

No evidence for widespread synchronized networks in binocular rivalry: MEG frequency tagging entrains primarily early visual cortex

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We investigated the spatio-temporal dynamics of the steady-state-visual-evoked field during perceptual switches in binocular rivalry using MEG. Several authors have previously used frequency tagging in MEG studies on binocular rivalry and have claimed to have found a widespread network of synchronized areas that are entrained by the stimulus, reaching up to frontal regions. Moreover, it has been claimed that the results prove that becoming aware of a stimulus is established by increased intra- and interhemispheric synchronization of brain areas, separated by large distances. Our results dovetailed nicely with previous findings such as power and coherence modulations as a function of perceptual state. However, while we also found stimulus-entrained activity across the entire scalp, a phase analysis revealed that the spatially extended nature of the frequency tag was produced by a limited set of occipital sources. Furthermore, we provide evidence that the coherence results from earlier studies are ambiguous in that they likely measured coherence between different sensors whose signals were dominated by the same sources. We conclude that the claims about widespread synchronized networks to consciously perceive flicker stimuli are currently unconvincing.

Keywords: binocular rivalry, MEG frequency tagging, coherence, synchronization

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Introduction

Integrative theories of brain function propose that higher cognitive functions, including perceptual awareness of our environment, result from the information integration across widespread brain areas (Edelman & Tononi, 2000; for review papers, see Engel & Singer, 2001; Varela, Lachaux, Rodriguez, & Martinerie, 2001; Cosmelli et al., 2004; but for a critical stance, see also Shadlen & Movshon, 1999). Such theories propose that although local cortical areas contribute to distinct aspects of conscious perception, global integration of locally present information is required to establish a unified conscious experience. Consciousness is thus predicted to correlate with the co-activation and functional coupling of a whole network of cortical areas, presumably spanning the entire cerebral cortex.

Binocular rivalry in combination with frequency-tagged stimuli has become a particularly popular technique to investigate the relation between conscious experience and information integration across multiple cortical areas (Brown & Norcia, 1997; Cosmelli et al., 2004; Lansing, 1964; Lawwill & Biersdorf, 1968; Srinivasan & Petrovic, 2006; Srinivasan, Russell, Edelman, & Tononi, 1999; Tononi, Srinivasan, Russell, & Edelman, 1998). Binocular rivalry arises when the two eyes are presented with two unfusible images. Rather than perceiving two superimposed images, this type of stimulation results in alternating perception of the left and right eye images (for a review on binocular rivalry, see Blake, 2001). Lansing (1964) first demonstrated that when flashing a monocular image at a distinct frequency within a binocular rivalry setup, the power at the tagging frequency of an occipitally placed electrode correlated directly to the reported perceptual awareness of the corresponding

image. Lawwill and Biersdorf (1968) later supported these results using for the first time distinct tagging frequencies for each eye separately. Brown and Norcia (1997) went on to show that this technique provided a sufficient signal-to-noise ratio for power fluctuations to be visible on a single-trial basis.

Tononi et al. (1998) were first to investigate the spatial extent of these power modulations. They reported that although stimulus-induced power is most prominent in sensors overlying occipital cortex, the frequency tag extends well into temporal, parietal, and even frontal sensors. Srinivasan et al. (1999) went a little further by also looking at the frequency-specific coherence of MEG sensors relative to each other. Coherence is a measure of phase and amplitude correlation between two signals and reflects the degree of functional coupling between them. This study found perceptual awareness to correlate with a general increase not only in raw power modulations at the tagging frequency but also in coherence measured between different sensors, even separated over large distances. Sensors that expressed higher coherence with other sensors were organized primarily in two clusters over the right and left side of the brain. In most cases, the spatial topographies of coherence modulations overlap with the topographies of power modulation and essentially form a pattern reminiscent of the cortical hemispheres. Srinivasan et al. interpreted these findings as evidence that intra- and interhemispheric synchrony mediates conscious awareness of the stimulus. Regarding the specific sources involved in perceptual awareness, Cosmelli et al. (2004) applied a source reconstruction algorithm based on binocular rivalry data and reported that an abundance of cortical sources spanning the entire cortex are susceptible to the frequency tag. Although the modulated sources were inconsistent across subjects, within subjects they did find coherence between the sources to increase as the tagged image became perceptually dominant.

These findings are generally taken as evidence that perception of the tagged stimulus in binocular rivalry indeed correlates with a pan-cortical increase in coordinated activity at the tagging frequency, just as information integration theories of consciousness predict.

Here we argue that the results from the mentioned experiments exploiting the frequency tagging paradigm are ambiguous and need further investigation. We first produced findings dovetailing with earlier findings that power at the tagging frequencies indeed modulates as a function of perception and that these modulations are visible in a large number of MEG sensors covering nearly the entire scalp. We then calculated coherence of each MEG sensor with respect to the stimulus and found coherence to modulate with perception as well. Although our coherence analysis slightly differs from the coherence analyses used in related articles (Cosmelli et al., 2004; Srinivasan et al., 1999), our coherence modulations supported those found in these earlier studies. However, when calculating each sensor's average phase with respect

to the flickering stimulus, we found the phase angle topographies to be less heterogeneous than one would expect from a complex network of sources. Moreover, our analyses show that the two “cortical hemispheres” found in earlier studies (e.g., Srinivasan et al., 1999; Tononi et al., 1998) are actually 180 degree phase shifted relative to each other. This finding is much better explained by the positive and the negative field components of a single occipital dipole than activity generated by a multitude of sources covering separate cortical hemispheres. This occipitally generated activity appears strong enough to even dominate activity measured by frontal sensors, and the application of a source reconstruction algorithm indeed projects its source back to early visual cortex. This finding casts doubt on the validity of earlier claims stating that binocular rivalry with frequency tagging demonstrates that conscious experience is correlated with enhanced co-activation, or information integration, across large cortical networks. While we do not exclude that such enhanced information integration exists, the results reported so far do not unambiguously show this and may be explained in a much more trivial way.

Materials and methods

Subjects

Six subjects participated and informed written consent was obtained prior to every experimental session. Subjects had normal or corrected-to-normal vision and good stereo acuity. All procedures were approved by the F.C. Donders Centre for Cognitive Neuroimaging.

Stimuli

Stimuli were two orthogonal white square wave gratings of 2.1 visual degrees and a spatial frequency of 1.87 cycles per degree (see Figure 1). The gratings were embedded in a red fusible background and contained a red



Figure 1. Left and right eye stimuli. The left eye flickered at 7.5 Hz, the right eye at 12 Hz.

fixation dot to aid proper alignment of the eyes. Presentation of the stimuli was controlled through the software package Presentation (Neurobehavioral Systems), using a 60-Hz LCD monitor for display purposes. The flashing frequencies were 7.5 Hz and 12 Hz for the left and right eye, respectively.

Binocular rivalry was induced in the MEG system by presenting the stimuli spatially apart but making them overlap subjectively by letting subjects view them through optically diverging glasses. To fully separate the ocular images and to prevent inter-ocular leakage of the frequency tag, each grating was viewed through a separate tube internally lined with black velvet that connected each lens to its respective image on the screen.

Procedure and task

Rivalry data were collected over 20 sessions lasting 2 min each, with each session being preceded by a baseline period of 5 s where only the background and fixation dot were visible. During rivalrous viewing, subjects pressed a button with their right index finger whenever a perceptual switch occurred toward the left eye image, pressing the right middle finger button whenever the switch was toward the right eye image. Subjects were encouraged to blink only between sessions and could autonomously choose to start the next session by pressing the button corresponding to the left index finger.

Data recording

Magnetoencephalography was recorded with a whole-head 151 sensor axial-gradiometer MEG system (Omega 2000, CTF Systems, Port Coquitlam, Canada), installed at the F.C. Donders Centre, Nijmegen, The Netherlands. Button presses were stored within the same data set, as well as the onset of each flickering rivalry image. The latter resulted in two reference signals for the left and right eye flicker sequence, respectively. These signals were later used for the calculation of sensor coherence with respect to each ocular image separately.

The electro-oculogram (EOG), useful for the detection of eye movements and blinks, was measured by placing electrodes below and to the left of the left eye. The electro-cardiogram was additionally measured by placing electrodes to the right of the neck and on the left waist but was not used for later analyses. All data were sampled at a rate of 1200 Hz and stored for offline analysis.

The position of the head relative to the sensors was additionally measured at the beginning and end of the experiment using three magnetic coils. One such coil was placed at the nasion, the other two in the left and right ear. The positions of these coils were later used by the source reconstruction algorithm to overlay its results on an anatomical scan of each subject's brain. These scans were

made separately by the Siemens Sonata 1.5-T MRI scanner available at the F.C. Donders Centre.

Data analysis

Data were analyzed using the Fieldtrip software package developed by the F.C. Donders Centre (<http://www.ru.nl/fcdonders/fieldtrip/>). Pre-processing steps included down sampling the data to 200 Hz and the detection and subsequent rejection of artefacts due to eye blinks and sudden jumps in the MEG signal.

The artefact-free data were cut into trials starting 3 s before and ending 3 s after each button press. Each trial was sorted according to whether it represented a perceptual switch toward or away from the left eye image. This resulted on average in 223 trials per condition with a standard deviation of 58 across subjects.

A time-frequency analysis was then applied to these data around the periods of a perceptual switch; the signals were Fourier-transformed, using a sliding window approach with window length 1 s, step size 0.05 s, incorporating a Hanning taper. The window length was chosen in a way to optimally balance frequency resolution (to increase SNR and selectively get the steady state activity) and time resolution (to capture the temporal dynamics of activity around the perceptual switch).

In order to calculate coherence, in principle the same procedure was applied as for obtaining the time-varying estimates of power (Fourier transform on Hanning-tapered sliding time windows). Additionally, two virtual “reference sensors” were created, carrying a sinusoidal signal at each of the tagging frequencies phase locked to the flickering stimuli. The complex cross-spectral density of each MEG sensor's signal relative to the reference sinusoid was then calculated at each tagging frequency and multiplicatively normalized on the autospectra of both signals—resulting in a measure called coherence (e.g., Mitra & Pesaran, 1999).

This complex coherence value shows the coupling of neuromagnetic activity recorded by the sensor with respect to the reference signal. While the magnitude of the complex coherence metric (ranging between 0 and 1) shows the strength of coupling between two oscillatory signals, the polar angle reflects the average phase angle between the signals at the given frequency.

As mentioned previously, raw power and coherence differ in the sense that power reflects the energy within a specific frequency band, while coherence measures the consistency in phase angle differences (or functional coupling) between two signals. Coherence, in this context, has a number of advantages over raw power. First of all, coherence is more sensitive to weak signals since it is normalized on the power amplitude. Secondly, when taking the flashing stimulus as the reference signal, stimulus-induced activity at the tagging frequency may be separated from background activity at the same

frequency as the tag. The underlying rationale is that activity not generated by the stimulus has random phase angles with respect to the stimulus, resulting in a drop close to zero of the unrelated activity's coherence values. For these reasons, in this article we look at coherence of sensors relative to the stimuli rather than raw power.

The results of the frequency analysis was finally passed through a DICS (Dynamic Imaging of Coherent Sources) algorithm and overlaid on an anatomical MRI. DICS is a beamformer implementation ideally suited for locating brain areas firing coherently with respect to a reference signal (Gross et al., 2001). It is important to note, however, that DICS does not work optimally when sources are correlated. Because in our study this condition is violated, the results shown here reflect the general center(s) of gravity of coherent activity rather than the true locations of each individual source.

Results

Figure 2 presents the analysis results of subject LM's recorded brain activity during perceptual switches toward

the 7.5-Hz left eye percept. The top left panel (Figure 2A) plots the average time course of 7.5 Hz stimulus-locked coherence relative to button press. Coherence modulations can be observed in almost every sensor, attaining a maximum of over 0.45 in some sensors. The peak amplitude is reached in all sensors around 300 ms before button press.

Figures 2B and 2C present the coherence topographies at time points of minimum ($t = -1.2$ s) and maximum ($t = -0.3$ s) general coherence, respectively, presumably corresponding to the moments of maximum perceptual suppression and dominance. Note that the dominant features of the two topographies are very similar, with primarily the general level of coherence changing as a function of perceptual awareness.

The coherence topographies are indeed reminiscent of the two cortical hemispheres, as was suggested earlier by Srinivasan et al. (1999). To show that these coherence hemispheres do not translate to actual cortical hemispheres, however, we also plot the phase angles between the stimulus and the MEG sensors at the time of maximum coherence ($t = -300$ ms, see Figure 2D, eccentricity = coherence). Most sensors are either 90 or 270 degrees out of phase with respect to the stimulus. Figure 2E further reveals this 180 degree phase shift to

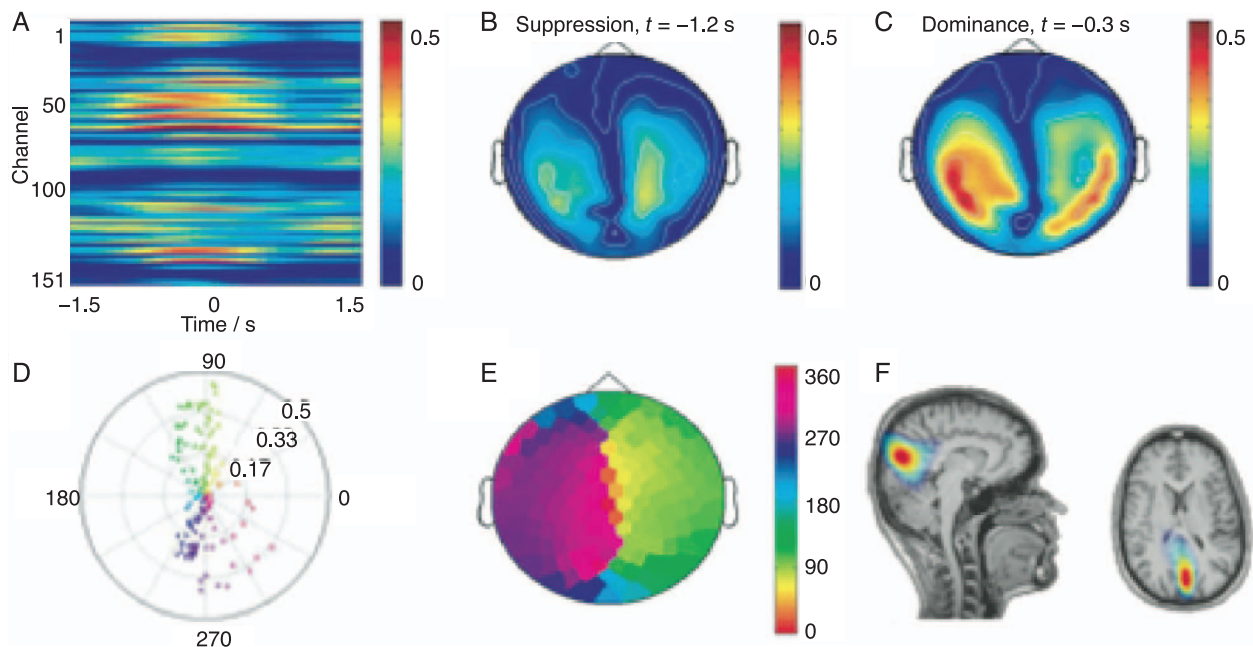


Figure 2. Subject LM's results for 7.5 Hz (left eye) dominance. (A) Time course of coherence relative to button press. Coherence increases in many sensors when the left eye image is perceived. (B) Spatial topography of coherence during suppression. This topography corresponds to a snapshot taken of Figure 2A at $t = -1.2$ s. (C) Spatial topography of coherence during dominance at $t = -0.3$ s. Although the coherence is higher during perceptual dominance than suppression, the topographies are the same. (D) Phase angles relative to stimulus per channel at $t = -0.3$ s (angle = phase, eccentricity = coherence). Most sensors belong to either of two dominant phase angles lying 180 degree apart. Colors are angle dependent and equivalent to the ones used in 2E. (E) Spatial topography of phase angles at $t = -0.3$ s. The 180-degree phase shift overlaps with the high coherence regions and extends even to frontal channels. The topographies suggest that all recorded activity is dominated by a very limited set occipitally generated dipoles. (F) The beamformer algorithm projects the dominant source of coherent activity to early visual cortex. No other consistent sources were found.

overlap almost precisely with the two hemispheres. Deeming it unlikely that the two cortical hemispheres process the stimulus in anti-phase, we interpret them to reflect the positive and the negative components (influx–efflux) of a

single dipole (for a thorough discussion on the bi-phasic nature of MEG signals induced by dipolar activity, see Hämäläinen & Sarvas, 1989; Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993). In Figure 2F, the DICS

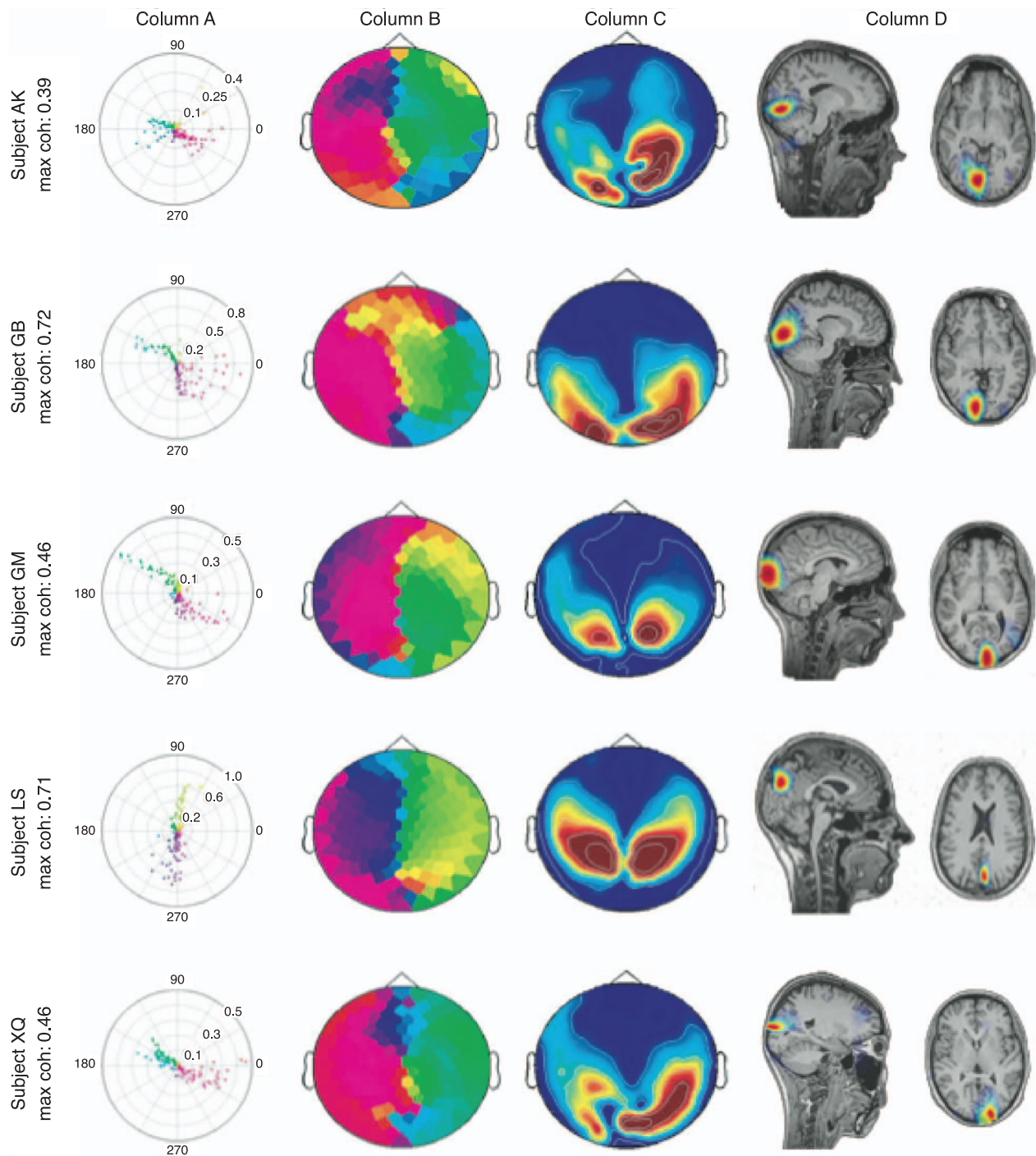


Figure 3. Column A: phase angles and coherence relative to stimulus per sensor (angle = phase, eccentricity = coherence). For all subjects, most sensors belong to either of 2 phase angle clusters that are 180 degrees out of phase with respect to each other. Columns B and C: the spatial topographies of phase angles and coherence, respectively (coherence topographies are scaled per subject). The 180-degree phase shifts coincide with the areas of large coherence and extend across the entire scalp. This suggests that the recorded activity is dominated by a very limited set of occipitally generated dipoles. Column D: the beamformer algorithm projects the source of maximum coherence back to early visual cortex for all subjects. No other consistent sources could be found in any subject.

beamformer algorithm supports this suspicion by projecting the dominant activity back to a single source in early visual cortex.

For the remaining subjects, column A in Figure 3 shows the 7.5-Hz coherence and phase angles at the moment of maximum dominance. The 180-degree phase shift that is the telltale sign of dipolar activity is clearly visible in each subject. Some subjects (e.g., subject GB) show a slightly more scattered distribution of phase angles, however, indicating the presence of more than one dipole.

The spatial topographies of phase angles and coherence are plotted in columns A and B, respectively. Some subjects (e.g., subjects AK and XQ) show a slightly more intricate spatial distribution of coherence than others, but the 180-degree phase shifts are always clearly present and extend across the entire scalp. The DICS beamformer algorithm projects all subjects' dominant activity back to early visual cortex, as is presented in column D.

Discussion

For all subjects, our results are consistent with earlier findings that power and coherence modulate as a function of perception. Contrary to previous claims that flicker stimuli during conscious states activate a variety of brain areas spanning the entire cortex, our phase analyses suggest that the widespread nature of frequency-tagged activity can better be accounted for by a very limited set of occipital dipoles. While the present results do not exclude possible (weaker) entrainment of higher cortical sources by the stimulus, the results do show that activity in most sensors is highly dominated by these medial occipital dipoles. This makes identification of such higher cortical sources very difficult using the frequency tagging paradigm.

In many subjects, the dipolar pattern resulted in a field-topography that is reminiscent of the two cortical hemispheres, as has been previously observed by Srinivasan et al. (1999). That these field topographies do not translate to actual cortical hemispheres, however, is suggested by the 180-degree phase shift between them and the fact that a DICS beamformer algorithm localized the most dominant sources back to early visual cortex, presumably including V1.

Our analysis differs from previous analyses (e.g., Srinivasan et al., 1999; Tononi et al., 1998) in one important respect. While they look at raw power and general inter-sensor coherence at the tagging frequency, we primarily look at coherence with respect to the stimulus. Our method exploits the fact that the signals induced by the tag have a strictly defined phase relative to the stimulus, enabling us to effectively filter out all activity not related to the stimulus, even at the tagging

frequency itself. This provides us with a much cleaner view of stimulus-induced activity than the raw power or inter-sensor coherence methods. Another advantage of taking the stimulus as a reference rather than arbitrary MEG sensors is that it allows us to investigate the phase distribution of all sensors with respect to a highly controlled reference signal. It is precisely this fact that reveals the dipolar nature of the “two hemispheres” of flicker-related activity. In this context, it may also be noteworthy that our coherence analysis indeed emphasizes signals strictly phase locked to the stimulus reference function, unlike the analysis used by Srinivasan et al. (1999). Importantly, small variations in the phase of a neural population to the flicker stimulus (as they might result from intrinsic processes in the brain) will not lead to total cancellation of such activity in our metric. Thus, while our analysis approach efficiently suppresses physiological processes that have *random phase* with respect to the stimulus, it will not eliminate brain responses that have small variations in their phase to the stimulus due to internal brain processes. Their contribution will only appear attenuated (depending on the variance of the phase to the stimulus). We consider it unlikely that in a steady-state paradigm, stimulus-related activity at the tagging frequency can have random phase with respect to the stimulus.

Our results have strong implications for previous frequency tagging studies claiming that perceptual awareness requires the co-activation and functional coupling of multiple cortical areas, as is predicted by the information integration theories of consciousness. While the present results do not exclude possible (weaker) entrainment of higher cortical sources, our results do show that activity in most sensors is dominated by medial occipital dipoles. These dipoles produce the field topography that was earlier interpreted as belonging to the two cortical hemispheres and reveal the ambiguity and the difficulty inherent to interpretation of sensor-to-sensor coherence estimates, even for sensors that are located far apart from each other. Since our power and coherence topographies are very similar to those reported in earlier studies (e.g., Srinivasan et al., 1999; Tononi et al., 1998), we argue that the original claim of Srinivasan et al. (1999) and Tononi et al. (1998) that conscious perception is reflected in increased intra- and interhemispheric synchronization cannot be substantiated by their and our findings. We strongly suspect that their reported power and coherence patterns are essentially caused by signals from just one or a few occipital dipoles and that phase analyses would reveal this source structure in these data as well. Clearly, these issues need to be addressed with techniques that overcome the shortcomings of the currently used analyses.

To our knowledge, only Cosmelli's work investigated coherence modulations in binocular rivalry at source-level rather than sensor-level using a minimum-norm estimation (Cosmelli et al., 2004). Their article reports enhanced

levels of synchrony around the tagging frequency in widespread cross-cortical networks during perceptual awareness. However, their experimental paradigm differs substantially from ours in that (1) they only present a flickering stimulus into one eye and (2) this flickering stimulus is a spatially non-stationary stimulus (a ring expanding in discrete steps at the flicker frequency). This radically changes the pattern of stimulus-related brain responses that one expects compared to our and Srinivasan et al.'s (1999) experiments. Specifically, in Cosmelli's case, each instantiation of the expanding ring will activate different patches of sources in retinotopic areas, and in areas higher up in the visual stream, the temporal activation characteristics will almost certainly be different than in lower level areas due to convergent inputs from different spots that are sequentially activated in retinotopic areas. This makes it more difficult to speak of frequency tagging in the first place and reduces the comparability to our and Srinivasan et al.'s (1999) results. With respect to their specific results, we think it is crucial that they explicitly do not condition their source estimate to pick up primarily stimulus-related activity (as they write themselves) but will rather non-specifically pick up ongoing activity as well (e.g., in an attentional control network). Their source constellations and the synchronized networks also show little consistency across subjects. With that, and the relatively broad frequency resolution of their analysis, we think it is unclear whether the reported network is really involved in the actual representation of the stimulus and whether the reported increase in synchrony is related to the content of the consciously perceived stimulus rather than reflecting a state change. In this report, we focus on stimulus-related activity and how stimulus-related activity changes as a function of perception. Thus, we do not think that Cosmelli's results prove that widespread cortical networks are entrained by the flicker stimulus and that perceptual awareness is mediated by enhanced synchrony between neuronal populations involved in stimulus representation.

To our knowledge, there is only one other study that investigated phase characteristics in frequency tagging for a binocular rivalry paradigm (Srinivasan & Petrovic, 2006). However, this study investigated binocular rivalry between two images that were flickered one to each eye but were never presented simultaneously. Rather than tagging the two ocular images at different frequencies, they tagged both eyes with the same frequency, but in anti-phase to each other. Because the resulting signal at the tagging frequency is the summation of the two anti-phase signals (which interfere with each other, as the authors also state themselves), their results cannot be easily compared to ours.

In this discussion, we focussed on binocular rivalry studies. Quite a few other topics have been studied using frequency tagging in MEG. It remains to be discussed for other tagging studies whether conclusions on wide spread brain activity are warranted. The present results are

consistent with the suggestion that changes in neural activity from unconscious to conscious states in binocular rivalry occur in early visual areas (Lee, Blake, & Heeger, 2005; Tong, 2003) and are consistent with recent work using rivalrous stimuli in EEG (Kornmeier & Bach, 2004, 2005; Pitts, Nerger, & Davis, 2007) and TMS (Pearson, Tadin, & Blake, 2007) on visual rivalry. This statement does even hold for high-level-driven voluntary attentional control over visual rivalry (Meng & Tong, 2004; van Ee, van Dam, & Brouwer, 2005): A recent physiologically and mechanistically plausible model for binocular rivalry (Noest, van Ee, Nijs, & van Wezel, 2007) provided computational evidence that high-level-driven attentional control data (Klink et al., *in press*) could be fully explained through a gain change at the input to a low neural level where neurons both adapt and cross-inhibit one another. In fact, our initial goal here was to validate the computational model predictions. We wished to study whether there was a temporal order in source modulations related to percept switching and attentional control. Although our findings are consistent with the computational model, unfortunately MEG frequency tagging appears unsuitable to allow a systematic study of higher cortical sources. Nevertheless, note that our data does not allow us to reject the hypothesis on involvement of large-scale interactions between brain areas, neither for binocular rivalry nor for other topics.

Conclusion

Using binocular rivalry within a MEG frequency tagging paradigm, we support earlier findings that power and coherence with respect to the stimulus modulate as a function of perception. However, phase analyses and a source reconstruction algorithm revealed that recorded activity was dominated by a limited set of occipital dipoles most likely generated in early visual cortex. These results cast doubt on earlier claims stating that conscious awareness of visual flicker stimuli is mediated by enhanced intra- and interhemispheric synchronization at the flicker frequency.

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