Behavioral/Cognitive

Reduced Occipital Alpha Power Indexes Enhanced Excitability Rather than Improved Visual Perception

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Several studies have demonstrated that prestimulus occipital alpha-band activity substantially influences subjective perception and discrimination of near-threshold or masked visual stimuli. Here, we studied the role of prestimulus power fluctuations in two visual phenomena called double-flash illusion (DFI) and fusion effect (FE), both consisting of suprathreshold stimuli. In both phenomena, human subjects' perception varies on a trial-by-trial basis between perceiving one or two visual stimuli, despite constant stimulation. In the FE, two stimuli correspond to veridical perception. In the DFI, two stimuli correspond to an illusory perception. This provides for a critical test of whether reduced alpha power indeed promotes veridical perception in general. We find that in both, DFI and FE, reduced prestimulus occipital alpha predicts the perception of two stimuli, regardless of whether this is veridical (FE) or illusory (DFI). Our results suggest that reduced alpha-band power does not always predict improved visual processing, but rather enhanced excitability. In addition, for the DFI, enhanced prestimulus occipital gamma-band power predicted the perception of two visual stimuli. These findings provide new insights into the role of prestimulus rhythmic activity for visual processing.

Introduction

Despite physically constant sensory stimulation, subjective perception can vary substantially across subjects. Subjective perception can also vary within individual subjects on a trial-by-trial basis or over time, for example in ambiguous, bistable visual stimuli. It has been shown that peristimulus fluctuations of rhythmic neuronal activity are related to changes of subjective perception (Rodriguez et al., 1999; Parkkonen et al., 2008). In recent years, there has been cumulative evidence that also modulations of ongoing rhythmic neuronal activity before sensory stimulation can influence perception of the subsequent stimulus (van Dijk et al., 2008; Hipp et al., 2011; Keil et al., 2012). Especially ongoing rhythmic activity in the alpha-band (~10 Hz) has drawn much attention recently. Some studies have found the power of prestimulus alpha-band activity in parieto-occipital areas to correlate negatively with the subjective perception in visual detection and discrimination tasks (Worden et al., 2000; Hanslmayr et al., 2007; van Dijk et al., 2008; Wyart and Tallon-Baudry, 2009; Romei et al., 2010). Other studies have found prestimulus alpha-power in the visual and somatosensory domain to correlate to perception and poststimulus evoked responses as an inverted-U function: intermediate levels of alpha-power enhance perception and evoked responses while low and high levels have a negative effect (Linkenkaer-Hansen et al., 2004; Zhang and Ding, 2010; Rajagovindan and Ding, 2011; Lange et al., 2012). In addition, prestimulus gamma-band power has been shown to influence perception (Wyart and Tallon-Baudry, 2009).

Alpha-band power is modulated by attention (Worden et al., 2000; Thut et al., 2006; Haegens et al., 2011; Rajagovindan and Ding, 2011; van Ede et al., 2011) and has been linked to inhibition of task irrelevant areas (Händel et al., 2011; Jensen and Mazaheri, 2010). Similarly, gamma-band power is modulated by attention (Fries et al., 2001b, 2008; Bauer et al., 2006; Buffalo et al., 2011; Kahlbrock et al., 2012). Both processes are believed to gate neuronal processing and thus increase neuronal stimulus processing in task related neuronal groups (Fries, 2005; Fries et al., 2007; Romei et al., 2008a; Schroeder and Lakatos, 2009; Jensen and Mazaheri, 2010). Specifically, decreased prestimulus alpha-band power has been interpreted by some studies to improve visual perception in the sense that it leads to better detection performance of near threshold stimuli or more veridical perception in visual discrimination tasks (Hanslmayr et al., 2007; van Dijk et al., 2008; Mathewson et al., 2009; Wyart and Tallon-Baudry, 2009; Romei et al., 2010).

Here, we study prestimulus rhythmic neuronal activity in two phenomena called double-flash illusion (DFI) and fusion effect (FE). In the visuotactile DFI, subjects receive one visual stimulus accompanied by two tactile stimuli, and this stimulation is misperceived as two visual stimuli (Violentyev et al., 2005; Lange et al., 2011). By contrast, the FE occurs when two visual stimuli are

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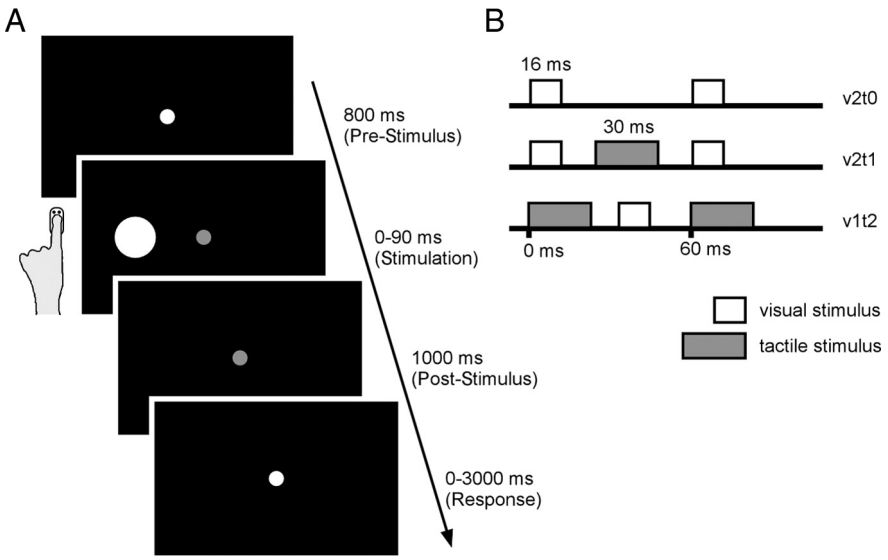

Figure 1. Illustration of the paradigm. ***A***, Each trial started with the presentation of a central fixation. The luminance of the dot decreased and 800 ms later, visuotactile stimulation followed. The visual stimulus was a white disc (2.5° diameter) that appeared at 17° eccentricity in the left hemifield. Tactile stimulation was applied to the left index finger. After stimulation, only the fixation dot was visible for another 1000 ms before subjects were allowed to respond with their right hand. ***B***, Illustration of stimulation sequences for the critical conditions v2t0, v2t1, and v1t2. Visual stimuli (white rectangles) were presented for 16 ms, tactile stimuli (gray rectangles) for 30 ms.

presented with no or one tactile stimulus, and this stimulation is misperceived as a single visual stimulus (McCormick and Mamassian, 2008). In both the FE and the DFI, varying perception occurs in the face of constant physical stimulation. The comparison of the DFI and the FE provides for a critical test: If reduced prestimulus alpha-band activity indeed promotes veridical perception in general, it should reduce illusory misperception in both the DFI and the FE. Here, we test this prediction using MEG recordings in 33 subjects.

Materials and Methods

Subjects

Thirty-three right-handed volunteers [15 male, mean age (± SD) 22.2 ± 2.8 years] participated in this study. All participants had normal or corrected-to-normal vision and no known history of neurological disorders. The experiment was approved by the local ethics committee, and each subject gave written informed consent before the experiment, according to the Declaration of Helsinki.

Paradigm and stimuli

Paradigm and stimuli were reported in detail previously (Lange et al., 2011). Here, we will present a comprehensive overview; for details, see the study Lange et al. (2011).

Subjects were lying in supine position with their head placed inside the MEG helmet while they received visuotactile stimulation. Visual stimuli were presented via a projector (60 Hz refresh rate) placed outside the magnetic shielded room and backprojected via a mirror system on a translucent screen. The visual stimulus consisted of a gray disc (2.5° diameter) presented 17° left of the center of the screen. The luminance of the disc was adjusted individually (average across subjects 2.3 cd/m^2) to obtain balanced responses during illusion trials (see below). Visual stimuli were presented for one monitor frame (16 ms). Tactile stimuli were presented via a piezoelectric stimulation device (Metec) that was taped to the subjects' left index finger. The device consisted of 4 × 2 pins that were raised simultaneously for 30 ms. To mask clicking sounds produced by the stimulator, subjects' hands and the stimulator were covered by sound attenuating foam and subjects received white noise via headphones.

Each trial began with the presentation of a central gray fixation dot (Gaussian of diameter 0.5°, luminance 7 cd/m^2). A decrease of luminance served as a warning cue and after 800 ms visuotactile stimulation began (Fig. 1*A*). Stimulation consisted of 0, 1, or 2 visual stimuli, accompanied by 0, 1, or 2 tactile stimuli. We will address the different conditions as "vxty" for a condition with x visual and y tactile stimuli, e.g., conditions potentially showing the DFI effect are labeled v1t2. We applied all nine combinations of visuotactile stimulations in random order. In the critical condition v2t0 the onset of both visual stimuli was separated by 60 ms (Fig. 1*B*). In the bimodal conditions v1t2 and v2t1, stimuli were presented in the order t-v-t (v-t-v, respectively), with the onset of the two tactile (visual) separated by 60 ms and the visual (tactile) stimulus presented in between. We used only the stimulation order t-v-t for v1t2 trials (Fig. 1*B*). This choice was motivated by a previous study on the auditory–visual DFI (Shams et al., 2002). This study had shown that perception of the DFI occurs if the visual stimulus is presented in between the two auditory stimuli (or simultaneous to one auditory stimulus) and that the gap of the onsets of visual and auditory stimuli needs to be within ±70 ms.

After stimulation, only the fixation dot was visible for 1000 ms before its luminance increased, indicating the start of the response period (Fig. 1*A*). Subjects were asked to report how many visual stimuli they perceived while ignoring tactile stimulation. Responses were given by button presses with the thumb, index, and middle finger of right hand. After button press or maximally 3000 ms, the next trial started.

Overall, each condition was presented in 100 trials. To increase statistical power, the condition v1t2 was presented 200 times. The trials were presented in 10 blocks with each block containing all nine conditions (v1t2 twice) in pseudorandom order. After 10 blocks, subjects were allowed to take a short self-paced break.

The experiment was controlled using the software "Presentation" (Neurobehavioral Systems).

MEG and MRI recordings

Electromagnetic brain activity was recorded using a 151-channel MEG system for 22 subjects and a 275-channel MEG system for the other 11 subjects (both CTF Systems). Data from the 275-channel system were interpolated to a common 151-channel template using a procedure that was also used to compensate for differences in subjects' head position (for details, see Preprocessing, below) (Lange et al., 2011).

Subjects were measured in supine position. An electro-oculogram (EOG) was recorded for offline detection of eye-movements. MEG/EOG data were low-pass filtered at 300 Hz and sampled continuously at a rate of 1200 Hz. Subjects' head position relative to the sensor array was determined before and after the recording session by measuring the position of reference coils placed at the subjects' nasion and at the left and right ear canals.

Structural MR images were acquired using standard T1-weighted sequences on a 1.5 T or 3 T whole-body scanner (Siemens). MRI and MEG data were aligned according to reference coils at nasion and at the left and right ear canals.

Data analysis

Preprocessing. Data were analyzed using FieldTrip (Oostenveld et al., 2011), Matlab (MathWorks), and SPM8 (Litvak et al., 2011).

To average the data from the 275-channel and the 151-channel system, the individual subjects' MEG data were interpolated to a common 151-channel-template position for the MEG sensors with respect to the head (for details, see Lange et al., 2011). Power line noise was removed using a Fourier transformation of 10-s-long signal periods and subtracting the

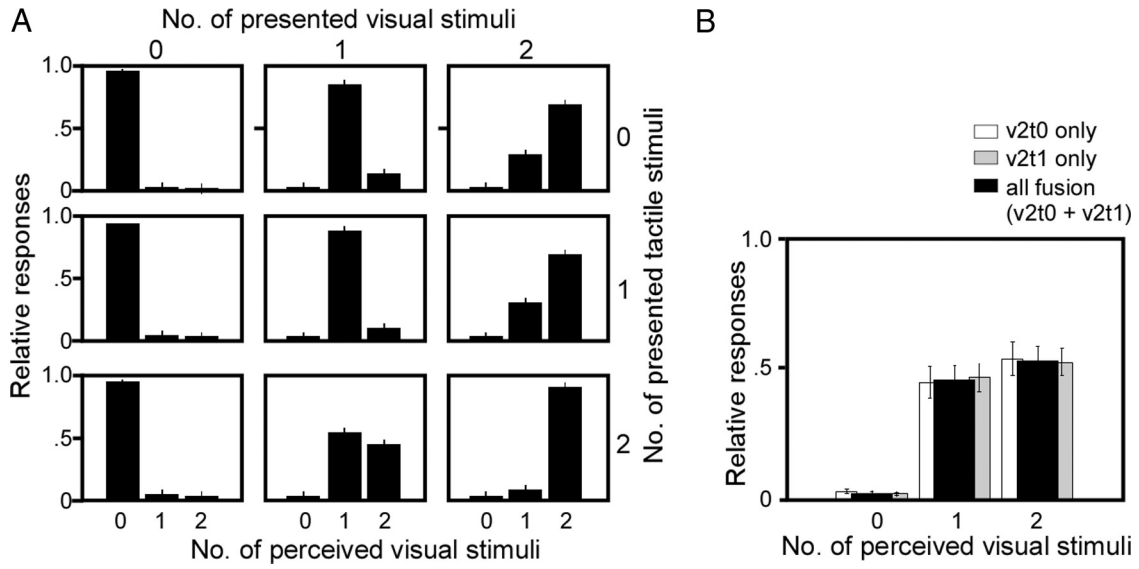

Figure 2. Behavioral results. ***A***, Relative proportion of subjective reports for all nine conditions, averaged across all 33 subjects. ***B***, Subjective reports for conditions v2t0 (white bars), v2t1 (gray bars), and pooled across both conditions (fusion trials, black bars), averaged across all 17 subjects showing a reliable fusion effect.

50, 100, and 150 Hz components. Artifacts caused by eye-movements, muscle activity, or sensor jumps were removed using a semiautomatic procedure. Trials shorter than 800 ms were completely rejected. Trials in which subjects gave no response or the response was given too early (i.e., within the 1000 ms poststimulus period) were also rejected.

Time-frequency analysis. We analyzed spectral power in two distinct frequency ranges. For the low-frequency range (4–40 Hz), we applied a discrete Fourier transformation on sliding temporal windows with a length of 400 ms, shifted in steps of 20 ms. Data segments were tapered with a single Hanning window resulting in a spectral smoothing of $\sim\pm 2.5$ Hz. For the high-frequency range (40–150 Hz), we used time windows of 200 ms length, shifted in steps of 20 ms. We applied a multitaper approach to the respective analysis windows to optimize spectral concentration over the frequency of interest (Mitra and Pesaran, 1999). We applied 11 Slepian tapers resulting in a spectral smoothing of $\pm$ 30 Hz. Spectral power was first estimated per trial and taper and then averaged across trials and tapers.

The focus of the present study was on the effect of prestimulus rhythmic neuronal activity on visual perception. We defined regions of interest (ROIs) in sensor space for the visual domain as defined in our previous study (Lange et al., 2011): The ROI for visual processing was defined by taking the 10 occipital MEG sensors overlying visual cortex centrally and contralaterally to stimulus presentation that revealed the strongest poststimulus effects in the alpha-, beta-, and gamma-band in response to visual stimulation (sensors RO21, RO22, RO31, RO32, RO33, RO41, RO42, ZO01, LO31, LO32).

Additionally, we studied effects in the somatosensory domain. We defined sensors of interest as defined in our previous study (Lange et al., 2011), i.e. by taking the 10 sensors over somatosensory areas contralateral to tactile stimulation showing the strongest poststimulus effects in response to tactile stimulation (sensors RC13, RC14, RC15, RC21, RC22, RC23, RC24, RC31, RC32, RP34).

Statistical analysis of spectral power. Subjects frequently misperceived trials of the condition v1t2 as two visual stimuli (DFI trials). In addition, subjects frequently reported only one visual stimulus in the conditions v2t0 and v2t1 (FE trials, Fig. 2).

We performed two statistical analyses. First, we sorted all trials of the condition v1t2 into DFI (2 stimuli perceived) and non-DFI (1 perceived) trials. Second, we pooled trials of the conditions v2t0 and v2t1 and sorted the trials into fusion (1 perceived) and nonfusion (2 perceived) trials. Pooling the two conditions was motivated by the fact that they showed very similar proportions of perceptual fusions (Fig. 2) and very similar effects in the time-frequency analyses. Statistical comparison was performed by first pooling spectral power over sensors of interest for each subject individually. This was done separately for DFI, non-DFI, FE, and non-FE trials. Next, we compared DFI to non-DFI and non-FE to FE trials, i.e., we always compared conditions with two perceived stimuli to conditions with one perceived stimulus. Within each subject, we computed a time-frequency-wise independent samples t test between the conditions compared in a given contrast, leading to a time-frequency t-map. For the actual statistical inference, these t-maps were forwarded to a group-level statistics where the consistency of the effect across subjects was tested by using a nonparametric randomization test (Maris and Oostenveld, 2007). The t-maps were pooled across subjects. Pooled values were thresholded at a value of $t = 1.96$, and neighboring time-frequency-points exceeding this threshold were clustered. Values within a cluster were summed, giving our cluster-level test statistic. Under the null hypothesis, the conditions compared in the t-maps can be randomly exchanged. Therefore, we generated a randomization distribution by inverting the t-map sign of a random subset of subjects before pooling. The cluster-statistics were recomputed for these new group-level pooled t-maps. By repeating this step 1000 times, a randomization distribution of cluster-level test-statistics was computed and the test statistics of the observed clusters were compared with this randomization distribution (for details, see Lange et al., 2011). This nonparametric approach avoids assumptions about underlying distributions, implements a random effect analysis, and corrects for multiple comparisons across time and frequency (Maris and Oostenveld, 2007).

For significant time-frequency clusters, we further studied the relation of prestimulus rhythmic activity to subjective perception. For each subject separately, we averaged prestimulus power over the sensor-ROI, and over the significant time-frequency bins. Based on these averages and separately per subject, we sorted the trials and divided into quartiles. Averaged perception rates were calculated for each quartile and normalized per subject by subtracting the mean perception rate across all trials [similar to the studies by van Dijk et al., 2008; Lange et al., 2012]. To study linear trends, a linear regression was fitted to the data. Detection rates in quartiles were statistically compared by repeated-measures ANOVA and *post hoc t* tests. The comparison was performed separately for the condition v1t2 and the combined conditions v2t0 and v2t1.

Source reconstruction. To determine the cortical sources of the significant time-frequency clusters identified on sensor level, we applied a beamforming approach in the frequency domain (Gross et al., 2001).

To this end, the brain was discretized into a three-dimensional grid. Leadfield matrices were computed for each grid location using a realistic single-shell volume conduction model based on the individual MRIs (Nolte, 2003). The grid locations were determined for individual subjects by the following procedure: First, a regular grid with a resolution of 1 cm

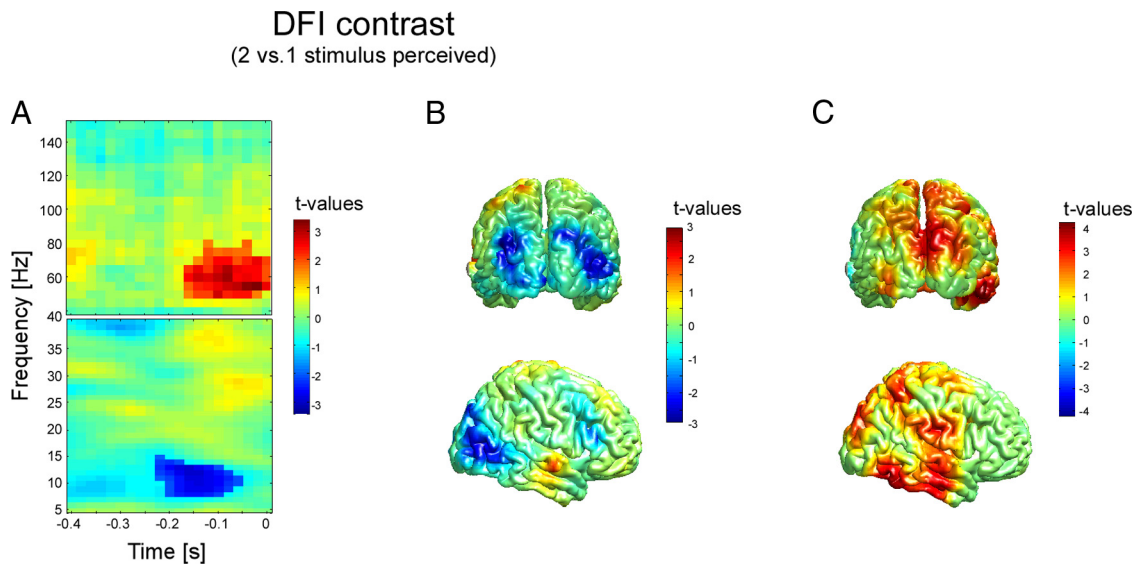

Figure 3. Results of the DFI contrast in visual sensors. ***A***, Time-frequency representations on sensor level. $t = 0$ indicates the onset of the first stimulation. ***B***, Source reconstruction projected on the MNI template brain for the significant effect in the alpha-band (~10 Hz in ***A***) viewed from the back (top row) and right (bottom row). ***C***, Same as in ***B*** but now for the significant effect in the gamma-band (~60 Hz in ***A***). Time-frequency representations and source plots are masked to highlight significant clusters. Red colors indicate greater spectral power in trials when subjects perceived two visual stimuli (i.e., the DFI) compared with trials in which they perceived one stimulus. Color bars apply to the significant (nonmasked) pixels/voxels.

was created in the Montreal Neurological Institute (MNI) template brain. Individual subject's structural MRIs were linearly warped into this template MRI and the inverse was applied to the template grid, resulting in individual grids. The advantage of this approach is that group level results can be computed by averaging results per grid point. Spatial filters were constructed for each grid location based on leadfield and cross spectral density (CSD) matrices. CSD matrices were computed between all MEG pairs for the time period and frequency of interest. Time-frequency bands of interest were determined by the significant clusters of the abovementioned time-frequency analysis on sensor level. For each contrast (DFI vs non-DFI and nonfusion vs fusion), we first pooled all trials of the respective condition (v1t2 or v2t0 and v2t1) and computed a common filter per subject and condition. Next, the single trials of each condition were projected through the respective filter and sorted according to subjective perception. Statistical comparison was performed in line with the statistical comparison on the sensor level except that clusters were now based on spatiotemporal proximity rather than on time-frequency proximity. Source parameters estimated this way per subject were statistically tested across subjects (see above) and group results were plotted on the MNI template brain.

Inter-trial coherence. To study the role of phase entrainment, we computed intertrial coherence (ITC). ITC is a measure of phase consistency across trials. We measured ITC in the prestimulus period separately for trials in which subjects perceived two stimuli and for trials in which subjects perceived one stimulus. At each time t and frequency f, the we computed ITC following the formula (Busch et al., 2009):

$$\mathrm{ITC}_{t,f} = \frac{1}{k}\sum_{n=1}^{k} e^{-i\varphi_{k(t,f)}},$$

with k the number of trials. The number of trials was stratified between conditions. ITC was computed in two ways: averaged across the whole prestimulus period or in sliding time windows of 300 ms length in steps of 20 ms. Differences of ITC between conditions (two vs one stimulus perceived) were statistically tested using the randomization approach described above.

Interaction metrics: coherence and power correlation. To quantify interactions between visual and somatosensory channels, we calculated two metrics: coherence and power correlation.

Coherence quantifies the consistency of phase differences between two signals and across multiple trials (Siegel et al., 2008; Schoffelen et al., 2011). If phase differences are random, coherence tends toward zero. If all trials have the same phase difference, coherence can reach one. Power correlation is the Pearson correlation coefficient between the trial-by-trial fluctuations in the power (at the same frequency) of two signals (Nieuwenhuis et al., 2012).

Results

Behavioral data

Subjects made only negligible errors when reporting the number of visual stimuli in six of the nine conditions (Fig. 2*A*). However, in trials with one visual stimulus paired with two tactile stimuli (v1t2), subjects perceived a second, illusionary visual stimulus in 43.0 ± 3.3% (mean ± SEM) of the trials, which constitutes the double flash illusion (DFI). By contrast, in trials with two visual stimuli paired with no (v2t0) or one tactile stimulus (v2t1), subjects missed one visual stimulus (the fusion trials) in 29.3 ± 5.8% and 30.8 ± 4.5%, respectively, which constitutes the FE. Closer inspection of the behavioral data revealed that 16 out of 33 subjects did not experience an FE, i.e., they reliably perceived two visual stimuli in the majority of trials (>90%). For the remaining 17 subjects who experienced a reliable FE, the fusion occurred on 44.3 ± 6.2% (v2t0) and 46.2 ± 5.4% (v2t1) of the trials. Since the stimulation conditions v2t0 and v2t1 revealed highly similar FEs, we pooled both conditions to a common "fusion" condition (Fig. 2*B*).

DFI contrast

To study the effect of prestimulus rhythmic activity on the perception of the DFI, we sorted trials of the condition v1t2 according to the subjective perception. We contrasted trials in which subjects reported two visual stimuli versus trials in which subjects reported one visual stimulus, despite physically constant stimulation.

In the time-frequency analysis of power in occipital MEG sensors (see Materials and Methods for details), we found a significant negative cluster between 8–15 Hz and −220 to −60 ms ($p < 0.05$), i.e., alpha-power was significantly decreased in the prestimulus period if subjects perceived the DFI after the subse-

quent stimulation (Fig. 3*A*). The cortical sources of this effect were localized to bilateral visual areas (Brodmann areas 17, 18, 19), extending on the right hemisphere (contralateral to stimulus presentation) to more ventrolateral sites (Fig. 3*B*).

In addition, we found prestimulus gamma-band (50–80 Hz) power to be significantly enhanced for DFI trials compared with non-DFI-trials between −180 and 0 ms (Fig. 3*A*). Source localization of this effect revealed a widespread network of cortical areas, covering bilateral occipitoparietal areas, right inferior temporal gyrus, as well as parts of middle and superior temporal gyrus, and finally right primary and secondary somatosensory cortex (Fig. 3*C*).

Prestimulus alpha-power (averaged between −200 and −80 ms and 8–12 Hz, sensor level) was negatively correlated with subjective perception rates ($r = 0.98$, $p < 0.05$), i.e., lower prestimulus alpha power predicted a higher probability to perceive the DFI (see Fig. 5*C*). An ANOVA revealed a significant difference between power bins ($p < 0.05$). *Post hoc* analysis revealed that perception rates were significantly larger in the first bin than in the third and fourth bin (both $p < 0.05$). In addition, prestimulus gamma-power (averaged between −180 and 0 ms and 50–70 Hz) showed a strong trend toward a positive correlation with subjective perception rates ($r = 0.94$, $p = 0.055$), i.e., higher prestimulus gamma-power tended to predict a higher probability to perceive the DFI. An ANOVA revealed a significant difference between power bins ($p < 0.05$). *Post hoc* analysis revealed that perception rates were significantly larger in the fourth bin than in the second ($p < 0.05$) and an almost significant trend between the fourth and first bin ($p = 0.055$) (see Fig. 5*A*).

Because the interval between warning signal and stimulus was fixed (800 ms), it was conceivable that some kind of phase entrainment may occur, which in turn might impact stimulus processing. Therefore, we quantified phase entrainment by computing intertrial coherence (Busch et al., 2009). No significant differences were found.

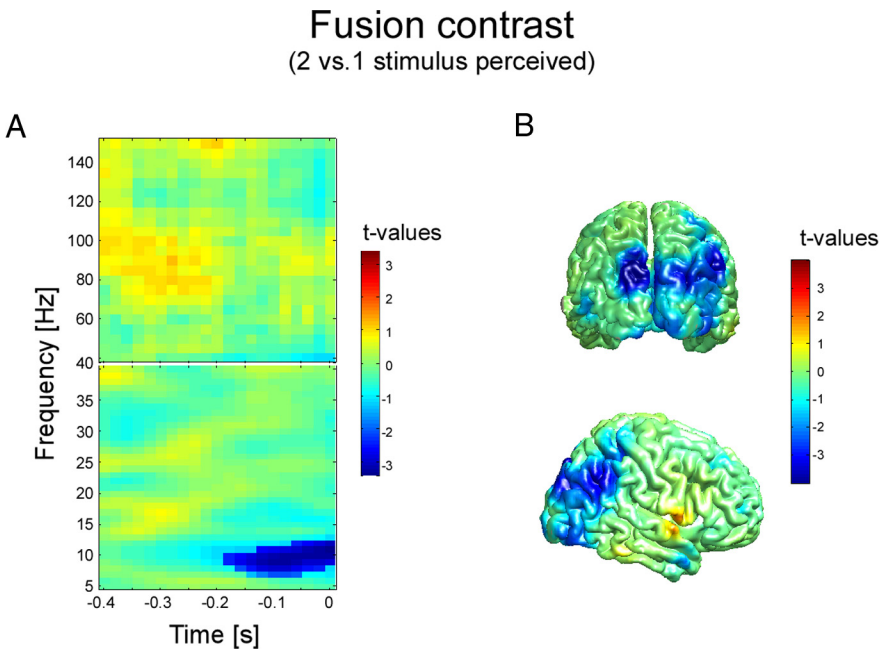

Figure 4. Results of the fusion contrast in visual sensors. ***A***, Same as in Figure 2*A* but now for the contrast two versus one stimulus perceived in the pooled fusion trials conditions (v2t0 and v2t1). ***B***, Source reconstruction of the significant effect in the alpha-band (~10 Hz in ***A***). All formats as in Figure 2.

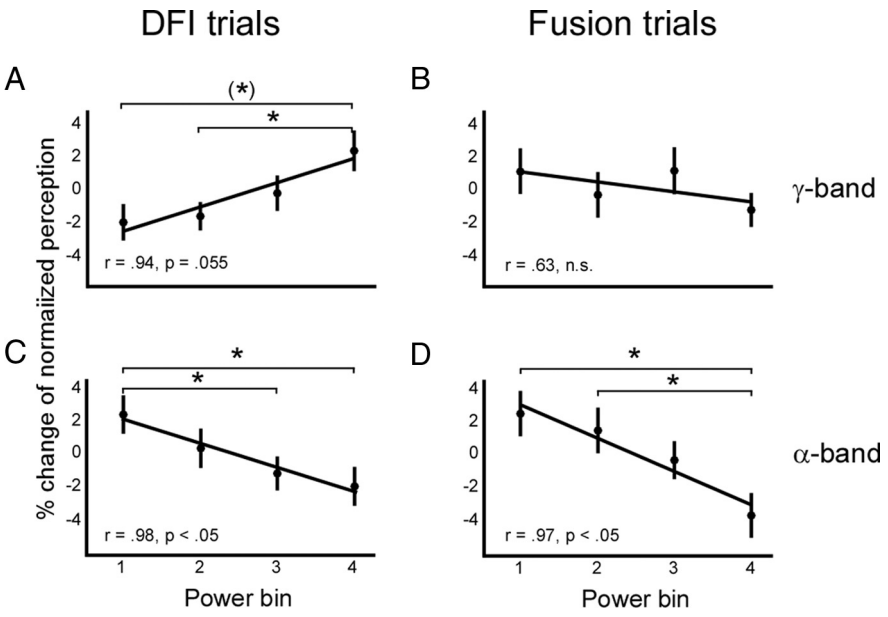

Figure 5. Results of the correlation analysis of spectral power and normalized subjective perception. Power was averaged for DFI trials in the gamma- (***A***) and alpha-band (***C***) or for the fusion trials in the gamma- (***B***) and alpha-band (***D***). $^{*}p < 0.05$; $^{(*)}p = 0.055$; n.s., not significant ($p > 0.05$). Insets show results of the regression analysis. Higher bin numbers indicate higher spectral power.

Time-frequency analysis in the somatosensory sensors (see Materials and Methods for sensor selection details) did not reveal any significant DFI effect (see Fig. 6*A*).

We also analyzed two different metrics of interaction between visual and somatosensory channels: coherence and power-power correlation. First, we calculated the average coherence between all possible pairs of visual and somatosensory channels in the same time-frequency range for which we had analyzed power. This did not reveal any significant DFI effect. Next, we calculated the average correlation between power fluctuations in all possible pairs of visual and somatosensory channels. This was again for the same time-frequency range and always considering somatosensory and visual sensor power of the same frequency. This analysis revealed a significant DFI effect: When subjects perceived two as compared to one flash, there was enhanced power correlation ~180 and 0 ms before stimulation and ranging from ~14–26 Hz (see Fig. 7*A*).

FE contrast

To study the effect of prestimulus rhythmic activity on the perception of the FE, we pooled trials of the conditions v2t0 and v2t1

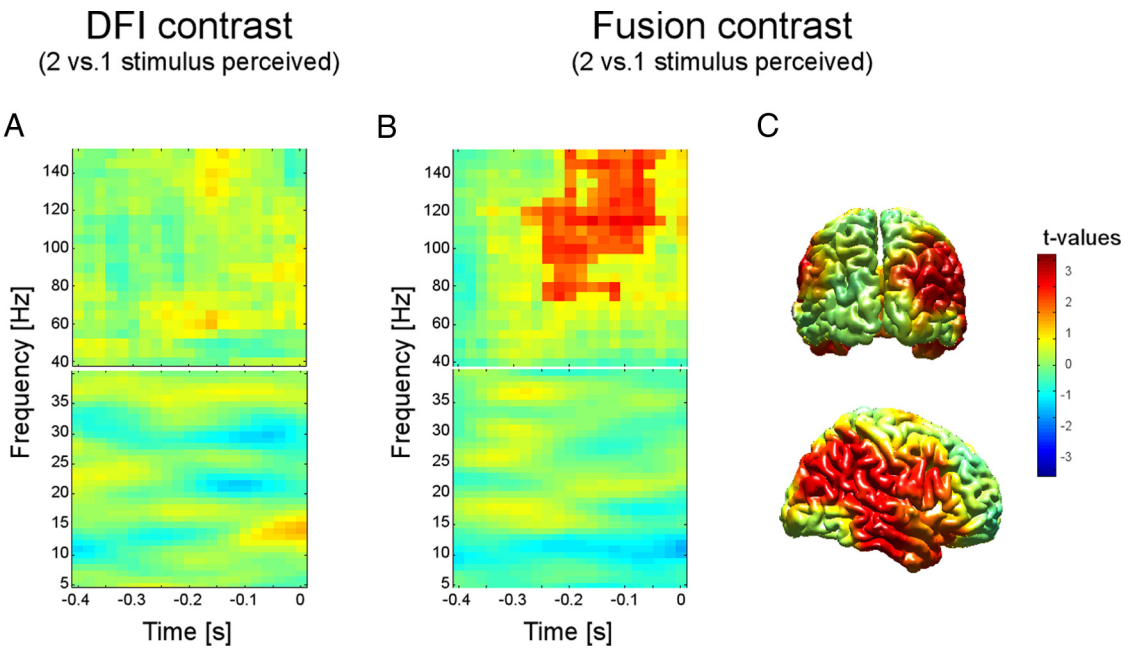

Figure 6. Results of the DFI and FE contrast in somatosensory sensors. ***A***, Time-frequency representations for the DFI contrast on sensor level. $t = 0$ indicates the onset of the first stimulation. ***B***, Time-frequency representations for the FE contrast on sensor level. ***C***, Source reconstruction projected on the MNI template brain for the significant effect in the gamma-band (70–150 Hz in ***B***) viewed from the back (top row) and right (bottom row). All formats as in Figure 3.

and sorted all trials according to the subjective perception. We contrasted trials in which subjects reported two visual stimuli versus trials in which subjects reported one visual stimulus. Analysis was restricted to the 17 subjects that showed a reliable fusion effect.

The time-frequency analysis of power in the same occipital MEG sensors as used for the DFI analysis revealed a significant negative cluster between −180 and 0 ms and 7–12 Hz ($p < 0.05$), i.e., alpha-power was significantly decreased in the prestimulus period if subjects perceived no fusion effect after the subsequent stimulation (Fig. 4*A*). The cortical sources of this effect were localized to bilateral visual areas (Brodmann areas 17, 18, 19), with the effect slightly lateralized to the right hemisphere (Fig. 4*B*). No significant effect was found for the high frequencies.

Prestimulus alpha-power (averaged between −180 and 0 ms and 8–12 Hz, sensor level) was negatively correlated with perception rates ($r = 0.97, p < 0.05$), i.e., lower prestimulus alpha power correlated with higher probability to perceive no FE (Fig. 5*D*). An ANOVA revealed a significant difference between power bins ($p < 0.05$). *Post hoc* analysis revealed that perception rates were significantly larger in the first and second bin than in the fourth bin (both $p < 0.05$). Gamma-band power (averaged between −180 and 0 ms and 50–70 Hz, see above analysis for DFI trials) showed no significant correlation to perception rates in the FE (Fig. 5*B*).

As for the DFI contrast, we tested for potential differences in intertrial coherence, but found no significant difference also for the FE contrast.

In somatosensory channels, a time-frequency analysis for the fusion effect revealed a significant positive cluster between −240 and −50 ms and 70–150 Hz, i.e., gamma-power was significantly increased in the prestimulus period if subjects perceived no fusion effect after the subsequent stimulation (Fig. 6*B*). The source reconstruction revealed that this effect was not specific to the somatosensory domain, but spread over a large right hemispheric network covering temporal, visual, and parietal areas (Fig. 6*C*).

Additionally, we analyzed average coherence and power correlation between all possible pairs of visual and somatosensory channels. This did not reveal any significant difference in the FE contrast (Fig. 7*B*).

Finally, we compared prestimulus alpha-power (averaged between −180 and 0 ms and 8–12 Hz) between the 17 subjects with FE and the 16 subjects without reliable FE. Prestimulus alpha-power was lower in subjects without FE than with FE ($p < 0.05$). This difference held when non-FE subjects were compared with FE subjects in trials with ($p < 0.01$) or without FE ($p < 0.05$) occurring (Fig. 8).

Discussion

We studied the influence of prestimulus rhythmic activity on subjective perception in two perceptual phenomena called DFI and FE. In both phenomena, subjective perception can vary on a trial-by-trial basis despite constant physical stimulation. In DFI trials, one visual stimulus was paired with two tactile stimuli, but subjects frequently perceived two visual stimuli. In FE trials, two visual stimuli were paired with zero or one tactile stimulus, but subjects frequently "fused" the two physical stimuli to one perceived stimulus. For both phenomena, we found that prestimulus power in visual areas in the alpha-band directly before the stimulation (~−200–0 ms) correlated with subjective perception, i.e., decreased alpha-power increased the likelihood to perceive two visual stimuli during constant physical stimulation. Interestingly, while in DFI trials, a power decrease predicted an illusory perception, in FE trials, a power decrease predicted a veridical perception. In addition, prestimulus (~200–0 ms) gamma-band power correlated positively with perception in DFI trials.

Several studies have reported an inverted-U relationship between on the one hand prestimulus alpha power and on the other hand stimulus evoked responses and/or behavioral performance, with intermediate alpha levels leading to largest responses and best performance (Linkenkaer-Hansen et al., 2004; Zhang and Ding, 2010; Rajagovindan and Ding, 2011; Lange et al., 2012).

Other studies have found that an enhanced detection performance for single visual stimuli is monotonically related to occipital prestimulus alpha-band power, with lower alpha levels leading to better performance (Thut et al., 2006; Hanslmayr et al., 2007; van Dijk et al., 2008; Mathewson et al., 2009). The precise reason for the discrepancy between these results is not yet known and requires future research. Our results from the FE analysis are in line with the studies reporting a monotonic relationship by demonstrating that trial-by-trial fluctuations of occipital prestimulus alpha-band power predict the temporal resolution of visual perception. Low temporal resolution (i.e., the fusion effect) was predicted by high alpha-power, while high temporal resolution (i.e., perception of two visual stimuli) was predicted by low alpha-power. This effect was visible both when we compared in individual subjects the trials with and without FE, and also when we compared subjects with FE to subjects not experiencing the FE: For a subgroup of subjects, which did not perceive FEs, we found absolute levels of alpha-power to be significantly decreased relative to subjects frequently experiencing the fusion effect. These findings are in line with previous studies arguing that reduced prestimulus alpha-power improves visual perception (van Dijk et al., 2008; Mathewson et al., 2009; Wyart and Tallon-Baudry, 2009; Jensen and Mazaheri, 2010; Jensen et al., 2012).

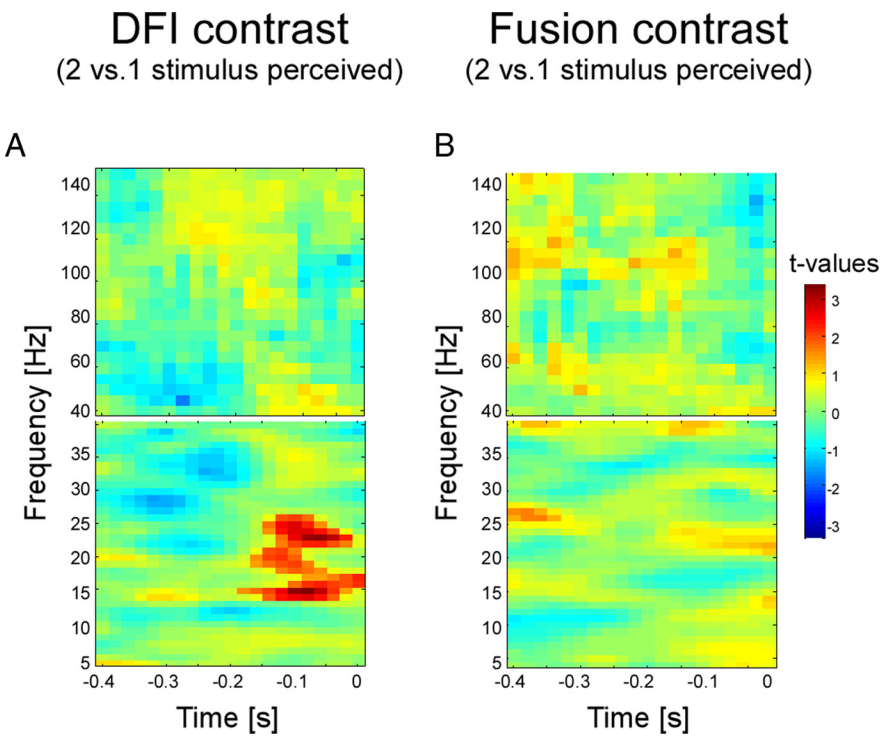

Figure 7. Results of the power correlation analyses. ***A***, Averaged difference in power correlation for the DFI contrast on the sensor level. Power correlation was computed between all predefined somatosensory and visual sensors (see Materials and Methods for sensor selection). $t = 0$ indicates the onset of the first stimulus. ***B***, Averaged difference in power correlation for the FE contrast. Time-frequency representation plots are masked to highlight significant clusters. Red colors indicate greater power correlation in trials in which subjects perceived two visual stimuli (i.e., the DFI) compared with trials in which they perceived one stimulus. Color bars apply to the significant (nonmasked) pixels.

Our analysis of the DFI effect revealed that reduced prestimulus alpha-band activity is not always related to improved perceptual performance in the sense of a more veridical perception. Rather, in trials with one visual stimulus paired with two tactile stimuli (v1t2, DFI trials), decreased occipital alpha-power promotes the perception of a visual illusion. We propose that reduced alpha-band power in general indexes enhanced excitability of visual cortex rather than improved visual perception per se. This hypothesis is in line with recent TMS-studies showing that a larger number of TMS-induced phosphenes are perceived when pre-TMS alpha-band power is reduced (Romei et al., 2008a,b, 2012). We suggest that enhanced excitability might render visual cortex in general more susceptible to input, including heteromodal input, e.g., from somatosensory cortex. If somatosensory activity induced by two tactile stimuli merges with low alpha-power in visual cortex, it is more likely to induce two visual sensations during the DFI, showing that increased excitability is not always related to more veridical visual perception.

Our analyses revealed also two effects in the gamma-frequency band. The time-frequency analyses of occipital sensors revealed that the perception of two flashes during DFI trials was predicted by enhanced prestimulus power in the gamma-band. The corresponding analysis of somatosensory sensors revealed that the perception of two flashes as compared with one in the fusion contrast was predicted by enhanced gamma-band power. The precise temporal and spectral extensions of these effects differed and the spatial extensions overlapped only partly. Yet, in both cases, prestimulus gamma power predicted the perception of two flashes. This is in line with previous studies linking prestimulus gamma-band activity to attention, enhanced excitability, and reduced neuronal and behavioral response times (Engel et al., 2001; Fries et al., 2001a,b; Gonzalez Andino et al., 2005). Prestimulus occipital gamma-band power is also posi-

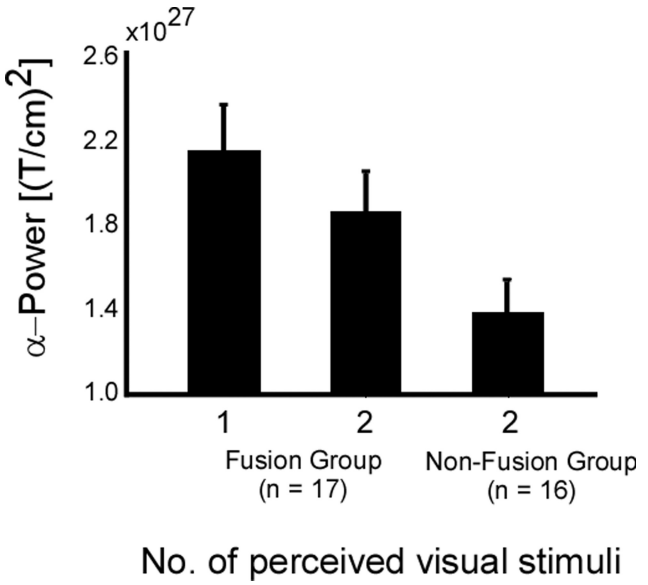

Figure 8. Absolute power levels in the alpha-band for subjects ($n = 17$) showing a reliable fusion effect (left and middle bar) and subjects ($n = 16$) showing no fusion effect. The fusion group was split into perceived 1 (left bar) and perceived 2 stimuli (middle bar). All bars are significantly different from each other ($p < 0.05$).

tively related to detection performance in a unimodal visual task (Wyart and Tallon-Baudry, 2008, 2009). The prestimulus gamma increase reported in these studies was highly similar in time and frequency to our observed gamma-band increase in the DFI contrast.

Our analysis of correlations between power fluctuations in somatosensory and visual regions revealed that the perception of two flashes in DFI trials was predicted by higher interareal power correlations in the beta-frequency band. This supports the hypothesis that the perception of the DFI is mediated by an interaction between visual and somatosensory cortex.

In summary, our results complement recent studies demonstrating that fluctuations of prestimulus rhythmic activity and interareal interactions are more than mere background noise, but substantially influence subjective perception despite constant physical stimulation. Our study critically extends previous studies in three aspects. First, we demonstrate within and across subjects that prestimulus alpha-power in visual cortex predicts the temporal resolution of visual perception: The lower the prestimulus alpha-power the more likely subjects perceive the veridical two stimuli. Second, we demonstrate that low prestimulus alpha-power is not always correlated to more veridical perception. During DFI trials, low prestimulus alpha-power correlated with an illusory perception of a second stimulus. We propose that prestimulus alpha power indexes excitability of visual cortex rather than improved perception per se. Low alpha-power renders visual cortex more susceptible to unimodal, but also heteromodal input, leading to improved perception in most cases, but to illusory perception in the case of DFI. In addition, we report fluctuations of prestimulus gamma-band power in a widespread network. Gamma-band power correlates with the perception of two flashes in both, the DFI and the FE contrast. Finally, we show that the DFI is preceded by enhanced beta-power correlation between visual and somatosensory regions. Taking these results together, we conclude that prestimulus fluctuations in power and power correlations play a functional role in unimodal and heteromodal perception.

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