially suppressed image  $\sim I$ . Accordingly,  $p(I)$  denotes the percentage of valid trials in which  $I$  continues to be perceived after the interruption pattern, with  $p(\sim I) = 100 - P(I)$ , and  $p(E)$  denotes the percentage of valid trials in which the same *eye* continues to be dominant after the interruption pattern, with  $p(\sim E) = 100 - p(E)$ . Invalid (failed) trials were not further analyzed, however, their proportions appear in the figures as *fails*.

### 1. Upright Stimuli

Rivalry between a pair of upright house/face stimuli yielded results that are largely consistent with those obtained by Bartels and Logothetis (2010) presenting images of flowers. Thus, after short dominance (0.3 s), the percept was very stable in same-eye conditions but tended to change in exchanged-eye conditions (same eye:  $p(\sim I) = 17.99\% \pm 3.8$  S.E; exchanged-eye:  $p(\sim I) = 58.11\% \pm 3.8$  S.E.), implying a primary role of processes related to the eye-of-origin in determining the perceptual outcome; i.e. whichever stimulus was shown to the initially dominant eye tended to be dominant after the brief stimulus disruption (Fig. 4).



**Figure 4. Results obtained using upright house/face images.** Percentages of percepts following the presentation of the binocular interrupting pattern, for each of the four conditions. P(I) and P(~I) denote the percentages of valid trials in which the initially dominant stimulus continues to be perceived after the interruption pattern and where it changed, respectively ( $p(I)+p(\sim I)=100\%$ ). Invalid trials (e.g. due to a spontaneous switch preceding the interruption or to piecemeal rivalry), are indicated as 'fails'. After short dominance (0.3 s) it was primarily the eye-of-origin that dictated the perceptual outcome (top row). Conversely, after prolonged dominance (3.0 s), the percept tended to switch to the previously suppressed image, with weaker contributions of the eye-of-origin. Errorbars: S.E. across eleven subjects.



Results further indicate an additional, albeit smaller stabilizing contribution of the initial percept, in that exchanged-eye results do not mirror same-eye result:  $p(\sim I)_{\text{exchange-eye}}$  is significantly smaller than  $p(I)_{\text{same-eye}}$  ( $p < 0.0001$ , 2-tailed t-test,  $n = 11$ ).

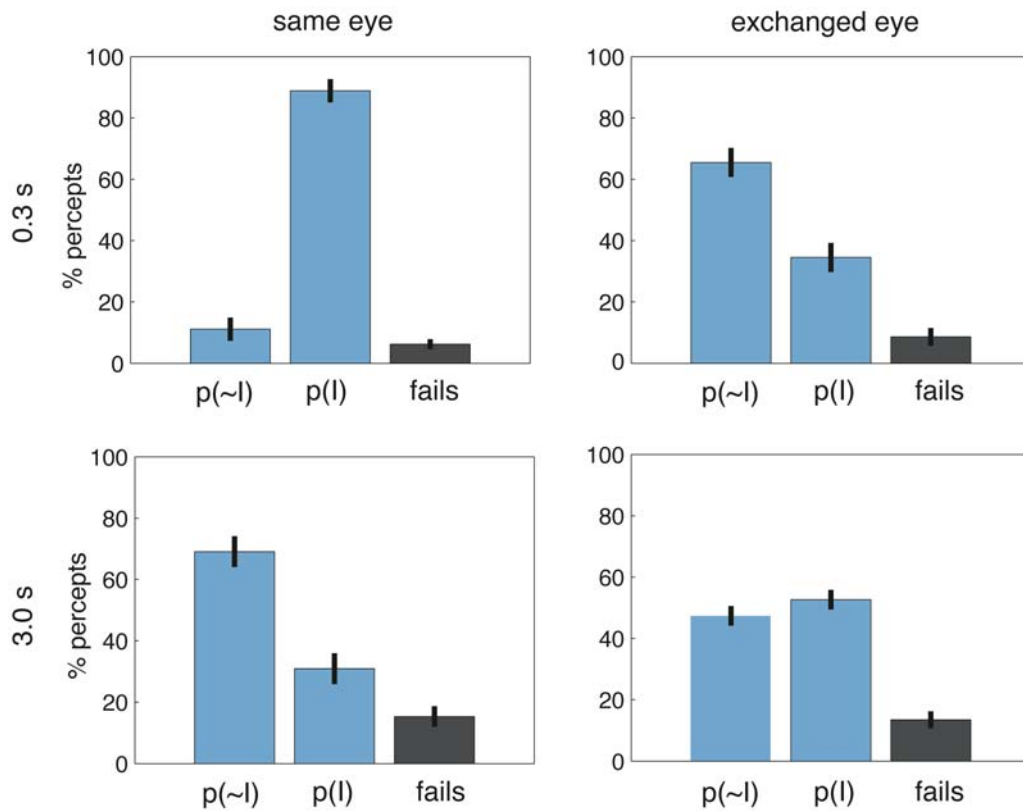
Therefore, after short dominance time, there was a strong tendency of the initially dominant eye to stay dominant and a weaker tendency of the initial percept to stay dominant.

Conversely, after long dominance (3 s), the interruption tended to result in a perceptual switch (same-eye:  $p(\sim I) = 63.55 \% \pm 6.2$  S.E.; exchanged-eye:  $p(\sim I) = 52.13 \% \pm 3.9$  S.E.), suggesting a switch-favouring influence of both the initial percept and the eye-of-origin. But most importantly, the *change* of the eye-based contribution is reflected in a significant interaction between the two factors ‘duration’ and ‘eye’ for  $p(\sim I)$  ( $p < 0.0001$  two-way ANOVA,  $F=32.01$ ,  $df=1$ ,  $n = 11$  subjects). The main factors also achieved significance in the group analysis (eye:  $p < 0.0031$ ,  $F=9.93$ ,  $df=1$ ; duration:  $p < 0.0001$ ,  $F=18.88$ ,  $df=1$ ). Likewise, a significant interaction between factors ‘duration’ and ‘percept’ for  $p(E)$  reflects the change of the initial percept contribution ( $p < 0.0001$ , two-way ANOVA,  $F=18.88$ ,  $df=1$ ,  $n=11$ ).  $P(E)$  equals  $P(I)$  in same-eye trials and  $P(\sim I)$  in exchanged-eye conditions. Thus, within a single dominance phase, initially stabilizing contributions of both eye- and image-related processes declined over time, turning into de-stabilizing forces that eventually favour a perceptual switch.

Taken together, our data reveal an initially strong stabilizing contribution of processes related to the eye-of-origin, as well as a weaker, yet significant stabilizing effect of the initial percept, both decreasing within a single dominance phase and eventually turning into de-stabilizing forces. Significantly, results do not differ in exchanged-eye conditions, implying that the amount of change in eye-of-origin- and higher-level image contributions was roughly equal, neutralizing each other at any given time in exchanged-eye conditions (Fig. 4). Therefore, replicating the results obtained by Bartels and Logothetis (2010) using flower stimuli, we show that the initially stabilizing contributions of both eye- and percept-related processes – albeit differing in magnitude – decline in parallel over time, eventually de-stabilizing a current percept.

## 2. Inverted Stimuli

Presenting the same pictures of a house and of a face, but upside down, yielded overall results similar to that obtained with upright stimuli; i.e. after short dominance a given percept was very stable in same-eye conditions but tended to change after prolonged dominance time (Fig. 5). Similar to upright stimuli, factors ‘eye’ and ‘duration’, as well as their interaction, each achieved significance in a 2-way ANOVA (eye:  $p=0.00044$ ,  $F=14.7$ ,  $df=1$ ; duration:  $p=0.000034$ ,  $F=21.81$ ,  $df=1$ ; interaction:  $p<0.000000$ ,  $F=79.67$ ,  $df=1$ ;  $n = 11$  subjects), as did the interaction between factors ‘percept’ and ‘duration’ for  $P(E)$  ( $p=0.000034$ , two-way ANOVA,  $F=21.81$ ,  $df=1$ ,  $n = 11$  subjects).



**Figure 5. Replication of the first experiment using the same house/face stimuli, but this time presented upside down.** As shown with upright stimuli a given percept was very stable after short dominance but tended to change after prolonged dominance duration. Note however the significant difference between exchanged-eye conditions after 0.3 s and 3.0 s dominance time, implying an unequal amount of change in contributions related to the eye-of-origin and to binocular percept-related processes. Errorbars: S.E. across eleven subjects.

Therefore, stabilizing contributions of both, eye- image-related processes declined over time, ultimately de-stabilizing a given percept. Although it was primarily the eye-of-origin that determined the percept after short dominance, our data again reveal a weaker stabilizing contribution of the initial percept, in that  $p(\sim I)_{\text{exchange-eye}}$  was smaller than  $p(I)_{\text{same-eye}}$  ( $p=0.001$ , 2-tailed t-test,  $n = 11$ ).

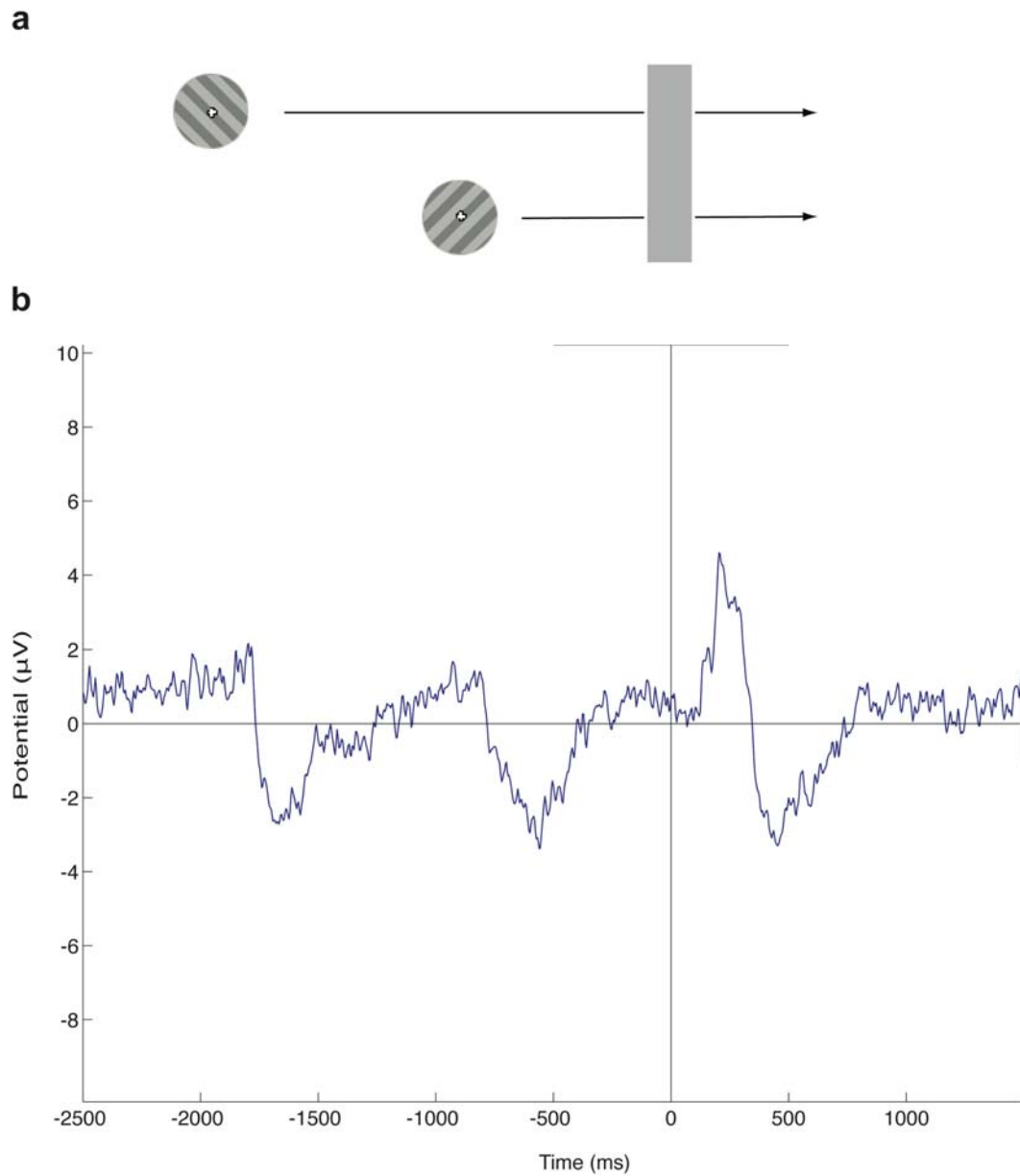
Importantly, however, and contrasting results obtained with upright stimuli, exchanged-eye results after short (0.3 s) and long dominance times (3.0 s) differ significantly ( $p=0.019$ , two-tailed t-test,  $n=11$ ) (Fig. 5). This implies an unequal amount of change in contributions related to the eye-of-origin and to the initial percept, which consequently fail to cancel each other in exchanged-eye conditions.

The effect of stimulus-inversion could be substantiated using a 3-way repeated-measures ANOVA with the factors (stimulus, channel, duration), revealing a significant interaction of the factors ‘stimulus’ (upright vs. inverted) and ‘duration’ (short vs. long dominance) for  $p(E)$  ( $p=0.0082$ ,  $F=10.78$ ,  $n=11$ ).

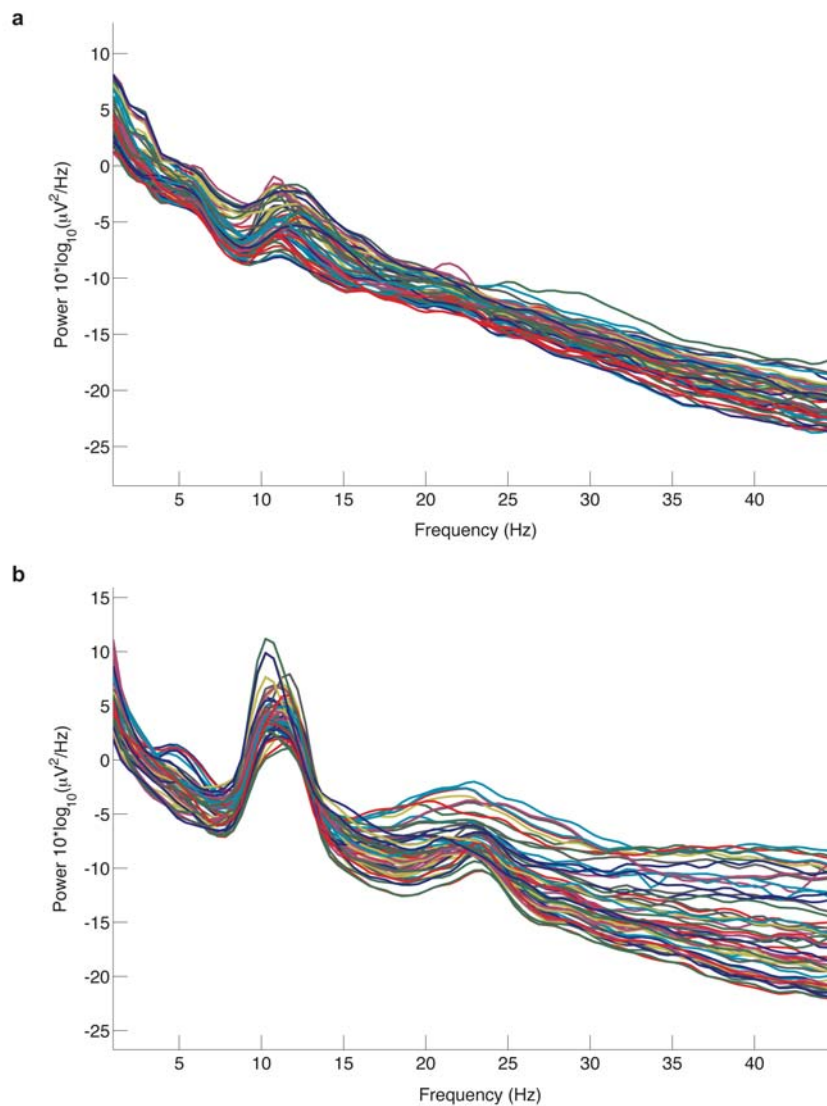
It might be worth noting that there is a seeming *trend* towards a greater net-influence of processes related to the eye-of-origin both early and late during a dominance phase for inverted stimuli; i.e. after short dominance  $p(\sim I)_{\text{exchanged-eye}}$  was slightly higher for inverted than upright stimuli ( $65.49\% \pm 4.7$  S.E and  $58.11\% \pm 3.8$  S.E respectively;  $p=0.051$ , 2-tailed t-test), suggesting a stronger tendency of the eye-of-origin to stay dominant with inverted stimuli. Conversely, after long dominance duration, an initially dominant percept had a tendency of becoming dominant again in exchanged-eye conditions (Fig. 5), consistent with a relatively stronger destabilizing influence of eye-based processes for inverted house/face images.

## **B. The effect of oscillatory phase on rivalry dynamics**

The presentation of the sinusoidal gratings, as well as that of the binocular mask, elicited a characteristic sequence of clearly definable ERPs (Fig. 6). Because we were primarily interested to see whether the distributions of phases preceding mask-onset differed for switch and no-switch trials, we initially computed the circular statistics for every time-frequency point in a window between onset of the second stimulus (flash suppression) and that of the interrupting pattern.

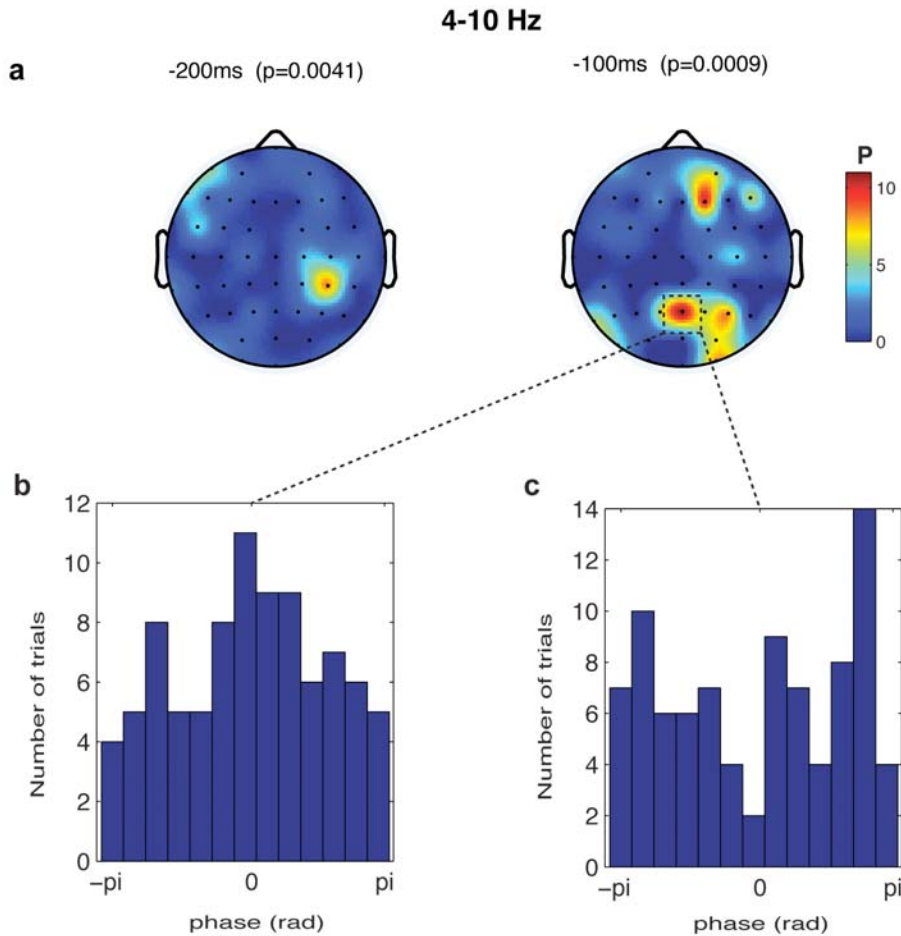


**Figure 6. Illustration of experimental paradigm and evoked EEG response.** (a) The same flash suppression setting as in the psychophysical experiments was used (c.f. Figure 2), presenting oriented gratings instead of house/face stimuli. Note however that stimuli were never exchanged between eyes. For each subject, a time-interval between onset of the second grating and that of the binocularly presented interrupting pattern was determined in order to obtain an approximately equal number of switch and no-switch trials (ranging from 500-1200 ms depending on the subject) (b) Event related potentials (averaged over 330 trials) from a representative participant. The presentation of each stimulus, as well as that of the brief mask each elicited a clearly identifiable ERP. In this particular example, the second grating was shown 900 ms before mask onset. The figure in (a) is meant to be a schematic illustration of the paradigm only, and therefore does not reflect the exact temporal relationships depicted in (b).



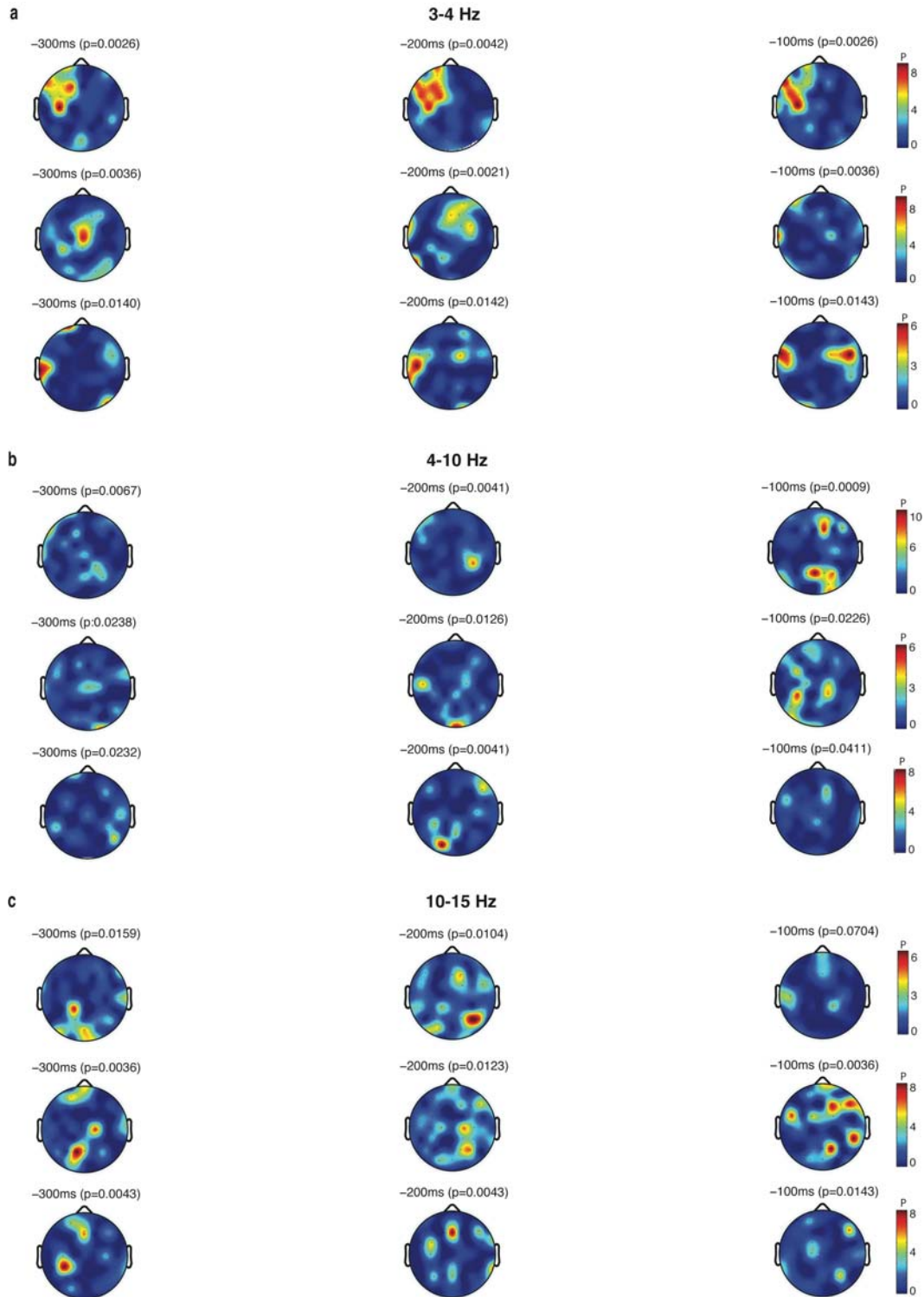
**Figure 7. Mean log power spectra at 59 channels, and for two different subjects.** Each coloured trace in the bundle represents one out of 59 channels (excluded are the eye-electrode and four outer channels). Though most subjects had slightly enhanced power in a frequency range from 10-15 Hz, it was excessive in some participants. Shown as an example are the spectra for one of the five subjects that were finally considered in further analyses (a), and for one that was excluded due to overly alpha power in the EEG data (b). Note the prominent peak around 10 to 12 Hz in (b), corresponding to the traditionally defined alpha-band. The whole epoch time range [4000 ms] and data from 173 (a) and 202 (b) trials were used to compute the spectrum in a frequency range from 1 to 45 Hz.

Figure 8 displays the statistical results for a 4-10 Hz (*theta*-) oscillation of a single subject, showing the strongest effect at -100ms and at electrode *Pz*. The phase distributions at that time-frequency point clearly differed for switch and no-switch, and were almost locked to opposite phase angles (Fig. 8b & c).



**Figure 8. Phase distributions for *switch* and *no-switch* trials.** We applied a ‘multi-sample test for equal medians’ (a circular analogue of the Kruskal-Wallis test) to test the hypothesis that switch and no-switch trials were locked to different phase angles. **(a)** The results of the circular statistics plotted on a topographic map at -200 and -100ms relative to mask onset. High and low values of the test statistic  $P$  are colour-coded as red and blue, respectively. For presentational purposes the data are shown for a single subject and for the theta band (4-10 Hz) only. In this example the strongest effect ( $P=11.0$ ,  $p=0.0009$ , uncorrected for multiple comparisons) was found at -100ms relative to mask onset, and at electrode  $Pz$  (highlighted by the dotted outline). The histograms in **(b)** and **(c)** display the ‘preferred’ phase angles at that specific time-frequency point for no-switch and switch trials. Whereas it was a phase angle around  $0^\circ$  that was most frequent in no-switch trials, the preferred phase in trials that subsequently led to a perceptual reversal was closer to the trough of the theta oscillation; i.e. at  $\pm \pi$  (c.f. Figure 3). Data from a representative subject ( $n=176$  trials); histograms show the number of trials that fall in each of 13 phase bins  $[-\pi, \pi]$ .

However, while phase effects in at least one of the frequency bands were found in all five subjects, their spatiotemporal distribution was highly variable both within and between subjects (c.f. Fig. 9). Indeed, narrowing down the analyses to those time-frequency points that looked most informative initially did not change this very much inconclusive picture, and we finally decided to abandon the experiment at this stage.



**Figure 9. Results of the circular statistics in different subjects.** Results are plotted for each of 3 subjects ( $n=176, 104$  and  $96$  trials) in 3 frequency bands (a-c) and at 3 time points relative to mask onset. Data shown in the upper row in (b) at  $-200$  and  $-100$ ms are identical with those in Fig. 8 and belong to the same subject respectively. Note the variability in the distribution of phase effects. Values of the test-statistic  $P$  are colour-coded for each subject separately;  $p$ -values are uncorrected for multiple comparisons (c.f. Fig. 8).

## IV. DISCUSSION

### A. The effect of high-level stimulus content

A prior rivalry study demonstrated that eye- and image-based contributions vary to the same extent over time (Bartels & Logothetis, 2010); i.e. initially stabilizing contributions of both, processes related to the eye-of-origin as well as of binocular, stimulus-related processes decline in parallel during a dominance phase, eventually de-stabilizing a current percept. As it was the stabilizing contribution of the eye-of-origin that had a greater net-influence early during dominance, it was first the influence of the initial percept that turned into a de-stabilizing force. Such a co-varying change of eye- and image-based contributions is indicative of direct interactions between the two, consistent with the hypothesis that rivalry dynamics critically depend on feedback from higher-level percept representations to early eye-based processing stages (Gilbert & Sigman, 2007; Jiang et al., 2007; Leopold & Logothetis, 1999; Sterzer et al., 2009; Watson et al., 2004).

Results from the current study confirm the findings of Bartels and Logothetis (2010), showing that stabilizing contributions of both eye- and image-based processes – though differing in magnitude – decline in parallel with time and to the same extent, respectively. Again it was the contribution of the eye-of-origin that had a greater net-influence initially, and therefore higher-level processes that were favouring a switch first. Importantly, however, we here extended these findings in an additional experiment, demonstrating that the co-variation between eye- and image-based contributions was considerably reduced when rivalling house/face stimuli were inverted from their canonical upright orientation. Indeed, contrary to upright stimuli, eye- and image-based contributions did not change to the same amount over time, therefore failing to cancel each other in exchanged-eye conditions. Similar results were obtained by Bartels and Logothetis (2010) using simple gratings instead of images of flowers. However, since flower and grating stimuli were not matched in low-level visual features, and were presented to different subjects, it was not clear whether the observed effect was actually due to the difference in stimulus complexity. Crucially, we here sought to rule out these alternative explanations and presented identical pictures of a house and a face – either upright or inverted – to the same 11 subjects. This procedure allowed us to keep the low-level feature composition of rivalling stimuli pairs de facto identical, while at the same time changing considerably higher-level stimulus information (i.e. familiarity) (Gilaie-Dotan, Gelbard-Sagiv, & Malach, 2010; Jiang et al., 2007).



Taken together, these results may add to a growing literature showing that the amount of shared neural substrate between stimuli can affect rivalry dynamics in various ways. For example, it was shown that diverting attention from bi-stable stimuli causes a slowing of perceptual alternations as a function of attentional load (Paffen, Alais, & Verstraten, 2006; Pastukhov & Braun, 2007). Interestingly, this effect is less pronounced for grating rivalry than for rivalry between upright house/face stimuli or ambiguous figures (Alais et al., 2010). Similarly, stimulus complexity critically affects the depth and coherence of rivalry suppression (Alais & Melcher, 2007; Nguyen, Freeman, & Alais, 2003). While rivalry between complex visual objects like faces and houses – both processed in high-level visual areas (Aguirre, Singh, & D'Esposito, 1998; Epstein & Kanwisher, 1998; Kanwisher, McDermott, & Chun, 1997) – exhibits deep suppression and coherent perceptual alternations, rivalry between a pair of simple gratings exhibits shallow suppression, as does a combination of simple and complex stimuli, suggesting that suppression depth primarily depends on the level of *shared* stimulus complexity (Alais & Melcher, 2007). Moreover, rivalry between inverted faces displays suppression as shallow as rivalry between gratings, inverted faces also rivaling less coherently than pairings of upright face/house stimuli (Alais & Melcher, 2007). Together, these data indicate that the processing of faces viewed upside down entails rivalry characteristics similar to simple gratings, and suggest that high-level cortical involvement and feedback may be similarly reduced for simple and unfamiliar objects. Consistently, Jiang and colleagues (2007) showed that familiar objects – like upright faces, or words from one's native language – are more likely to break inter-ocular suppression than inverted faces or unknown words from a foreign language. This implies that coherent or familiar information is processed differently, even when perceptually suppressed and invisible (Jiang et al., 2007). Interestingly, functional neuroimaging in conjunction with multivariate pattern analysis recently demonstrated the presence of category-specific information in higher order visual areas (i.e. the fusiform face area, FFA, and the parahippocampal place area PPA) during perceptual suppression of house/face stimuli (Sterzer, Haynes, & Rees, 2008). Neural stimulus representations like these could engage in competitive interactions with those encoding the currently dominant percept, and it would be interesting to see whether similar decoding in high-level areas would have been possible for perceptually suppressed house/face stimuli viewed upside down.

The reduced co-variation of eye- and image-based contributions for inverted, relative to upright house/face stimuli, may thus be accounted for by fewer competitive interactions at higher levels of processing, and a reduced amount of feedback to early

visual processing stages. Feedback projections are an integral part of the brain (e.g. Felleman & Van Essen, 1991), and top-down modulations of activity in early visual cortex were shown to affect visual perception in multiple ways (Gilbert & Sigman, 2007; Hsieh, Vul, & Kanwisher; Murray, Kersten, Olshausen, Schrater, & Woods, 2002; Pascual-Leone & Walsh, 2001). Consistently, psychophysical studies demonstrated top-down/perceptual influences on eye-based processing stages repeatedly. For example it was shown repeatedly, that the perceptual state of an adaptor significantly affects the formation of its monocular afterimage (Bartels et al., *in revision*; Gilroy & Blake, 2005; Tsuchiya & Koch, 2005; van Boxtel et al., 2010). And a further compelling example was provided by Watson and colleagues (2004), revealing that perceptual grouping of biological motion promotes rivalry in binocular stimuli whose local elements would not engage in rivalry by themselves.

These findings possibly relate to an intriguing discrepancy between rivalry studies using functional imaging in humans, and single-unit recordings in monkeys. In short, whereas perceptual modulations of neuronal spiking activity are remarkably modest or even absent in the lateral geniculate nucleus (LGN) and V1, the percentage of neurons that change their firing rates as a function of perceptual state increases substantially in higher stages (Gail, Brinksmeier, & Eckhorn, 2004; Lehky & Maunsell, 1996; Leopold & Logothetis, 1996; Logothetis & Schall, 1989; Sheinberg & Logothetis, 1997; Wilke, Logothetis, & Leopold, 2006). In contrast, local field potentials (LFP), reflecting primarily the inputs to and local processing within a cortical area (Bartels, Logothetis, & Moutoussis, 2008; Berens, Keliris, Ecker, Logothetis, & Tolias, 2008; Logothetis, 2003, 2008), as well as fMRI signals, show robust percept-related modulations in V1 (Maier et al., 2008; Wilke et al., 2006) and even in the LGN (Haynes, Deichmann, & Rees, 2005; Wilke, Mueller, & Leopold, 2009; Wunderlich, Schneider, & Kastner, 2005). The curious mismatch between actual spiking activity and the BOLD/LFP signal might be related to feedback from higher-level areas to V1 or LGN, possibly affecting LFPs more than spiking output of neurons at these early processing stages (Bartels, Logothetis, & Moutoussis, 2008; Logothetis, 2008; Saalmann & Kastner, 2009).

Adopting a novel rivalry paradigm recently introduced by Bartels and Logothetis (2010) we here confirm their findings, showing that eye- and image based contributions to perception vary over time and within a signal dominance phase of binocular rivalry. Importantly, whereas both contributions declined in parallel over time for upright images of a house and a face, their coupling was found to be reduced when subjects were

exposed to the very same stimuli presented upside down. In sum, these results may be interpreted in terms of mutual interactions between percept- and eye-of-origin representations that are substantially reduced for stimuli engaging less competitive interactions at higher levels of cortical processing.

### **B. The effect of oscillatory phase**

Traditionally it is neural activity in response, and thus succeeding to some event, that is of primary interest in the (cognitive) neurosciences. However, there exists convincing evidence that ongoing neural activity not just influences the way in which incoming inputs are processed, but may also have important functional roles (e.g. Raichle, 2010; Ringach, 2009). Three recent studies, investigating the impact of spontaneous EEG oscillations on visual perception in humans may be relevant to the current study in particular, showing that detection thresholds for briefly presented visual targets greatly depend on their onset relative to the phase of spontaneous 5-10 Hz oscillations (Busch, Dubois, & VanRullen, 2009; Mathewson et al., 2009). Intriguingly, a follow-up study by Busch and VanRullen (2010) not only confirmed these initial results but also demonstrated that the correlation between pre-stimulus phase and perceptual performance exists primarily for attended, but not for unattended stimuli. Though it is known that the instantaneous phase of neural oscillations at stimulus-onset is related to manual reaction times (Callaway & Yeager, 1960; Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008) and to the strength/amplitude of neural responses (Jansen & Brandt, 1991; Kruglikov & Schiff, 2003; Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008) – as confirmed in a recent study using optogenetic tools (Cardin et al., 2009) – its impact on subsequent visual perception certainly constitutes a conceptual advance (Busch et al., 2009). These results also lend further support to the idea that oscillatory activity reflects a rhythmic shifting between high and low excitability states of neural ensembles, implying the existence of an ‘ideal’ phase – during which arriving inputs are optimally processed – and a ‘worst’ phase, during which inputs may be suppressed (Bishop, 1933; Buzsaki & Draguhn, 2004; Schroeder & Lakatos, 2009; Schroeder et al., 2008; Wang, 2010).

Therefore, several lines of evidence suggest that ‘spontaneous’ fluctuations in brain activity influence the response to sensory input at both the neural and the behavioural level, and can even influence whether a visual stimulus is perceived at all. Using a novel rivalry paradigm that allows to exactly track a subject’s perception while controlling for possibly confounding motor effects (Fig. 5), we were curious to see whether ongoing

brain activity, in the form of oscillatory phase, might be affecting perceptual dynamics during binocular rivalry. In particular, we hypothesized that switch and no-switch trials are each associated with different distributions of phase angles in a time-window preceding the onset of the brief mask, allowing the ‘prediction’ of perceptual switches on a trial-by-trial basis. However, we could not find convincing support for this hypothesis.

It is possible, of course, that the phase of EEG oscillations actually does not provide information about the occurrence of a coming perceptual switch during binocular rivalry. However, lack of evidence is not evidence of lack. Indeed, given the literature reviewed above such a scenario may even be rather unlikely. Accordingly, two recent EEG studies on bi-stable perception investigated the ‘momentary state of the brain’, defined by the authors as the spatial configuration of the scalp potential map immediately preceding the onset of intermittently presented bi-stable stimuli and reflecting the sum of all momentary ongoing brain processes, and found that perceptual reversals are associated with greater activity in right inferior parietal cortex (Britz, Landis, & Michel, 2009; Britz, Pitts, & Michel, 2010). Though not testing for any effects of oscillatory phase, these results may be interesting for several reasons. In particular, the identified regions are known to exhibit stronger BOLD contrast fMRI signals during subjective perceptual changes in rivalry, relative to physical (i.e. non-rivalrous) stimulus alternations (e.g. Lumer, Friston, & Rees, 1998). And while conclusions from both EEG and fMRI must be drawn with care due to our still incomplete understanding of the exact neural underpinnings – despite significant progress in this direction (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001; Whittingstall & Logothetis, 2009) – the superior temporal resolution of EEG may be better suited to make inferences about a potentially causal role of some brain area. Therefore, activity changes in the right parietal lobe preceding the occurrence of perceptual reversals, as shown by Britz and colleagues using EEG, could add critical support for a causal role of higher brain in instigating perceptual reversals during multistable perception, possibly by initiating reorganizations of activity throughout the visual cortex (c.f. Leopold & Logothetis, 1999).

Though temporal precedence could give a hint to some causal role of a brain area, the disruption of the same region by means of transcranial magnetic stimulation (TMS) might be a valuable alternative. Consistently, a recent study revealed an intriguing relationship between the structure of bilateral parietal cortex (i.e. cortical thickness and gray-matter density) and individual percept durations for a bi-stable structure-from-motion stimulus, and further found that TMS applied over this parietal regions significantly decreases the rate of perceptual alternations (Kanai et al., 2010). Interpreted

by the authors as evidence for a causal role, their results at least show that ‘normal’ functioning of these areas is required for ‘normal’ percept durations, providing strong support for a critical role of parietal regions in multistable perception.

In sum, there is ample evidence from multiple sources that activity in fronto-parietal cortex is related to perceptual transitions in binocular rivalry and related phenomena. For having a causal role, such changes in activity should *precede* a perceptual switch, possibly reflected in the phase of neural oscillations. After all, our results do not convincingly support this assumption, lacking consistent and clearly distinct phase distributions for switch and no-switch trials across 5 subjects. However, given the peculiarities of binocular rivalry, and the fact that oscillatory phase reflects the state of a neural network on a very short timescale, the lack of a consistent effect may not be that surprising. On the other hand, keeping in mind that ‘some’ differences were found in every single subject tested here, it could pay off to consider the use of more refined statistical methods (e.g. Busch, Dubois, & VanRullen, 2009) or the data of a larger sample of subjects, though beyond the scope of this work.

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## ZUSAMMENFASSUNG

Binokulare Rivalität beschreibt eine visuelle Illusion, welche durch spontane Wechsel in der bewussten Wahrnehmung zweier unterschiedlicher Bilder gekennzeichnet ist. Da der sensorische Input im Gegensatz zum fluktuierenden Perzept stets unverändert bleibt, erlaubt dieses Phänomen der Wahrnehmung eine Dissoziation der neuronalen Aktivität, welche mit den physikalischen Eigenschaften eines Sinnesreizes assoziiert ist, von der mit der bewussten Wahrnehmung *per se* korrelierenden. Obwohl ein gewisser Konsens hinsichtlich einer Rolle neuronaler Prozessen sowohl auf früher („augenbasierter“) als auch höherer („perzeptbasierter“) Ebene kortikaler Verarbeitung erreicht scheint, gibt es eine Reihe offener Fragen bezüglich ihrer spezifischen Wirkungen und zeitlichen Variation. Umso interessanter erscheinen die Resultate einer kürzlich veröffentlichten Studie, wonach anfänglich stabilisierende Einflüsse neuronaler Stimulus-Repräsentationen sowohl auf frühen (vermutlich monokularen) als auch auf höheren Verarbeitungsebenen parallel zueinander in einer Dominanzphase binokularer Rivalität abnehmen, um letztendlich ein aktuelles Perzept zu destabilisieren (Bartels & Logothetis, 2010). Eine solche Co-Variation lässt die Existenz direkter Interaktionen vermuten, deren Ausmaß von jenem des involvierten neuronalen Substrates und damit indirekt auch von der Komplexität des zu verarbeitenden visuellen Reizes abhängt. Zur Prüfung dieser ersten Hypothese wurden den Probanden identische Photos eines Hauses und eines Gesichtes gezeigt, entweder in gewohnt aufrechter Position oder aber auf den Kopf gestellt. Bei den letzteren fanden wir tatsächlich eine Reduktion in der ‚Koppelung‘ augenbasierter und perzeptbasierter Einflüsse, möglicherweise als Effekt einer geringeren Beteiligung höherer Zentren und einer damit einhergehenden Reduktion neuronalen Feedbacks zu früheren Ebenen visueller Verarbeitung. Aufgrund zahlreicher Studien, welche auf eine essentielle Rolle ‚spontaner‘ Gehirnaktivität auf mehreren Ebenen neuronaler Verarbeitung schließen lassen, untersuchten wir zusätzlich die Frage, ob die Phase neuronaler Oszillationen die Dynamik unsere Wahrnehmung im Zuge binokularer Rivalität beeinflusst und ob (Hypothese 2) die Phase eines oder auch mehrerer EEG-Bänder die ‚Vorhersage‘ eines Wahrnehmungswechsels erlaubt. Während die experimentellen Resultate unsere erste Hypothese stützen und einen signifikanten Effekt der Stimulus-Inversion auf den zeitlichen Einfluss augenbasierter und perzeptbasierter Prozesse zeigen, bleiben die Ergebnisse der EEG-Analyse uneindeutig und scheinen unsere zweite Hypothese nicht zu bestätigen.



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