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Prestimulus Oscillatory Phase at 7 Hz Gates Cortical Information Flow and Visual Perception

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Summary

Although we have the impression that visual information flows continuously from our sensory channels, recent studies indicate that this is likely not the case. Rather, we sample visual stimuli rhythmically, oscillating at 5–10 Hz [1–3]. Electroencephalography (EEG) studies have demonstrated that this rhythmicity is reflected by the phase of ongoing brain oscillations in the same frequency [4–6]. Theoretically, brain oscillations could underlie the rhythmic nature of perception by providing transient time windows for information exchange [7], but this question has not yet been systematically addressed. We recorded simultaneous EEG-fMRI while human participants performed a contour integration task and show that ongoing brain oscillations prior to stimulus onset predict functional connectivity between higher and lower level visual processing regions. Specifically, our results demonstrate that the phase of a 7 Hz oscillation prior to stimulus onset predicts perceptual performance and the bidirectional information flow between the left lateral occipital cortex and right intraparietal sulcus, as indicated by psychophysiological interaction and dynamic causal modeling. These findings suggest that human brain oscillations periodically gate visual perception at around 7 Hz by providing transient time windows for long-distance cortical information transfer. Such gating might be a general mechanism underlying the rhythmic nature of human perception.

Results

Thirteen healthy volunteers (mean age 24.2 years; six male, seven female) performed a perceptual integration task while their electroencephalogram (EEG) and fMRI were recorded simultaneously. We adopted a contour detection task where the target is defined by the relative orientation as well as by the spatial arrangement of distributed Gabor patches [8]. The orientation of the patches is known to be coded at initial stages of processing and represented within retinotopic feature maps

in visual areas V1–V4 [9, 10], as well as in posterior parts of the lateral occipital complex, LO1 and LO2 [11]. Because of the limited receptive field size of orientation-selective neurons, a spatial reference, presumably provided by the parietal brain, is then needed to select target candidates from the low-tier units and integrate them across space [12, 13]. A contour detection task is therefore ideally suited for investigating neural long-range communication between higher- and lower-order visual processing regions [14].

Stimuli were composed of 100 Gabor patches each. On half of the presentations, the displays contained a contour consisting of patches with a partially aligned orientation, whereas on the other half, no contour was present (Figure 1A). The task was to indicate the presence or absence of a contour by means of a button press. Participants responded with either the left or the right hand, with the mapping of the response hand to the contour/noncontour stimulus being counterbalanced across subjects. Stimuli were shown very briefly (194 ms) in order to avoid eye movements (Figure 1B) and were constructed for each volunteer individually such that each participant achieved approximately 75% correct responses (obtained by preliminary testing; see [Supplemental Experimental Procedures](#) and [Figure S1](#) available online). All participants were able to discriminate between contour and noncontour stimuli in the main experiment, as reflected in a mean hit rate of 72.34% (SD 8.59%) and a mean false-alarm rate of 23.96% (SD 10.87%). The mean d' measure was 1.37 (SD 0.53).

Prestimulus EEG Phase Predicts Perceptual Integration

After denoising the EEG data from artifacts induced by the scanning environment, the EEG trials corresponding to contour stimuli were divided into those where the contour was detected (hits) or not detected (misses). Noncontour trials were discarded from the analysis. Following prior studies, the phase distributions of hits and misses were compared by means of the phase-bifurcation index [15, 16], which is greater than zero when the mean phase direction between two conditions is maximally different, i.e., shows a 180° phase difference ([Supplemental Experimental Procedures](#)). As shown in [Figure 2A](#), a pronounced increase in the phase bifurcation index (randomization test; $p_{\text{corr}} < 0.05$) was evident shortly before stimulus onset (around –250 ms) in a frequency range centered at 7 Hz. Note that this effect disappears at stimulus onset, which can be attributed to temporal smearing induced by the filter (i.e., smearing the poststimulus event-related potential [ERP] into the prestimulus interval, thus decreasing the phase opposition between hits and misses). This effect was most pronounced over frontocentral and left parietal electrodes. Both the topography and the time-frequency window of this effect closely replicated previous findings [15, 16], showing that reliable EEG results were obtained despite the background noise induced in the EEG by fMRI. Examining prestimulus phase distributions (–250 ms; 7 Hz) at frontocentral electrode sites between hits and misses revealed that across participants, hits clustered around $-\pi$ or π , whereas misses clustered around 0 phase angle ([Figure 2B](#); Kuiper test; $K = 117$; $p < 0.05$). To test for a continuous relationship

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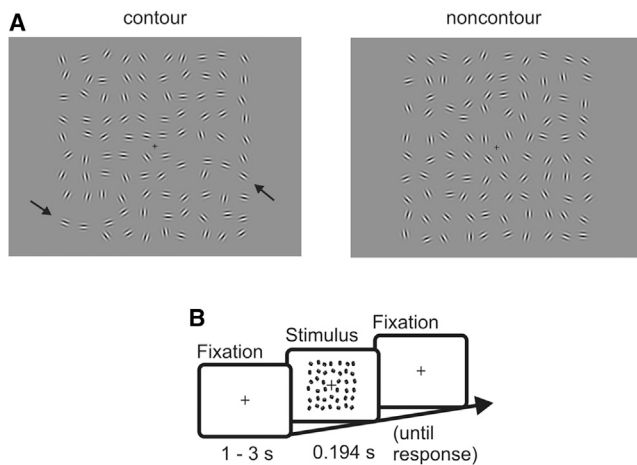


Figure 1. Stimuli and Procedure
Typical examples for contour and noncontour stimuli (A) and schematic depiction of a trial sequence (B).

between EEG phase and performance, we sorted single trials according to prestimulus phase (7 Hz; -250 ms), and we then averaged perception performance with a sliding moving window (Supplemental Experimental Procedures). As shown in Figure 2C, behavioral performance clearly followed an inverted cosine function, with perceptual performance being lowest at 0 and highest at $-\pi$ or π phase angles (circular-to-linear correlation; $\rho = 0.97$; $p < 0.001$; Figure 2C).

This phase difference between hits and misses was also observable in the ERP data, which showed a significant difference around 250 ms (~ 1.5 cycles at 7 Hz) prior to stimulus presentation (randomization test; $p_{\text{corr}} < 0.05$), with opposite polarities over frontocentral and left parieto-occipital electrodes (Figure 3A). This topography is suggestive of a parieto-occipital dipole structure (Figures 3B). Crucially, a similar effect emerged roughly 145 ms later (105 ms; < 1 cycle prior to stimulus presentation; Figure 3A). Additional analyses on the ERP difference waveforms (misses $-$ hits) revealed a peak at around 7 Hz in the prestimulus interval (Figure 3C),

and applying a notch filter centered at 7 Hz reduced this difference considerably (Figure S2A). To minimize the possibility that the observed phase differences at 7 Hz were driven by saccades, we performed a control analysis on vertical and horizontal electro-oculogram (EOG) signals. Contrasting oscillatory amplitudes between hits and misses for these EOG signals revealed no significant difference ($p_{\text{corr}} > 0.5$), suggesting that the observed phase effects were not driven by saccades (Figures S2B and S2C). Together, these data suggest that the phase difference is indeed driven by a 7 Hz oscillation. Note that even though stimulus duration in the current experiment covered more than one cycle of a 7 Hz oscillation [17], the phase at stimulus onset nevertheless determines how many duty cycles, i.e., open windows for neural communication, a stimulus will encounter during its presentation, thereby impacting on perceptual integration (see Figure S3).

Prestimulus Phase Effect Is Generated in Occipital and Parietal Regions and Gates BOLD

To examine the sources generating the prestimulus phase difference (-280 to -220 ms), we applied source localization over this interval to both the ERP for hits and the ERP for misses, making use of the individual MRI scans of each subject, and contrasted the resulting source reconstructions (see Supplemental Experimental Procedures). The results revealed that the prestimulus phase difference was indeed generated in visual processing regions in the left occipital cortex and the right superior parietal cortex (Figure 4A). We next investigated whether prestimulus phase influenced activity in visual processing regions [18], by calculating correlations between EEG phase (7 Hz; -250 ms; averaged over significant fronto-central electrodes) and the blood oxygen level-dependent (BOLD) signal on a single-trial level. Since phase is a circular variable, we used the cosine function of the phase values as a single-trial modulator of the BOLD signal. A specific effect of phase on BOLD amplitude emerged in the right intraparietal sulcus (rIPS; \sim BA 7; Montreal Neurological Institute [MNI] coordinates: $x = 30$, $y = -51$, $z = 63$; $p_{\text{uncorr}} < 0.001$; $k > 10$ voxels; Figure 4B), where the BOLD signal closely followed an inverted cosine function (Figure 4B). Paralleling the behavioral results, BOLD signal was highest when the stimulus was presented

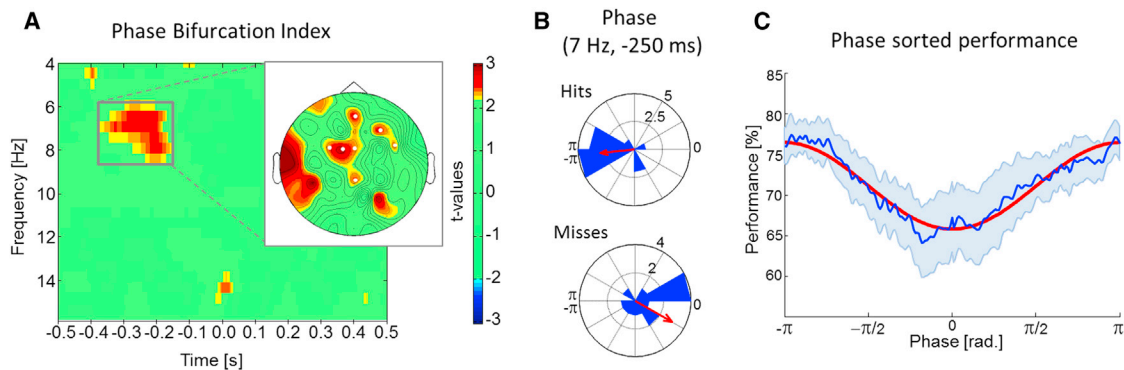


Figure 2. Ongoing Phase Modulates Perception

(A) Significant differences between hits and misses as measured by the phase bifurcation index (accumulated across all electrodes) are plotted in the time (x axis) and frequency (y axis) domains. A significant cluster (p corrected for multiple comparisons) emerged centered at 7 Hz and 250 ms prior to stimulus presentation and showed a frontocentral and left parietal topography.

(B) The prestimulus phase direction averaged across all subjects is shown for the electrodes highlighted in (A). Hits clustered around $-\pi$ or π , whereas misses clustered around 0.

(C) Performance sorted according to prestimulus phase (7 Hz; 250 ms; same electrodes as in B) is plotted (blue). The best-fitting inverted cosine function is shown in red. The shaded area represents the mean SE.

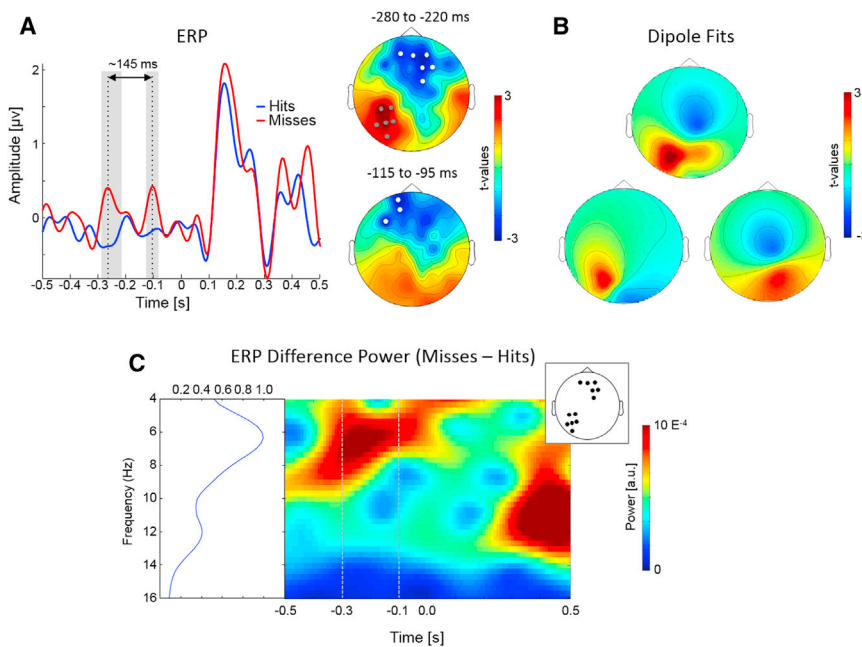


Figure 3. Event-Related Potential Results and Dipole Fits

(A) The event-related potential (ERP) averaged over frontocentral electrodes (white dots in the upper adjacent topography). The topographies of the prestimulus differences -280 to -220 ms (top) and -115 to -95 ms (bottom) between hits and misses are shown on the right. Significant electrodes are highlighted.

(B) Results of the dipole simulation. The upper plot shows the best-fitting topography (-280 to -220 ms) predicted by two dipoles: one in the left LO1, and one in the right intraparietal sulcus (rIPS). Dipole locations were derived from the peak voxels obtained by the fMRI analysis (Figure 4). The residual variance of the dipole fit was 0.252, indicating that nearly 75% of the variance could be explained by these two dipoles. The lower plot shows the best-fitting topographies separately for the left occipital dipole (left) and the right parietal dipole (right). Note that neither of these two dipoles could fit the real topography adequately alone.

(C) The time-frequency transformation (power) of the ERP difference waveforms (misses $-$ hits) is shown in the upper panel for the electrodes showing a significant difference in the ERP (highlighted in the right inset). a.u., arbitrary units.

at the optimal phase ($-\pi$ or π), compared to when the stimulus was shown at the nonoptimal phase (0). Accordingly, prestimulus phase at 7 Hz appears to gate activity in the intraparietal sulcus. No effect was observed in the opposite direction (i.e., $-\pi$ or $\pi < 0$), and no effect in any other brain region emerged. Additionally, we tested whether the parietal effect was driven by differences between detected (hits) and undetected (miss) stimuli rather than prestimulus phase. However, no significant effects were obtained in this analysis (threshold $p_{\text{uncorr}} < 0.001$; $k > 10$ voxels) in any direction (hits $>$ misses or misses $>$ hits) in any brain region, suggesting that the BOLD signal was indeed primarily driven by the prestimulus 7 Hz phase.

Prestimulus Phase Predicts Bidirectional BOLD Connectivity between Visual Processing Regions

Central to our hypothesis, the effect of prestimulus phase on information transfer between the rIPS and lower visual processing regions was examined in a two-step analysis. In a first step, the effect of prestimulus phase on BOLD functional connectivity (measured via BOLD correlation) was investigated by means of a psychophysiological interaction analysis (PPI [19]; Supplemental Experimental Procedures). PPI addresses the question of whether functional connectivity between a seed region and any other brain region is modulated by an independent variable. In the present study, rIPS served as a seed region, and the phase at 7 Hz, 250 ms prior to stimulus presentation, was the independent variable. For this analysis, single trials were split into quartiles depending on prestimulus phase ($-\pi$ or π ; $-\pi/2$; 0; $\pi/2$), and BOLD connectivity was then compared between the quartile corresponding to the most optimal ($-\pi$ or π) and the least optimal (0) phase. Following our hypothesis, PPI was restricted to the occipital cortex (see Figure S4B for whole-brain analysis). The only region where connectivity with the rIPS was predicted by prestimulus phase (Figure 4C) was in the posterior part of the left lateral occipital complex, LO1 (\sim BA 19; MNI coordinates: $x = -36$; $y = -87$; $z = 12$). Area LO1 holds a retinotopic

representation of the visual input and, in contrast to the anterior section of the lateral occipital complex, is selective for simple features like orientation [11]. Strikingly, when the stimulus was presented during the least optimal phase at 0, there was virtually no functional connectivity between left LO1 and rIPS, whereas pronounced functional connectivity was evident when the stimulus was shown during the optimal phase at $-\pi$ or π (Figure 4D). Having established functional connectivity between rIPS and left LO1, we used dynamic causal modeling (DCM; [20]) in a second step to test whether the prestimulus phase affected information transfer between the two regions in a bottom-up, top-down, or bidirectional manner. Importantly, DCM for fMRI data relies on not only temporal order but also the spatiotemporal structure of the input signal and can thus detect subtle changes in directionality [21] as evaluated with invasive electrophysiology [22]. The DCM analysis provided strong evidence for models implementing an effect of phase on bidirectional information flow (random effects analysis on family level; exceedance probability = 0.89; Figure S4A).

Discussion

The current results demonstrate that prestimulus phase of a low-frequency oscillation at 7 Hz predicts perceptual performance and effective connectivity between higher- and lower-level visual processing regions. The fMRI BOLD signal is tightly coupled to the firing rates of neurons and high-frequency oscillatory amplitudes [23, 24], suggesting that the BOLD signal represents a proxy of the output of a neural assembly. Moreover, it was demonstrated that ongoing low-frequency oscillations gate neural firing [25] and high-frequency oscillations [26, 27]. Extending these previous studies, our results suggest that the ongoing phase at 7 Hz synchronizes the neural output between task-relevant distributed cortical cell assemblies. This central result corroborates the recently proposed communication-through-coherence hypothesis [7], suggesting that oscillations route cortical information flow

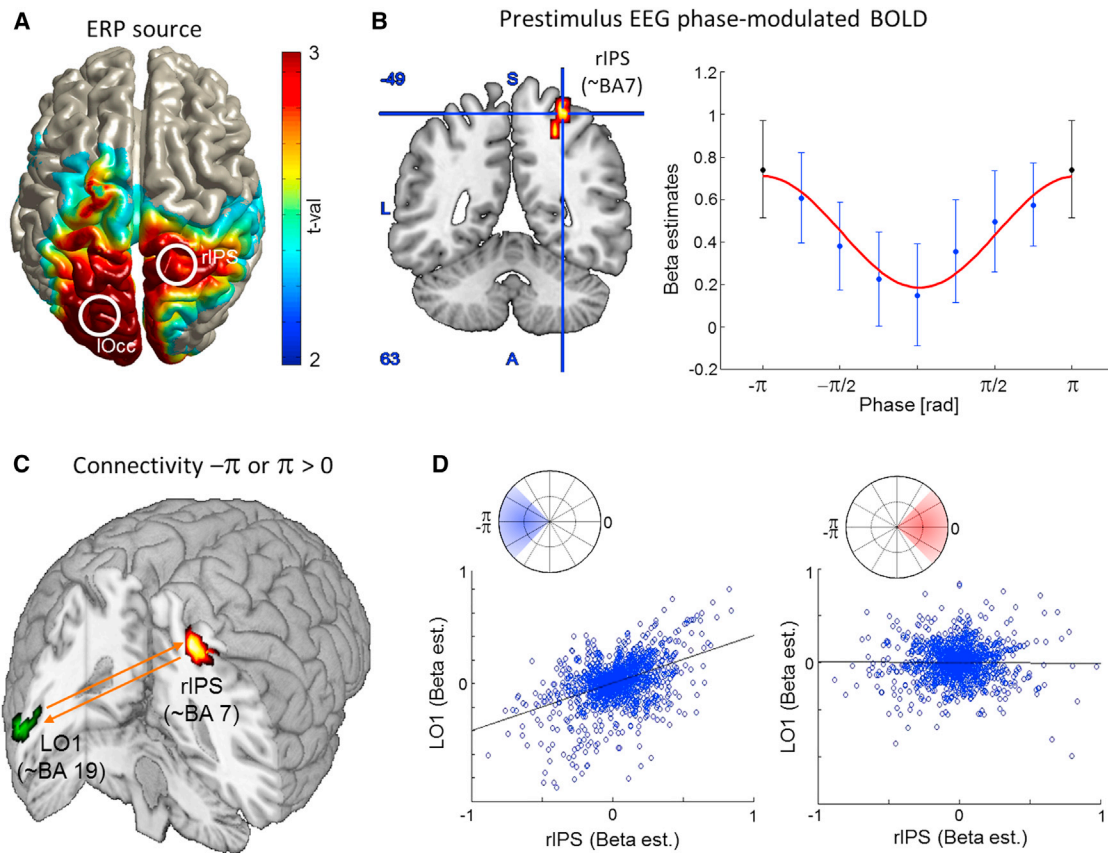


Figure 4. Prestimulus Phase Difference Is Generated in Parietal and Occipital Brain Regions and Modulates Parietal BOLD Signal and Connectivity

(A) The source localization of the prestimulus ERP difference (280–220 ms; linearly constrained minimum variance beamformer) between hits and misses. (B) The BOLD signal in the rIPS was modulated by prestimulus phase (7 Hz; -250 ms; $p < 0.001$; $k > 10$ voxels). The plot on the right shows the beta estimates of eight phase bins in the rIPS (blue) together with a fitted inverted cosine function (red). Note that the data points corresponding to $-\pi$ and π are identical (black dots). Error bars represent mean SE.

(C) When a stimulus was shown during the optimal phase ($-\pi$ or π), connectivity between rIPS and left LO1 was significantly higher ($p < 0.001$; > 10 voxels) compared to when the stimulus was shown during the nonoptimal phase (0). DCM analysis (Figure S4A) indicated that phase influenced information flow between LO1 and IPS in a bidirectional manner (orange arrows).

(D) Connectivity is shown by means of BOLD (normalized beta estimates) correlation plots for the optimal ($-\pi$ or π) and nonoptimal phase bin (0). Note that the BOLD correlation between LO1 and IPS was virtually absent when in the nonoptimal phase bin.

[28–30]. Crucially, however, our findings demonstrate that even when synchronized, two task-relevant brain regions will transmit information only during the optimal, putatively excitatory phase and not during the nonoptimal, inhibitory phase. These time windows for information transfer determine the perception of an incoming near-threshold stimulus.

Several prior studies demonstrate the importance of 10 Hz oscillations, the classical alpha band, for perceptual gating [3, 31–33]. The findings reported here emerged in the 7 Hz range, which falls in between the theta (~ 5 Hz) and alpha (~ 10 Hz) bands but replicates previous behavioral and EEG findings [2, 15, 16]. Future studies will need to investigate whether the two frequency bands play differential roles for perception, possibly depending on the task or stimulus material used. Other prestimulus events might impinge on the perception as well. For example, the cortical transfer of visual information is suppressed shortly before and during saccadic eye movements [34]. Saccadic suppression, even though unlikely to have an influence on the effects reported here, can therefore render a stimulus invisible even if it is shown at the optimal phase within the 7 Hz cycle.

Although the IPS preferentially connects to occipital areas within the same cerebral hemisphere [35], our results show an interhemispheric flow of information between the left area LO1 and rIPS during contour perception. Gabor arrays as used in the current experiment contain information on different spatial scales, from local details to global stimulus configurations. The lateralized pattern of activity mimics a known hemispheric specialization for processing local level (left) and global level (right) visual information that is prevalent within occipital and parietal areas [36–38]. Given this hemispheric difference, the present results indicate that a global percept emerges dynamically from interhemispheric communication between higher and lower visual brain structures. LO1 neurons are sensitive for orientation [11, 39] and colinearity [40–42], thus coding information on a more local scale. By synchronizing neural activity between this area and the parietal cortex, the firing rates of LO1 neurons at the relevant locations can be enhanced [14, 43], making the contour elements more salient and facilitating their segregation from the background. Presumably, contour segments can be integrated via this mechanism across space, according to their orientation as a local grouping cue.

Together, the present results suggest that a low-frequency oscillatory signal at 7 Hz dynamically opens and closes the time windows for sensory information transfer between lower-level occipital and higher-level parietal brain regions. Presumably, in the present perceptual integration task, ongoing phase modulated the likelihood of integrating distributed local features into a coherent stimulus representation, which can be consciously perceived and reported by the participant. This interpretation fits with neural models of consciousness stating that conscious perception requires the ignition of long-distance neural loops [44]. Considering that phase-modulated information exchange is bidirectional, our results suggest that both feedforward and feedback connections are required for the perceptual integration of distributed stimulus features [14]. Remarkably, the frequency in which we found these effects exactly matches the behavioral time constant of visual sampling [1, 2], suggesting that the oscillatory gating of information transfer between cortical regions underlies the rhythmic nature of our visual system.

Experimental Procedures

Stimuli and Procedure

The study was approved by the ethics committee of the University of Regensburg (reference number 10-101-0035). Stimuli were arrays or Gabor elements that did or did not contain a path of collinear-oriented elements (“contour” or “noncontour”; Figure 1A). Details for the generation of the stimuli are given in the [Supplemental Experimental Procedures](#). Prior to the EEG-fMRI experiment, a preliminary behavioral test was conducted outside of the scanner to determine the stimulus parameters such that each subject reached a performance of 75% hits.

EEG Recording and Analysis

The EEG was recorded inside the scanner using an MR-compatible 64-channel EEG system (Brain Products). Sixty-two channels were used to record scalp EEG (sampling rate 5 kHz) and were mounted in an elastic cap (EasyCap, Herrsching-Breitbrunn) positioned according to the international 10-10 system. The EEG was initially referenced to FCz and later rereferenced to average reference. The clock of the EEG amplifier was synchronized to the clock output of the MR scanner using a SynchBox device (Brain Products) to facilitate offline removal of the MR gradient artifact. Artifacts induced by the MRI scanner were removed carefully using the FMRIB plug-in for EEGLAB running under MATLAB (The Mathworks; see [Supplemental Experimental Procedures](#)).

fMRI Recording and Analysis

Imaging was performed using a 3 T MR head scanner (Siemens Allegra). For fMRI, 2,226–2,286 whole-brain volumes, consisting of 34 axial slices, were acquired in three sessions using an interleaved, standard T2*-weighted echo-planar imaging sequence (time repetition [TR] = 2000 ms; time echo [TE] = 30 ms; flip angle 90°; 64 × 64 matrices; in-plane resolution 3 × 3 mm; slice thickness 3 mm). Image preprocessing and statistical analysis were carried out using SPM5 and SPM8 (Wellcome Department of Cognitive Neurology, London; <http://www.fil.ion.ucl.ac.uk/spm>), running under MATLAB.

Supplemental Information

Supplemental Information includes four figures and Supplemental Experimental Procedures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2013.09.020>.

Author Contributions

S.H. and G.V. carried out the experiments. S.H. and G.V. analyzed the data with help from M.W. and S.S.D. S.H., G.V., and M.W.G. designed the experiment and wrote the manuscript with help from all authors.

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References

1. Landau, A.N., and Fries, P. (2012). Attention samples stimuli rhythmically. *Curr. Biol.* 22, 1000–1004.
2. VanRullen, R., Carlson, T., and Cavanagh, P. (2007). The blinking spotlight of attention. *Proc. Natl. Acad. Sci. USA* 104, 19204–19209.
3. Romei, V., Gross, J., and Thut, G. (2012). Sounds reset rhythms of visual cortex and corresponding human visual perception. *Curr. Biol.* 22, 807–813.
4. Vanrullen, R., Busch, N.A., Drewes, J., and Dubois, J. (2011). Ongoing EEG phase as a trial-by-trial predictor of perceptual and attentional variability. *Front. Psychol.* 2, 60.
5. Hanslmayr, S., Gross, J., Klimesch, W., and Shapiro, K.L. (2011). The role of α oscillations in temporal attention. *Brain Res. Brain Res. Rev.* 67, 331–343.
6. Jensen, O., Bonnefond, M., and VanRullen, R. (2012). An oscillatory mechanism for prioritizing salient unattended stimuli. *Trends Cogn. Sci.* 16, 200–206.
7. Fries, P. (2005). A mechanism for cognitive dynamics: neuronal communication through neuronal coherence. *Trends Cogn. Sci.* 9, 474–480.
8. Field, D.J., Hayes, A., and Hess, R.F. (1993). Contour integration by the human visual system: evidence for a local “association field”. *Vision Res.* 33, 173–193.
9. Livingstone, M., and Hubel, D. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science* 240, 740–749.
10. Tootell, R.B., Hadjikhani, N.K., Mendola, J.D., Marrett, S., and Dale, A.M. (1998). From retinotopy to recognition: fMRI in human visual cortex. *Trends Cogn. Sci.* 2, 174–183.
11. Larsson, J., and Heeger, D.J. (2006). Two retinotopic visual areas in human lateral occipital cortex. *J. Neurosci.* 26, 13128–13142.
12. Robertson, L.C. (2003). Binding, spatial attention and perceptual awareness. *Nat. Rev. Neurosci.* 4, 93–102.
13. Mevorach, C., Humphreys, G.W., and Shalev, L. (2006). Opposite biases in saliency-based selection for the left and right posterior parietal cortex. *Nat. Neurosci.* 9, 740–742.
14. Roelfsema, P.R. (2006). Cortical algorithms for perceptual grouping. *Annu. Rev. Neurosci.* 29, 203–227.
15. Busch, N.A., Dubois, J., and VanRullen, R. (2009). The phase of ongoing EEG oscillations predicts visual perception. *J. Neurosci.* 29, 7869–7876.
16. Busch, N.A., and VanRullen, R. (2010). Spontaneous EEG oscillations reveal periodic sampling of visual attention. *Proc. Natl. Acad. Sci. USA* 107, 16048–16053.
17. Wyart, V., and Sergent, C. (2009). The phase of ongoing EEG oscillations uncovers the fine temporal structure of conscious perception. *J. Neurosci.* 29, 12839–12841.
18. Scheeringa, R., Mazaheri, A., Bojak, I., Norris, D.G., and Kleinschmidt, A. (2011). Modulation of visually evoked cortical fMRI responses by phase of ongoing occipital alpha oscillations. *J. Neurosci.* 31, 3813–3820.
19. Friston, K.J., Buechel, C., Fink, G.R., Morris, J., Rolls, E., and Dolan, R.J. (1997). Psychophysiological and modulatory interactions in neuroimaging. *Neuroimage* 6, 218–229.
20. Friston, K.J., Harrison, L., and Penny, W. (2003). Dynamic causal modeling. *Neuroimage* 19, 1273–1302.
21. Stephan, K.E., Penny, W.D., Moran, R.J., den Ouden, H.E.M., Daunizeau, J., and Friston, K.J. (2010). Ten simple rules for dynamic causal modeling. *Neuroimage* 49, 3099–3109.
22. David, O., Guillemain, I., Saittet, S., Rey, S., Deransart, C., Segebarth, C., and Depaulis, A. (2008). Identifying neural drivers with functional MRI: an electrophysiological validation. *PLoS Biol.* 6, 2683–2697.

23. Logothetis, N.K., Pauls, J., Augath, M., Trinath, T., and Oeltermann, A. (2001). Neurophysiological investigation of the basis of the fMRI signal. *Nature* 412, 150–157.
24. Mukamel, R., Gelbard, H., Arieli, A., Hasson, U., Fried, I., and Malach, R. (2005). Coupling between neuronal firing, field potentials, and FMRI in human auditory cortex. *Science* 309, 951–954.
25. Haegens, S., Nàcher, V., Luna, R., Romo, R., and Jensen, O. (2011). α -Oscillations in the monkey sensorimotor network influence discrimination performance by rhythmical inhibition of neuronal spiking. *Proc. Natl. Acad. Sci. USA* 108, 19377–19382.
26. Schroeder, C.E., and Lakatos, P. (2009). Low-frequency neuronal oscillations as instruments of sensory selection. *Trends Neurosci.* 32, 9–18.
27. Canolty, R.T., Edwards, E., Dalal, S.S., Soltani, M., Nagarajan, S.S., Kirsch, H.E., Berger, M.S., Barbaro, N.M., and Knight, R.T. (2006). High gamma power is phase-locked to theta oscillations in human neocortex. *Science* 313, 1626–1628.
28. Saalmann, Y.B., Pinsk, M.A., Wang, L., Li, X., and Kastner, S. (2012). The pulvinar regulates information transmission between cortical areas based on attention demands. *Science* 337, 753–756.
29. Bressler, S.L. (1996). Interareal synchronization in the visual cortex. *Behav. Brain Res.* 76, 37–49.
30. Varela, F., Lachaux, J.P., Rodriguez, E., and Martinerie, J. (2001). The brainweb: phase synchronization and large-scale integration. *Nat. Rev. Neurosci.* 2, 229–239.
31. Mathewson, K.E., Gratton, G., Fabiani, M., Beck, D.M., and Ro, T. (2009). To see or not to see: prestimulus alpha phase predicts visual awareness. *J. Neurosci.* 29, 2725–2732.
32. Callaway, E., 3rd, and Yeager, C.L. (1960). Relationship between reaction time and electroencephalographic alpha phase. *Science* 132, 1765–1766.
33. Varela, F.J., Toro, A., John, E.R., and Schwartz, E.L. (1981). Perceptual framing and cortical alpha rhythm. *Neuropsychologia* 19, 675–686.
34. Vallines, I., and Greenlee, M.W. (2006). Saccadic suppression of retinotopically localized blood oxygen level-dependent responses in human primary visual area V1. *J. Neurosci.* 26, 5965–5969.
35. Bray, S., Arnold, A.E.G.F., Iaria, G., and Macqueen, G. (2013). Structural connectivity of visuotopic intraparietal sulcus. *Neuroimage* 82, 137–145.
36. Han, S., Weaver, J.A., Murray, S.O., Kang, X., Yund, E.W., and Woods, D.L. (2002). Hemispheric asymmetry in global/local processing: effects of stimulus position and spatial frequency. *Neuroimage* 17, 1290–1299.
37. Moses, P., Roe, K., Buxton, R.B., Wong, E.C., Frank, L.R., and Stiles, J. (2002). Functional MRI of global and local processing in children. *Neuroimage* 16, 415–424.
38. Weissman, D.H., and Woldorff, M.G. (2005). Hemispheric asymmetries for different components of global/local attention occur in distinct temporo-parietal loci. *Cereb. Cortex* 15, 870–876.
39. Larsson, J., Landy, M.S., and Heeger, D.J. (2006). Orientation-selective adaptation to first- and second-order patterns in human visual cortex. *J. Neurophysiol.* 95, 862–881.
40. Altmann, C.F., Bühlhoff, H.H., and Kourtzi, Z. (2003). Perceptual organization of local elements into global shapes in the human visual cortex. *Curr. Biol.* 13, 342–349.
41. Kourtzi, Z., Tolias, A.S., Altmann, C.F., Augath, M., and Logothetis, N.K. (2003). Integration of local features into global shapes: monkey and human FMRI studies. *Neuron* 37, 333–346.
42. Shpaner, M., Molholm, S., Forde, E., and Foxe, J.J. (2013). Disambiguating the roles of area V1 and the lateral occipital complex (LOC) in contour integration. *Neuroimage* 69, 146–156.
43. Roelfsema, P.R., and Houtkamp, R. (2011). Incremental grouping of image elements in vision. *Atten. Percept. Psychophys.* 73, 2542–2572.
44. Dehaene, S., Changeux, J.-P., Naccache, L., Sackur, J., and Sergent, C. (2006). Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends Cogn. Sci.* 10, 204–211.