

## COGNITIVE NEUROSCIENCE

# Spontaneous local alpha oscillations predict motion-induced blindness

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## Abstract

Bistable visual illusions are well suited for exploring the neuronal states of the brain underlying changes in perception. In this study, we investigated oscillatory activity associated with 'motion-induced blindness' (MIB), which denotes the perceptual disappearance of salient target stimuli when a moving pattern is superimposed on them (Bonneh *et al.*, 2001). We applied an MIB paradigm in which illusory target disappearances would occur independently in the left and right hemifields. Both illusory and real target disappearance were followed by an alpha lateralization with weaker contralateral than ipsilateral alpha activity (~10 Hz). However, only the illusion showed early alpha lateralization in the opposite direction, which preceded the alpha effect present for both conditions and coincided with the estimated onset of the illusion. The duration of the illusory disappearance was further predicted by the magnitude of this early lateralization when considered over subjects. In the gamma band (60–80 Hz), we found an increase in activity contralateral relative to ipsilateral only after a real disappearance. Whereas early alpha activity was predictive of onset and length of the illusory percept, gamma activity showed no modulation in relation to the illusion. Our study demonstrates that the spontaneous changes in visual alpha activity have perceptual consequences.

## Introduction

Perception depends not only on sensory input, but also on the actual state of the brain. What are the neuronal substrates of these brain states and how are they expressed in terms of measurable neuronal activity? Bistable visual illusions produce different perceptions, although the physical properties of the visual display remain unchanged. Thus, they are well suited for investigating the neuronal states of the brain underlying changes in perception. In this study, we investigated 'motion-induced blindness' (MIB), which denotes the perceptual disappearance of salient target stimuli when a moving pattern is superimposed on them (Grindley & Townsend, 1965; Bonneh *et al.*, 2001). As subjects fixate on the centre of the screen, the peripheral target stimuli seem to disappear randomly for periods of up to several seconds. It is now clear that MIB is neuronally induced and cannot be explained, for instance, by local retinal adaptation (Bonneh *et al.*, 2001; Hofstoetter *et al.*, 2004; Mitroff & Scholl, 2005; Caetta *et al.*, 2007).

Several mechanisms have been proposed to explain MIB. One possibility is that the moving pattern creates a filling-in effect, suppressing the perception of the targets (Ramachandran & Gregory, 1991). Such an explanation is supported by experiments using induced surfaces: if Kanizsa triangles were moved over the MIB targets, then the targets disappeared more frequently than on

non-induced surfaces (Graf *et al.*, 2002). Also, targets disappear more frequently and rapidly if they are perceived behind their surrounding region than if they are perceived in front of it (Hsu *et al.*, 2010). However, the filling-in account is challenged by other findings: if the target is surrounded by a background, which normally leads to the disappearance of filling-in effects, targets continued to disappear (Bonneh *et al.*, 2001). Additionally, whereas perceptual filling-in is enhanced when the luminance of the surrounding zone approaches that of the background, MIB is enhanced with increased contrast (Bonneh *et al.*, 2001; Hsu *et al.*, 2004). Therefore, although filling-in might be a factor, it does not explain all aspects of MIB.

A complementary explanation for the MIB illusion proposes competition for resources between the targets and the rotating pattern. If visual computational resources are low, a process comparable to a winner-take-all mechanism guided by attention might come into play, inducing the disappearance of the less salient input (Bonneh *et al.*, 2001). A well-known perceptual winner-take-all effect is observed in ocular rivalry. Interestingly, some features of MIB are shared with binocular and monocular rivalry (Bonneh *et al.*, 2001; Carter & Pettigrew, 2003; Caetta *et al.*, 2007; Kawabe *et al.*, 2007). Owing to mutual inhibitory competition underlying winner-take-all mechanisms, the MIB illusions might occur more often the more the stimuli compete (Scholvinck & Rees, 2009). This could explain the surprising finding that MIB occurs more frequently with an increase in target contrast (Bonneh *et al.*, 2001; Hsu *et al.*, 2004); that is, the more the two inputs compete, the greater the necessity to select one input over the other.

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Received 9 December 2013, accepted 29 July 2014

The aim of the current study was to identify the neuronal substrates associated with MIB. We specifically focused on oscillatory activity in the alpha band, which is thought to reflect local inhibition of neuronal processing (Klimesch *et al.*, 1999) [for reviews, see Klimesch *et al.* (2007); Thut & Miniussi (2009); Jensen & Mazaheri (2010); Foxe & Snyder (2011); Lopes da Silva (2013)]. This interpretation is supported by several lines of evidence. For instance, it has been demonstrated in numerous studies that alpha activity is reduced in task-relevant areas but increased in areas associated with distracting input (Foxe *et al.*, 1998; Fu *et al.*, 2001). Also, within one modality, when attentional resources are allocated to a specific location of input, alpha activity decreases contralateral to the relevant input while it increases ipsilaterally (Worden *et al.*, 2000; Yamagishi *et al.*, 2003; Kelly *et al.*, 2006; Rihs *et al.*, 2007; Haegens *et al.*, 2010; Snyder & Foxe, 2010). The level of alpha activity has direct consequences for performance (Ergenoglu *et al.*, 2004; Babiloni *et al.*, 2006; Hanslmayr *et al.*, 2007; van Dijk *et al.*, 2008; Haegens *et al.*, 2011). Not only does the local decrease in alpha activity predict performance, but so does the ipsilateral increase (Händel *et al.*, 2011). These findings support the notion that oscillatory activity in the alpha band reflects local functional inhibition [for an overview, see also Foxe & Snyder (2011)]. The suppression of processing is specifically important if the task at hand needs a lot of resources. Given that MIB can potentially be explained by competition between the rotating pattern and the targets, we predicted that the reduction in computational resources indicated by an alpha increase would make target disappearance more likely. Such a finding would strengthen the interpretation that competition for resources is partly responsible for MIB.

Whereas oscillatory alpha activity seems to reflect functional inhibition, activity in the gamma band more likely reflects actual processing. This is supported by a great number of human and animal studies [for overview, see, for example, Fries (2009) and Jensen *et al.* (2007)]. In humans, gamma activity is produced by moving visual input (Kreiter & Singer, 1992; Sokolov *et al.*, 1999; Kruse & Hoffmann, 2002; Hoogenboom *et al.*, 2006). However, gamma activity has also been shown to reflect illusory percepts: a human study based on the Kanizsa triangle illusion reported increased gamma activity over occipital sensors (Tallon-Baudry *et al.*, 1996; Herrmann *et al.*, 1999; Kaiser *et al.*, 2004). In the context of MIB, an interesting question is whether gamma activity reflects either the physical appearance or the perceptual change of the target stimuli.

Local changes in oscillatory activity in humans can be detected by the use of whole-head magnetoencephalography (MEG). This technique allows for recording of ongoing brain activity with a millisecond time resolution at fairly good spatial resolution (Hamalainen *et al.*, 1993). In this study, we implemented a version of the MIB paradigm in which two targets were presented such that the illusive disappearance could occur in the left and/or the right hemifield. This allowed us to identify hemispheric lateralization of oscillatory activity in the gamma and alpha bands. We investigate whether the lateralized brain activity was predictive of changes in visual perception.

## Materials and methods

Fourteen healthy subjects, four males and 10 females, with a mean age of  $23 \pm 3$  years, participated in the study. All subjects had normal or corrected-to-normal vision. The study was approved by the local medical ethical committee (committee for protection of human subjects of the Arnhem/Nijmegen region; CMO protocol number CMO2001/095). Informed consent was obtained from all subjects

according to the Declaration of Helsinki. Two subjects were excluded from further analysis because of significant differences in reaction times (RTs) between left and right disappearance.

### *Psychophysical task and eye movement control*

Subjects were seated upright in an MEG system and were instructed to sit as motionless as possible during the MEG recording. The MEG system was placed in a magnetically shielded room. The visual stimuli were rear-projected (LCD projector; frame rate, 60 Hz;  $1024 \times 768$  pixels) from outside the magnetically shielded room via mirrors onto a screen positioned at a viewing distance of 90 cm.

The visual stimuli were created with the psychophysics toolbox (PTB-3) for MATLAB (Fig. 1). A pattern composed of a blue grid ( $13^\circ \times 13^\circ$ ,  $8 \times 8$  equally spaced crosses) was rotated at  $\sim 50^\circ/s$  over a black screen. Subimposed were two target stimuli constructed of small ( $2^\circ \times 2^\circ$ ) rightwards-moving sine wave gratings (maximal contrast; speed,  $2^\circ/s$ ; spatial frequency, two cycles per degree) which were placed  $5^\circ$  to the left and the right and  $2^\circ$  above the centre of the rotating grid. The fixation dot changed colour from white to red and back with a frequency of 1 Hz, and was located  $4^\circ$  below the centre of the rotating grid. As described by Kawabe *et al.* (2007), the fixation dot can also disappear during a MIB paradigm. In order to minimize this possibility, they presented a fixation dot that was flickered at 1 Hz. We adopted this procedure. The fixation dot, rotating grid and moving gratings were displayed for 55 s. This period was followed by a 5-s pause during which only the fixation dot was shown. These 1-min epochs were presented 13 times within a block.

Subjects were instructed to focus on the fixation dot during the whole experiment, and to blink as little as possible during a 55-s trial period. Subjects also had to monitor the left and right targets, and report when the left target, the right target or both targets disappeared, and hold a left or a right button down, respectively, during the perceived disappearance. The left and right buttons were pressed with the right-hand index and middle fingers. During the illusion condition, target disappearance and reappearance were purely illusory. The onset and duration of these illusory disappearances were recorded via the button presses. The exact timing was played back as real disappearances in the control condition. Now subjects had to report the real disappearances and reappearances of the targets. This ensured that, during the control condition, both the timing and the number and distribution of button presses were identical. Each condition was presented blockwise, as an illusion condition followed by a control condition. A full experiment consisted of four blocks; that is, each condition was presented twice. There was a self-paced break between blocks.

In the following, a 'trial' refers to the period 0.5 s before and 1.5 s after the real or illusory disappearance of the target. Because MIB could also occur during the control condition, valid trials had neither a visual change (on the same or opposite side) nor a button press or button release. This strongly reduced the possibility of illusory disappearances for control trials. Trials in which the illusion was reported for both targets in the illusion condition were excluded from analysis.

### *MEG acquisition*

Neuromagnetic activity was recorded with a whole-head MEG system (CTF, Vancouver, BC, Canada) containing 275 first-order axial magnetic gradiometers and situated at the Donders Institute for Brain, Cognition and Behaviour in Nijmegen, The Netherlands. The

signals were sampled at a rate of 600 Hz and low-pass-filtered at 150 Hz. Recording was continuous. The subject's head location relative to the MEG sensors was measured before and after each session with marker coils placed at the nasion and the left and right ear canals. The horizontal and vertical electro-oculography data were co-registered with the MEG data for later detection of eye movements and blinks.

### Data processing

All analysis was performed in MATLAB 7.5.0 (The MathWorks) and the FIELDTRIP software package (<http://www.ru.nl/fcdonders/fieldtrip/>), a MATLAB-based toolbox for the analysis of electrophysiological data.

### Behavioural data and estimation of the time of illusory target disappearance

In the control condition, the time between a real disappearance (and reappearance) and the button press was calculated and averaged per subject. These values were used to estimate the time point of the illusory target disappearance ( $t = 0$  ms) and reappearance by subtracting this individual value from the RT in the illusion condition. The 2-s trials that are used in the following analysis were defined as 0.5 s before and 1.5 s after this estimated time point of illusion onset. For the control trials, the actual RTs were used. Over subjects, there was no significant difference in RTs between left and right answers and no significant difference in numbers of left and right disappearances.

### Preprocessing

Four sensors (MRF55, MRF56, MRF64, and MRF66) were excluded from analysis, owing to malfunction. In order to optimize analysis over subjects at the sensor level, the axial gradiometer information was converted to planar gradients (Bastiaansen & Knoche, 2000; van Dijk *et al.*, 2008). The horizontal and vertical components of the planar gradients were estimated at each sensor location by using the fields from the specific sensor and its neighbouring sensors. Importantly, the activity values for the horizontal and vertical components were summed for each sensor location after the spectral analysis (Osipova *et al.*, 2006). Planar gradiometers display mostly activity from sources that lie beneath the peak of the activation, whereas for axial sensors a single source would be displayed as a bipolar pattern. Changing the signal to a planar representation can therefore be very beneficial for comparing activity between subjects at a sensor level. Any linear trend and the mean of each trial were subtracted, and line noise was attenuated with a 50-Hz notch filter. Trials with ocular artefacts were removed if they had values exceeding four standard deviations (SDs) above the mean (the SD was calculated over trials).

### Spectral analysis

Time-frequency representations (TFRs) of low-frequency activity (4–40 Hz) were calculated by use of a 0.25-s sliding time window shifted in 0.1-s steps. After application of a Hanning window, the fast Fourier transforms were calculated. Frequencies increased in steps of 4 Hz. The activity in the gamma band (40–80 Hz) was estimated by first applying four Slepian tapers to the data per time window prior to the fast Fourier transformation (resulting in a frequency smoothing of  $\pm 10$  Hz). Only trials that showed a deviation in activity (calculated over whole trial within each frequency

band) below three times the mean SD were included for further analysis; that is, if any trial exceeded the mean + 3 SD border in any frequency band it was excluded. This approach resulted in a mean trial rejection of  $1.4 \pm 2$  SD per subject.

### The hemispheric lateralization index

The hemispheric lateralization of activity was calculated by contrasting the trials with respect to disappearances of left and right targets: for a given sensor, the power differences between left and right trials were calculated and then divided by the sum.

The alpha (8–12 Hz) and gamma (40–80 Hz) bands were analysed in detail, and were chosen on the basis of the data for the control condition, as these frequencies showed the strongest lateralization effects, namely in a time window from 0.4 to 0.6 s after target disappearance. Two parieto-occipital sensors were chosen that showed the strongest lateralization effect (positive or negative) for each side in the above-mentioned frequency bands and time window. This sensor selection was then also applied to the illusion condition (Fig. 2).

To statistically assess disappearance-specific effects for the control condition vs. the illusion condition, we performed a two-factor ANOVA, in which the first factor was a 250-ms time window before and after disappearance [250-ms time window centred 100 ms before and 400 ms after the (estimated) disappearance], and the second factor was illusion vs. real disappearance. The dependent variable was the lateralization of activity as described above. In a

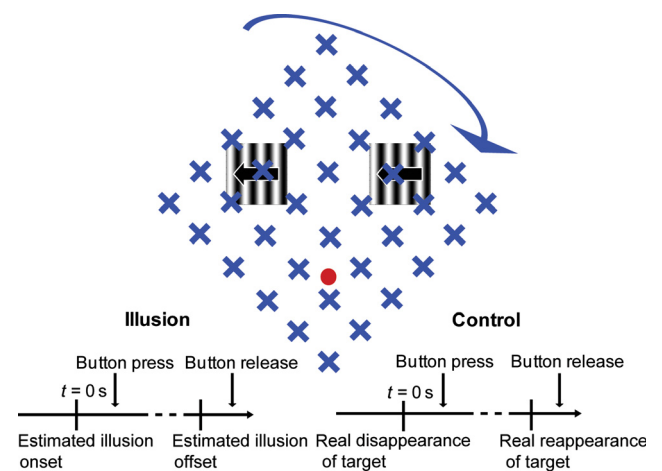


FIG. 1. Stimuli used for MIB. A pattern composed of a blue grid ( $13^\circ \times 13^\circ$ ,  $8 \times 8$  equally spaced crosses) was rotated at  $\sim 50^\circ/\text{s}$  over a black screen. Two target stimuli  $5^\circ$  to the left and the right and  $2^\circ$  above the centre were superimposed by the rotating grid. The target stimuli were constructed from small moving sine wave gratings ( $2^\circ \times 2^\circ$ ; speed,  $2^\circ/\text{s}$ ; spatial frequency, two cycles per degree). Subjects were instructed to fixate on a dot (changing colour from red to white at 1 Hz) placed  $4^\circ$  below the centre of the rotating grid, and had to indicate the disappearance of one or both targets by holding down the left, right or both buttons with the index and middle fingers of one hand. The experiment was composed of an illusion condition and a control condition. In the illusion condition, the targets were displayed continuously but were perceived by the subject as occasionally disappearing, owing to the illusion. In the control condition, the targets physically disappeared from the display. The timing, number and duration of disappearances were matched to the illusion condition. In the control condition, the time intervals between real target disappearance and button press were then used to estimate the onset of the illusory target disappearance per subject. Therefore,  $t = 0$  s refers to the exact time point of real disappearance and reappearance in the control condition, but to an estimation of illusory disappearance and reappearance in the illusion condition.

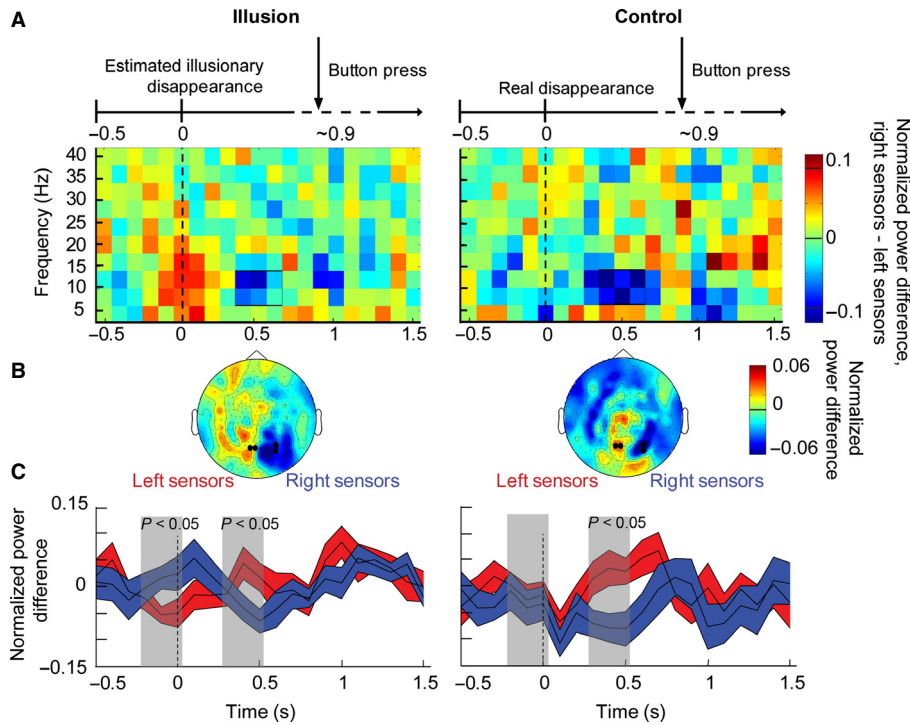


FIG. 2. Alpha activity during MIB. TFRs and topographies of alpha activity are shown separately for the illusion condition (left panels) and the control condition (right panels). (A) The timeline at the top indicates the trial timing. Note that  $t = 0$  s in the illusion condition marks the estimated onset of the illusory disappearance after correcting for the RT (as estimated from the control condition). In the control condition,  $t = 0$  s marks the physical disappearance of the target. The TFRs depict the normalized power difference, calculated as:

$$\frac{(\text{power}_{\text{left disappearance}}^{\text{left sensors}} - \text{power}_{\text{right disappearance}}^{\text{left sensors}}) / (\text{power}_{\text{left disappearance}}^{\text{left sensors}} + \text{power}_{\text{right disappearance}}^{\text{left sensors}}) - (\text{power}_{\text{left disappearance}}^{\text{right sensors}} - \text{power}_{\text{right disappearance}}^{\text{right sensors}}) / (\text{power}_{\text{left disappearance}}^{\text{right sensors}} + \text{power}_{\text{right disappearance}}^{\text{right sensors}})}{}$$

(B) The topographical distribution (combined planar gradient) of the normalized power difference is shown for the illusion and control conditions for time-frequency interval marked in A by a black box (8–12 Hz; 0.4–0.6 s). (C) The time course ( $\pm$ standard error over subjects) of the normalized power difference in the 8–12-Hz alpha band for the right and left sensor groups marked in B (black dots). Grey transparent boxes mark the time periods that were tested for significant differences [two-factor ANOVA: illusion vs. control, d.f. = 1,  $F = 5.35$ ,  $P = 0.041$ ; before disappearance (250-ms time window centred 100 ms before disappearance) vs. after disappearance (250-ms time window centred 400 ms after disappearance), d.f. = 1,  $F = 25.4$ ,  $P = 0.0004$ ] (*post hoc t*-test left vs. right sensors: illusion before,  $P = 0.039$ ; illusion during,  $P = 0.025$ ; control before,  $P = 0.69$ ; control during,  $P = 0.018$ ).

second step, we wanted to determine whether any specific frequency activation is predictive of the illusion. To this end, we calculated a linear regression between the length of the reported disappearance and the lateralization values assessed during the baseline period used previously, i.e.  $-0.1$  s before disappearance onset for the same sensor selection. We introduced an additional criterion, excluding all trials that exceeded the group mean plus three SDs in the reported length of disappearance. Additionally, stratification was introduced to secure the same number of trials for each subject, to exclude a more salient estimate (higher signal-to-noise ratio) if more trials were included.

## Results

### Behaviour

In the illusory condition, the subjects reported  $47 \pm 23$  and  $41 \pm 20$  disappearances exclusively in the left hemifield and in the right hemifield, with average durations of disappearance of  $928 \pm 1038$  ms and  $1022 \pm 919$  ms, respectively. There were no significant differences in trial number or trial length for left and right disappearances ( $P > 0.1$ ). Trials where the illusion appeared simultaneously on both sides were frequent but were excluded from the analysis.

In the control condition, the average durations of disappearance in the left and the right hemifields were, according to the study design, identical to the durations in the illusion condition. After artefact rejection, we ended up with  $37 \pm 23$  left and  $39 \pm 15$  right response trials in the illusion condition, with mean disappearance durations of  $1151 \pm 1712$  ms and  $1099 \pm 3185$  ms, respectively. There were no significant differences in disappearance duration or trial number between the control and illusion conditions. In the control condition, there was no significant difference in RT between left ( $681 \pm 76$  ms) and right ( $709 \pm 90$  ms) responses ( $P = 0.3$ ). These time intervals (between real target disappearance and button press) were then used to estimate the onset of the illusory target disappearance per subject. On the time axis in Fig. 2, time  $t = 0$  ms denotes the estimated disappearance of the left and the right targets.

### Results in the alpha band

When investigating the low-frequency bands, we considered the normalized power difference between left and right target disappearance. For each sensor, the activity values during right disappearance were subtracted from the activity values during left disappearance and divided by the sum. Fig. 2A shows the TFR of the activity modulation. The subsequent lateralization was then quantified by subtracting the normalized power differences in right selected sensors from those

in left selected sensors. The most salient effect was observed in the alpha band (8–12 Hz) in the 0.4–0.6-s interval after the target physically disappeared (control; right TFR) and during illusory target disappearance (illusion; left TFR). It reflected a contralateral decrease and an ipsilateral increase with respect to the hemifield of disappearance. Fig. 2B shows the topographical distribution of this alpha effect in the 0.4–0.6-s interval. The alpha modulation was strongest in posterior sensors for both the illusory and real target disappearance. Considering the sensors with the strongest alpha modulation in the control condition (marked in Fig. 2B as black dots), we next investigated the temporal evolution of alpha lateralization (Fig. 2C). In the illusion condition, we observed an early alpha lateralization preceding the estimated illusion onset by 100 ms. This early alpha activity was strongest contralateral to the disappearing target. In the control condition, no lateralization was observed prior to disappearance.

To statistically assess the disappearance-specific effects for the control condition vs. illusion condition, we performed a two-factor ANOVA in which one factor was the time before vs. time after disappearance (250-ms window, centred 100 ms before and 400 ms after the estimated illusion onset; see grey boxes in Fig. 2B). The other factor was illusion vs. real disappearance. The dependent variable was the lateralization index for the alpha band. The ANOVA showed a significant effect of both factors [illusion vs. control, degrees of freedom (d.f.) = 1,  $F = 5.35$ ,  $P = 0.041$ ; before vs. after disappearance, d.f. = 1,  $F = 25.4$ ,  $P = 0.0004$ ]. We did not find a significant interaction ( $F = 2.14$ ,  $P = 0.17$ ). *Post hoc t*-tests showed that the normalized alpha lateralization was significant in the illusion condition before ( $P = 0.039$ ) and after ( $P = 0.025$ ) illusory disappearance but, importantly, with different signs. In the control condition, the alpha lateralization was significant after the real disappearance ( $P = 0.018$ ) but not before ( $P = 0.69$ ). In summary, our data demonstrate a significant posterior lateralization in the alpha band predicting the onset of an illusory target disappearance. The lateralization was a consequence of stronger alpha activity contralateral to the target.

Next, we investigated whether the duration of disappearance could be explained by variations over subjects in alpha lateralization before disappearance onset. To this end, we correlated the normalized activity lateralization with the mean duration of the illusion. In order to exclude the possibility that the regression is affected by the different number of trials used per subject, we applied a stratification procedure whereby the same numbers of trials were randomly included for each subject. The linear regression was calculated during the pre-disappearance time period as used before (i.e. 250-ms time window centred 100 ms before the estimated illusory disappearance) and for the same sensors as indicated in Fig. 2B. This analysis revealed a significant regression between the alpha lateralization and the duration of the illusory disappearance (Fig. 3;  $P = 0.004$ ,  $R^2 = 0.58$ ,  $\beta = 6246$ ). There was no correlation for real disappearance or for the late time period (i.e. a 250-ms time window centred 400 ms after the estimated disappearance) of the illusion condition. In conclusion, subjects with stronger modulations in the hemispheric alpha band prior to the estimated illusion onset are also the subjects who perceive longer-lasting illusions.

### Results in the gamma band

The TFR of modulations in the gamma band (40–80 Hz) showed a contralateral increase and an ipsilateral decrease in the control condition (Fig. 4A). This lateralization effect was again most pronounced in the interval 0.4–0.6 s after the target physically disappeared (control, right TFR). However, it was absent during illusory target

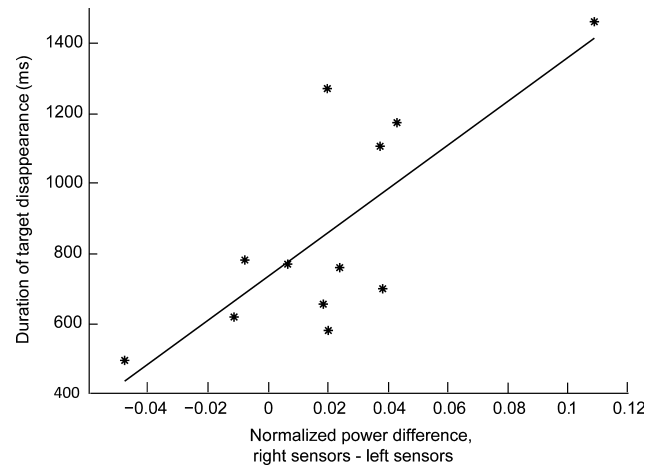


FIG. 3. Regression analysis of the early normalized alpha lateralization (250-ms time window centred 100 ms prior to the estimated target disappearance) and the duration of illusory target disappearances. Stratification was applied; that is, for each subject, the same number of trials was used. Subjects who perceived longer-lasting illusory target disappearance had stronger hemispheric alpha lateralization ( $P = 0.004$ ,  $R^2 = 0.58$ ,  $\beta = 6246$ ).

disappearance (illusion, left TFR). Fig. 4B shows the topographical distribution of the 40–80-Hz gamma activity during the time period of 0.4–0.6 s. The main effect occurred in occipital sensors. As the effect was not homogeneously distributed over frequencies, but rather had one peak at 55 Hz and a second peak at ~75 Hz, we decided to analyse the two frequency bands separately. Figs 4C and D show the temporal evolution of the gamma band lateralization for the sensors that showed the strongest modulation in the control condition (marked in Fig. 4B as black dots). Only in the control condition did we observe an effect on gamma activity (Fig. 4D, 60–80 Hz; Fig. 4C, 40–60 Hz) for the time period after the disappearance onset. However, the factorial ANOVA (factor 1, 250-ms time window centred 100 ms before and 400 ms after the disappearance; factor 2, condition vs. illusion) showed no significant effect in either band. A *t*-test (which we did not consider to be *post hoc*) showed that there was still a significant difference between left and right sensors in the control condition ( $0.4 \pm 0.125$  s) during real disappearance in the 60–80-Hz band ( $P = 0.0048$ , corrected for multiple comparisons in terms of tests).

### Discussion

We have investigated oscillatory activity associated with MIB. While recording the ongoing brain activity by using MEG, we applied a paradigm in which illusory target disappearances could occur independently in the left and right hemifields. The key findings were that illusory target disappearances were associated with posterior hemispheric lateralization of oscillatory brain activity: (i) the illusory target disappearance, as estimated from the RTs from the control condition, was preceded by stronger contralateral than ipsilateral alpha activity, and the duration of the illusory disappearance was predicted by the magnitude of this lateralization; (ii) after the onset of an illusory target disappearance, contralateral alpha activity decreased as compared with ipsilateral activity. This effect was comparable to alpha lateralization after real target disappearance onset. In contrast, activity in the gamma band showed no effects for illusory disappearances. In the control condition we observed a gamma power increase contralateral to real target disappearance.

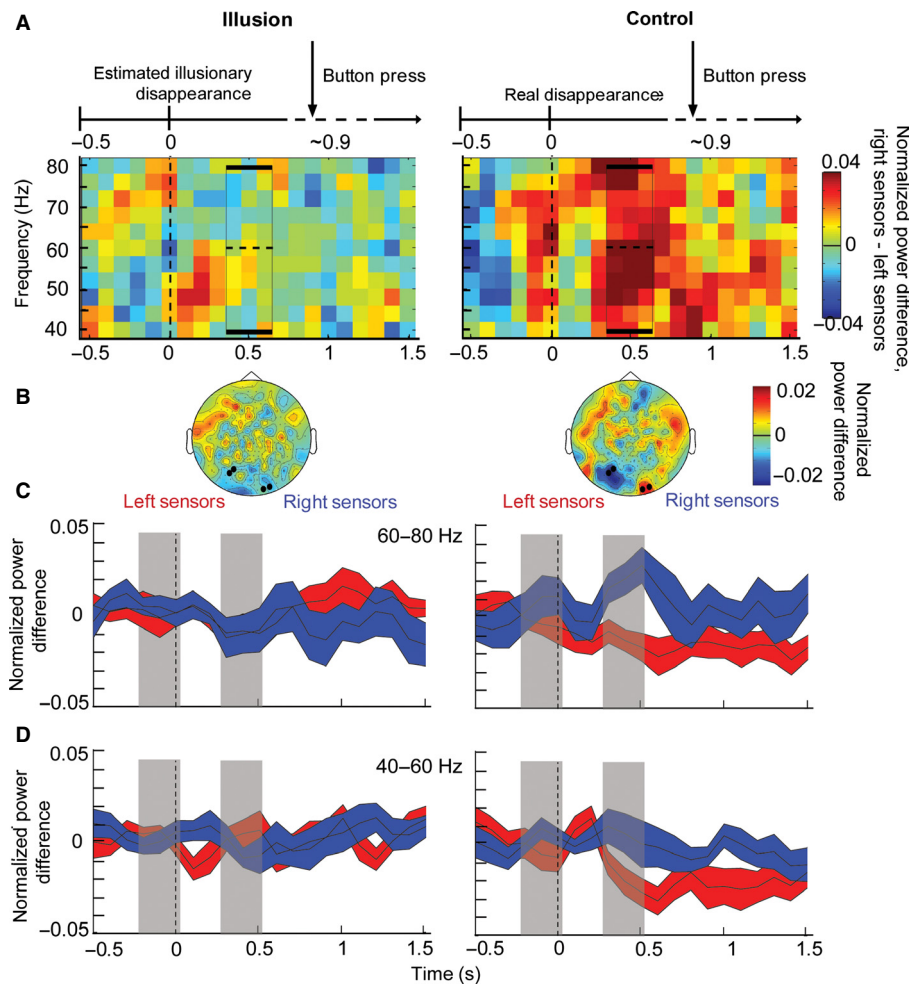


FIG. 4. Higher gamma activity during MIB. TFRs and topographies of gamma activity are shown separately for the illusion condition (left panels) and the control condition (right panels). (A) The timeline at the top indicates the trial timing as in Fig. 2. The TFR depicts the normalized power difference (as in Fig. 4) for right sensors minus left sensors. (B) The topographical distribution (combined planar gradient) of the normalized power difference is shown for the illusion and control conditions for the frequency (40–80 Hz) and time (–0.4 to 0.6 s) window marked in A by a black box. Sensor selection (black dots) is based on the time–frequency windows and analysis of the control condition only. (C and D) The time course ( $\pm$ standard error over subjects) of the normalized power difference in the high gamma band (C) (60–80 Hz) and low gamma band (D) (40–60 Hz) for right (blue) and left (red) for the sensors marked in B. Grey transparent boxes mark the time periods that were tested for significant differences with a two-factor ANOVA: no comparison was significant. A corrected *t*-test showed a significant effect in the control condition after the disappearance (250-ms time window centred 400 ms after disappearance;  $P = 0.0048$ , corrected) for 60–80 Hz.

#### Alpha activity predicting illusory perceptual changes

Numerous studies have demonstrated that posterior alpha activity is hemispherically lateralized when attention is covertly allocated to the left or right visual hemifield (Worden *et al.*, 2000; Yamagishi *et al.*, 2003; Kelly *et al.*, 2006; Thut *et al.*, 2006; Rihs *et al.*, 2007; Händel *et al.*, 2011). These modulations are explained by an increase in processing capabilities as the alpha activity decreases in the hemisphere contralateral to the attended hemifield. Likewise, the processing capabilities are thought to decrease in the unattended hemifield as alpha activity increases ipsilateral to the attended hemifield. The underlying cause of this change in processing capabilities is believed to be an inhibitory–disinhibitory process reflected by the alpha activity (see Klimesch *et al.*, 2007). Could such reduced processing also explain the sudden disappearance of our MIB target? We suggest that the hemispheric alpha lateralization reflects the allocation of computational resources when both the targets and the moving grid are processed during MIB. If the

alpha activity in the hemisphere contralateral to the target is high, the neuro-computational resources are reduced. As a consequence, only the moving grid is perceived, at the expense of the target. When the alpha activity is low, there will be sufficient computational resources to allow for both the target and the moving grid to be perceived. Changes in alpha activity might reflect the proposed winner-take-all mechanism believed to induce the disappearance of the less salient input (Bonneh *et al.*, 2001). The reason why the target but never the rotating grid disappears most likely lies in the fact that perception of the grid is dependent on more than one location. A filling-in effect as suggested by Ramachandran & Gregory (1991) created by the grid moving over large parts of the visual field could lead to a constant holistic perception of the grid. Even though the gratings of the targets are moving as well, their spatial dimension is very limited.

As discussed above, alpha activity is believed to be related to the allocation of resources. This resource allocation is usually observed in response to external stimuli changing spatial attention. In our

case, no external input induces an attentional shift, but we still observe spontaneous fluctuations of alpha activity. We therefore propose that fluctuation of alpha activity is (or at least can be) a spontaneous process. At this point, we would like to emphasize that, even though alpha activity is modulated by attention, this does not mean that any modulation of alpha activity is equivalent to a shift in attention. Therefore, the spontaneous changes in alpha activity do not necessarily reflect changes in spatial attention, but do reflect changes in neuro-computational resources.

In conclusion, we suggest that the spontaneous alpha activity increase marks the reduced processing capabilities in the hemisphere for the illusion whereby a winner-take-all process leads to the sole processing of the moving pattern at the expense of the target. Although, under normal circumstances, such alpha fluctuation might not introduce a noticeable breakdown of perception, the specific setting of MIB results in a mechanism allowing for the grid to be perceived at the expense of the targets.

As the illusion onset was only approximated by the mean RT to real disappearances, two questions must be asked. (i) Can the difference in brain response to real vs. illusory percepts be attributed to the absence of exact RTs in the illusion condition? It might be that a neuronal response is smeared over time, owing to jitter introduced by using the mean RTs of the control condition. However, our main finding is a lateralization prior to the illusion being in the opposite direction from the lateralization after both the true condition (control condition) and the illusory condition (Fig. 2A and C). This flip excludes the possibility that the pre-illusion effect is introduced by temporal smearing. (ii) Although this flip in alpha lateralization must be genuine for the illusion condition, can we conclude that it occurs around the estimated illusion onset? When inspecting the real disappearance (Fig. 3C, right panel), we observe a change in alpha lateralization emerging 400 ms after the onset of real disappearance. This time course is very compatible with the lateralization observed after the illusion (Fig. 2C, left panel). This is a strong indicator that we estimated the illusion onset correctly. In short, we conclude that the illusion onset is well estimated and that temporal smearing of the alpha lateralization cannot explain the pre-illusion alpha lateralization.

#### *Alpha lateralization after target disappearance*

Interestingly, if a target disappeared (illusory or real), strong lateralization was observed in the reverse direction as compared with the pre-disappearance interval: alpha activity decreased in the hemisphere contralateral to the target disappearance while it increased ipsilaterally.

A real disappearance of a target usually acts as an exogenous cue and relocates attention to the side of the perceptual event, accompanied by an alpha activity decrease contralateral to the attended hemifield. However, if the illusory disappearance of the target caught attention in such a bottom-up fashion, we would expect an immediate impact on the illusion. For instance, an exogenous cue such as a flashing stimulus near the target suppresses the perceptual disappearance (Kawabe *et al.*, 2007). Likewise, a flashing stimulus near the target can force a perceptual reappearance (Wu *et al.*, 2009). If the target itself is physically removed during the illusion, observers often report a target despite the fact that it is perceptually not present (Mitroff & Scholl, 2005). However, the illusory disappearance of the target does not lead to its immediate reappearance. On the contrary, the illusion can be very long-lived.

Two questions are triggered by this inconsistency. (i) If the sudden flip in alpha lateralization after illusion onset is not linked to an exogenous attentional allocation resulting from the illusion, what

triggered the shift in alpha activity? (ii) Independently of what caused the alpha lateralization after the illusion onset, why does alpha activity not have an influence on the illusion after its onset despite the fact that its lateralization beforehand is clearly linked to the illusion?

Concerning the first question, it might be the case that the illusory disappearance acts as an endogenous cue redirecting attention in a top-down fashion. This could explain the lateralization of alpha activity plus the absence of an immediate perceptual consequence, as there is a non-trivial relationship between endogenous cued spatial attention and the target disappearance in MIB. If covert attention is directed to a target by an endogenous cue, the disappearance is even enhanced on a longer time scale (Geng *et al.*, 2007; Scholvinck & Rees, 2009). For instance, Scholvinck has reported that endogenously allocating attention to the target actually increases the probability of the illusory disappearance. This effect, however, is not instantaneous (as observed for the exogenous cue), but occurs 6–7 s after the attentional cueing. Thus, the allocation of endogenous attention towards the target at trial onset does not force the target to disappear or reappear, but can still lead to a change in alpha activity.

It could also be the case that alpha lateralization is changing spontaneously. Attention cannot be constantly kept at a certain location. After a phase of increased processing, a phase of reduced processing seems to automatically follow, as, for instance, is the case for ‘inhibition of return’ (Posner *et al.*, 1985). Moreover, it has been demonstrated recently that attention fluctuates from the left hemifield to the right hemifield if there is one target presented in each (Landau & Fries, 2012). In the study by Landau and colleagues, the first attentional allocation is triggered by a cue; however, the reallocation to the opposite hemifield (~100 ms afterwards) is not. Such a mechanism could explain why the alpha fluctuation locked to the event of the illusion would show a peak and a consequent trough in power. Nevertheless, such alpha fluctuation might also take place over the whole visual field (and possibly also over modalities), which is indicated by the fact that both targets can disappear at the same time.

However, we have to deal with the fact that alpha activity does not influence the illusion after its onset despite the fact that its lateralization beforehand is clearly linked to the illusion. The mechanism forcing the perception of only the moving grid is apparently sufficiently strong to override the re-emergence of target perception even when, again, more processing resources are allocated. This interpretation is consistent with findings of bistable illusion in relation to selective attention. Although selective attention somewhat modulates these illusions, it does not override the illusory percept (Tong *et al.*, 2006).

#### *Gamma activity follows processing of change, not input*

The activity in the gamma band was revealing in several ways. Whereas we expected that gamma oscillations would be induced by the target (which was a moving grating at high contrast) and therefore be reduced when the target really disappeared, surprisingly, gamma activity increased with target disappearance. This finding was present at 60–80 Hz. Thus the gamma activity reported in this study did not reflect low-level processing of visual input as often is the case in single cells studies in animals (see Fries, 2009). Furthermore, the gamma activity increase was only observed contralateral to the real target disappearance, and not the illusory target disappearance. This suggests that gamma activity is also not reflecting a change in perception as such. Gamma activity has also been linked to attentional processes in visual, auditory and somatosensory tasks (e.g. Tiitinen *et al.*, 1993; Gruber *et al.*, 1999; Fries *et al.*, 2001;

Linkenkaer-Hansen *et al.*, 2004); for an overview see, for example, Womelsdorf & Fries (2007). The gamma increase following the real target disappearance might reflect such allocation of attention. However, it should be mentioned that we did not find gamma activity modulations in the illusion condition. This null finding has to be interpreted with care, as it might be an issue of insufficient signal-to-noise ratio.

Our findings need to be reconciled with those of other studies demonstrating an increase in gamma activity during the perception of illusions: activity in the gamma range (30–60 Hz) in the primary visual cortex was reported to coincide with the emergence of visual illusions (Adjamian *et al.*, 2004). Tikhonov *et al.* (2007) described increased gamma activity (~90 Hz) during a motion after-effect. However, our illusion consisted of less percept, not more, which might explain the difference in results.

## Conclusion

Our study suggests that an increase in local inhibition reflected by increased alpha activity can explain the illusive target disappearance as observed in MIB. We favour an explanation whereby MIB arises from competition between the targets and the moving grids. When the local alpha activity is relatively high, the computational resources are reduced. As a consequence, the perception of the moving grid wins over the perception of the target, owing to perceptual filling-in. Two independent phenomena, i.e. local inhibition and perceptual filling-in, might therefore lead to MIB.

It is worth pointing out that previous studies investigating hemispheric alpha lateralization have all relied on spatial cueing (e.g. Worden *et al.*, 2000; Yamagishi *et al.*, 2003; Kelly *et al.*, 2006; Rihs *et al.*, 2007; Händel *et al.*, 2011). Our study demonstrates that fluctuations in alpha activity not only result from input from the outside world, but are also subject to spontaneous modulations. These fluctuations in alpha activity have perceptual consequences. Furthermore, different subjects have larger modulations in alpha activity that result in longer-lasting illusions. Therefore, why people perceive the world around them differently can partly be explained by fluctuations in spontaneous brain oscillations.

## Acknowledgements

The authors gratefully acknowledge funding from The Netherlands Organization for Scientific Research (NWO); VICI grant number 453-09-002.

## Abbreviations

d.f., degrees of freedom; MEG, magnetoencephalography; MIB, motion-induced blindness; RT, reaction time; SD, standard deviation; TFR, time-frequency representation.

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