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Antiphasic 40 Hz Oscillatory Current Stimulation Affects Bistable Motion Perception

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Abstract When viewing ambiguous stimuli, conscious perception alternates spontaneously between competing interpretations of physically unchanged stimulus information. As one possible neural mechanism underlying the perceptual switches, it has been suggested that neurons dynamically change their pattern of synchronized oscillatory activity in the gamma band (30–80 Hz). In support of this hypothesis, there is correlative evidence from human electroencephalographic (EEG) studies for gamma band modulations during ambiguous perception. To establish a causal role of gamma band oscillations in the current study, we applied transcranial alternating current stimulation (tACS) at 40 Hz over occipital–parietal areas of both hemispheres during the presentation of bistable apparent motion stimuli that can be perceived as moving either horizontally or vertically. In this paradigm, the switch between horizontal and vertical apparent motion is likely to involve a change in interhemispheric functional coupling. We examined gamma tACS effects on the durations of perceived horizontal and vertical motion as well as on interhemispheric EEG coherence and found a decreased proportion of perceived horizontal motion together with an increase of interhemispheric gamma band coherence. In a control experiment using 6 Hz tACS, we did not observe any stimulation effects on behavior or coherence. Furthermore, external stimulation at 40 Hz was only effective when applied with 180° phase difference between hemispheres (anti-phase), as compared to in-phase stimulation with 0° phase difference. These findings suggest that externally desynchronizing gamma oscillations between hemispheres impairs interhemispheric motion integration and in turn biases conscious experience of bistable apparent motion.

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Introduction

The constructive nature of conscious perception becomes evident when visual awareness alternates continuously between alternative interpretations of an unchanged stimulus, as is the case with viewing ambiguous figures like the well-known Necker cube. This class of visual illusions allows the dissociation of neural activity related to basic sensory features from that correlated with conscious perception (Eagleman 2001; Sterzer et al. 2009). As one possible neural mechanism underlying the perceptual switches, it has been suggested that neurons dynamically change their pattern of synchronized oscillatory activity in the gamma band (30–80 Hz) (Engel et al. 2001). In support of this hypothesis, human electroencephalographic (EEG)

Fig. 1 Apparent motion stimuli. **a** Stroboscopic alternative motion (SAM). Alternating presentation of two diagonally opposed pairs of LEDs (*top*) induces spontaneous perceptual alternations between vertical and horizontal apparent motion (*bottom*). **b** Unambiguous apparent motion. Unambiguous motion percepts can be induced by alternating presentation of unambiguous horizontal (*left*) and vertical motion (*right*). *Open* versus *closed dots* indicate simultaneity of flashing, the green dot marks the fixation point
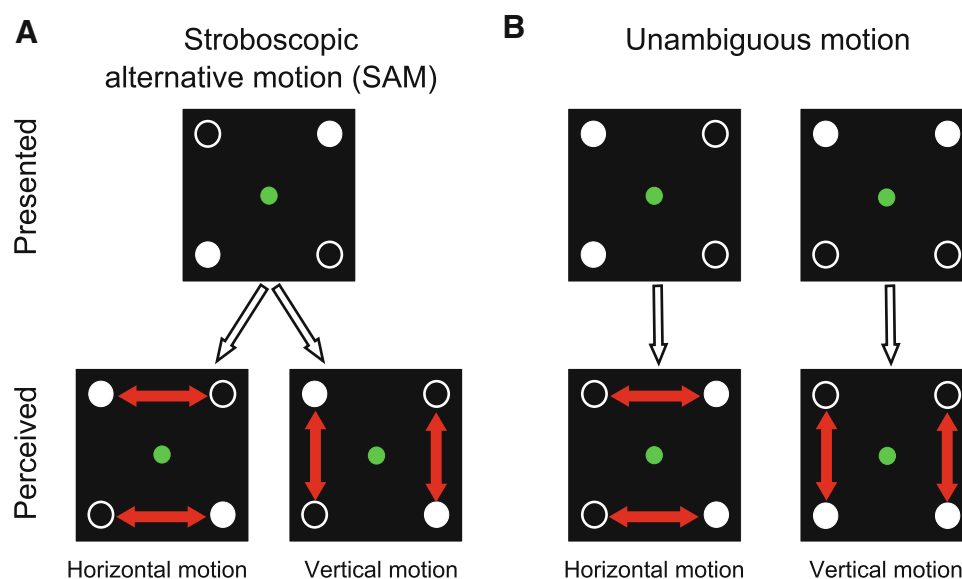
studies demonstrated gamma band modulations during ambiguous perception (Başar-Eroglu et al. 1996; Keil et al. 1999; Rodriguez et al. 1999; Ehm et al. 2011; Hipp et al. 2011).

However, the issue of whether gamma oscillations reflect a fundamental mechanism in cortical information processing or just an epiphenomenon is still unresolved. It has been argued that if oscillations are essential for any cognitive function, then this function should be disrupted by selectively interfering with the oscillations (Sejnowski and Paulsen 2006). While this has been considered to be a very difficult question to address empirically in healthy humans until recently (Rees et al. 2002), new techniques of noninvasive human brain stimulation are now available that allow for driving brain oscillations within the range of observable, physiologically relevant frequencies (Thut et al. 2011a).

One such technique is sinusoidally applied transcranial alternating current stimulation (tACS), which aims to directly interfere with ongoing cortical oscillations and which is expected to actively synchronize cortical oscillations (Paulus 2011). The effectiveness of tACS in modulating ongoing rhythmic brain activity has been demonstrated by frequency-dependent perceptual and behavioral consequences (Kanai et al. 2008; Pogosyan et al. 2009; Feurra et al. 2011; Laczó et al. 2012) and by direct electrophysiological evidence for an interaction between tACS and ongoing oscillatory EEG activity (Zaehle et al. 2010).

The aim of the present study was to substantiate a functional role of gamma band oscillations and their long-range interactions in conscious perception. To this end, we applied tACS in the gamma frequency band at 40 Hz bilaterally over motion sensitive regions of the cortex while observers reported spontaneous switches between perceived

horizontal and vertical motion directions of a bistable apparent motion display, called "stroboscopic alternative motion" (SAM) or "motion quartet" (Fig. 1a) (von Schiller 1933; Chaudhuri and Glaser 1991). In this paradigm, the switch between horizontal and vertical apparent motion is likely to involve a change in interhemispheric functional coupling, because information from both hemispheres has to be integrated in the case of perceived horizontal motion. As demonstrated previously by a correlative EEG study (Rose and Büchel 2005), interhemispheric gamma band coherence is increased during perceived horizontal motion compared to vertical motion of the SAM display with a prominent peak at 40 Hz. Therefore, we used 40 Hz as stimulation frequency within the gamma band and hypothesized that bilateral 40 Hz tACS would modulate interhemispheric coherence in the gamma frequency band and thereby affect the temporal dynamics of perceptual awareness during bistable motion perception. In order to demonstrate that the hypothesized effect is specific to 40 Hz, we compared it to 6 Hz tACS. In addition, we either stimulated the two hemispheres in-phase (Experiment 3) or with 180° phase difference (anti-phase, Experiments 1 and 2) to demonstrate that the hypothesized effect depends upon the phase difference between hemispheres.

Materials and Methods

Participants

A total of 45 healthy adults (27 female, mean age 24.9 ± 4.1 years) participated in the three experiments of the current combined tACS–EEG study. Participants were informed about all aspects of the study (excluding the main

hypothesis and the bistability of the SAM) and gave their written informed consent prior to the experiments. All participants were right handed and had normal or corrected-to-normal vision. They had no history of psychiatric or neurological disease, were under no current medication affecting the central nervous system. Participants were naïve with regard to the hypothesis of the study and the bistability of the SAM until the end of the study. The study protocol was designed and performed according to the declaration of Helsinki and was approved by the local ethics committee of the Carl von Ossietzky Universität, Oldenburg. From the 45 participants, 17 participated in Experiment 1 (anti-phase 40 Hz tACS), 13 in Experiment 2 (anti-phase 6 Hz tACS), and 15 in Experiment 3 (in-phase stimulation at 40 and 6 Hz). From the 17 participants of Experiment 1, two were excluded from the EEG analysis because of incomplete data (caused by accidental data loss).

Stimuli and Procedure

The SAM (Fig. 1a) was presented by means of four white light emitting diodes (LEDs) with a diameter of 5 mm which were mounted on a black box. A custom-written Matlab script (Matlab, The Mathworks) generated a digital 2 Hz sine wave which was converted to an analog voltage via a digital-to-analog converter (National Instruments USB-6229 BNC). The sine wave oscillated around 2.4 V with an amplitude of 0.15 V. This drives the LED in such a way that the luminance is modulated sinusoidally. All LEDs were situated equidistantly with a distance of 5 cm. A green LED at the center of the rectangular arrangement served as fixation point and was powered constantly. The visual angle for the horizontal and vertical distances of the LEDs at a participant-to-box distance of 130 cm was 2.2°.

After preparation of EEG and tACS electrodes (see below), participants accomplished two training runs of 5 min each to practice button presses. In both training runs, participants were instructed to fixate the green LED in the center of the display and to attend to the apparent motion pattern. If the perceived motion changed from a vertical to horizontal direction they were asked to press the left button with their left index finger. If the perceived motion changed from a horizontal to vertical direction they were asked to press the right button with their right index finger. In the first run, participants had to indicate motion direction changes between *unambiguous* vertical and horizontal apparent motion patterns (Fig. 1b). Participants were informed that the change of motion direction was externally controlled by the computer. In the second run, participants were presented with the bistable SAM pattern (Fig. 1a) and were again instructed to indicate changes of motion direction as they did in the first run. This run was

performed to familiarize the participants with the SAM. However, in order to keep the participants naïve with regard to the endogenous origin of the perceptual switches, the bistability of the SAM display was not explicitly pointed out to them. Instead, by presenting the ambiguous pattern subsequent to the unambiguous pattern it was indirectly suggested that for both patterns the change of motion direction is triggered externally by the computer. Keeping participants in a naïve state is important to prevent effects of voluntary control on the reversal rate and percept durations. A debriefing after the experiment was carried out to check whether participants stayed naïve throughout the second run. After the training sessions, there were two experimental conditions with the same protocol in Experiments 1 and 2 (Fig. 2c):

1. *Sham-condition*: Three minutes of spontaneous EEG (pre-stimulation) were recorded while participants fixated a green LED. Subsequently, the skin sensation and phosphene threshold were determined (see below for details). Then the stimulator was switched off and the participants had to perform the SAM task for 15 min, followed by the recording of another 3 min of spontaneous EEG (post-stimulation).
2. *TACS-condition*: Same procedure as in the sham-condition, except that participants received tACS at 40 Hz (Experiment 1) or 6 Hz (Experiment 2).

In Experiment 3, an additional sham-condition was presented following the tACS-condition to control for effects of fatigue, again preceded and followed by 3 min of spontaneous EEG (Fig. 2c).

We used the pre/post-stimulation EEG recordings to calculate interhemispheric coherence and, thereby, to study the electrophysiological consequences of tACS, because EEG recording online to stimulation was not feasible due to the tACS artifacts.

EEG Recording

Participants sat in a dimly lit, electrically shielded room. EEG was measured from Ag/AgCl electrodes mounted on an elastic cap (Easy cap, Falk Minow Services, Munich, Germany) according to the international 10–10 system and amplified using a BrainAmp amplifier powered by battery (Brain Products, Munich, Germany). An electrode placed on the nose served as reference and the ground electrode was located at Fpz. Electrode impedances were kept below 5 kΩ. EEG data were recorded with Brain Vision Recorder (Version 1.10, Brain Products, Munich, Germany) at a sampling rate of 500 Hz (0.1 μV steps resolution) and analog filtered (low pass filter DC, high pass filter 250 Hz). A fiber-optic cable transferred the digitized EEG to a computer outside the recording cabin.
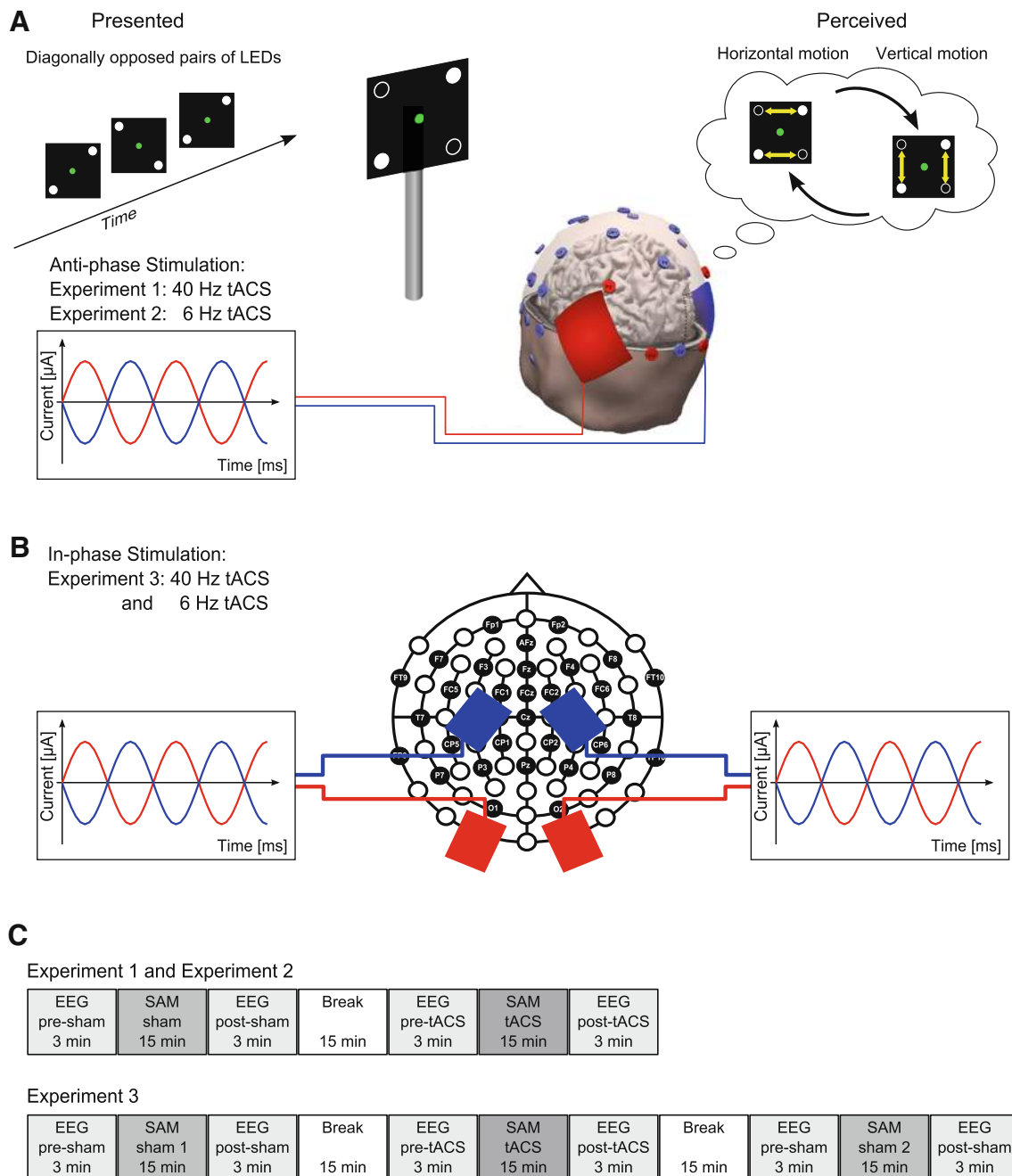
Fig. 2 Experimental setup. **a** Configuration of the SAM display together with the EEG and tACS electrode montage for anti-phase (180° phase difference between hemispheres) stimulation at 40 Hz (Experiment 1) and 6 Hz (Experiment 2). Those EEG electrodes that were used for analyzing interhemispheric coherence are indicated in *red* (P3, P4, O1, O2, international 10–10 system). The tACS sponge electrodes were placed bilaterally over the parietal–occipital cortex (*red* left hemisphere; *blue* right hemisphere) at electrode positions P7-PO7 and P8-PO8. **b** EEG and tACS electrode montage for in-phase (0° phase difference between hemispheres) stimulation at 40 and 6 Hz (Experiment 3). As in Experiments 1 and 2, EEG electrodes P3, P4, O1, and O2 were used for analyzing interhemispheric coherence. **c** Sequence of experimental events. In Experiments 1 and 2 (*top row*), the SAM was presented within two blocks for 15 min each (*dark grey squares*). Per block, the SAM presentation was preceded and followed by 3 min of spontaneous EEG recording (*light grey squares*). In the first block, participants received no tACS during the SAM presentation (sham condition), whereas in the second block tACS was applied during the SAM presentation (tACS condition). Blocks were separated by a 15 min break (*white squares*). In Experiment 3 (*bottom row*), the order of events within each block was identical to Experiments 1 and 2, but a third block (second sham-condition) was added. Note that participants in Experiment 3 were stimulated at both 40 and 6 Hz on two consecutive days in a counterbalanced order (within-subject design)

All devices inside the cabin were battery operated to avoid line frequency interference (50 Hz in Germany).

Experiments 1 and 2

Electroencephalogram was measured from 28 Ag/AgCl electrodes including 2 EOG electrodes (below right and left eye). Four electrodes (P7-PO7 and P8-PO8) of the original 32-channel setup were excluded for measurement because the tACS electrodes were situated at those locations (Fig. 2a).

Experiment 3

Electroencephalogram was measured from 31 Ag/AgCl electrodes including 2 EOG electrodes (below right and left eye). Three electrodes (C3–C4, Oz) of the original 32-channel setup were excluded for measurement because the tACS electrodes were situated at those locations (Fig. 2b).

Transcranial Alternating Current Stimulation (tACS)

Transcranial alternating current stimulation was applied by a battery-driven stimulator (NeuroConn, Ilmenau, Germany). Impedances were kept below 10 kΩ. We applied oscillating sinusoidal currents at 40 and 6 Hz. Stimulation and sham (no stimulation) conditions lasted for 15 min each.

All participants underwent a tACS-threshold-measurement procedure prior to the sham and stimulation conditions to determine the thresholds for phosphenes (visual flashes) and skin sensations induced by tACS. For that purpose, we applied tACS stimulation at 40 and 6 Hz with 1.5 mA and either increased or decreased the amplitude stepwise by 0.1 mA. Participants were asked to keep their eyes open and indicate the presence of a sensation. In the sham condition, stimulation was turned off after detection of the sensory threshold. In the stimulation condition, stimulation intensity was kept 0.1 mA below the lower threshold for either phosphenes or skin sensations. This procedure ensured that participants did not sense stimulation, but were convinced that they received stimulation in all conditions although they did receive stimulation only in the second. Hence, participants were not aware of the fact that only one of the conditions of the experiment included stimulation. Participants experienced neither skin sensation nor phosphenes at any time during the stimulation. A debriefing after the experiment was carried out in order to find out whether stimulation was sensed by the participants. TACS was not applied with a constant intensity, because skin sensation and/or phosphene thresholds differed intra- and interindividually, resulting in differences of the tACS mean intensity across experiments and conditions (see below).

Experiments 1 and 2

Two conductive rubber electrodes (5 × 7 cm, 35 cm^2; NeuroConn GmbH, Ilmenau, Germany), which were placed in saline-soaked sponges prior to measurement to ensure optimal conductive characteristics, were attached to the head bilaterally underneath the EEG recording cap over parietal–occipital locations (P7-PO7 and P8-PO8). This setup of stimulation electrodes caused an anti-phase stimulation protocol, i.e., it induced 180° interhemispheric phase difference between the stimulated areas (Fig. 2a).

The large size of the stimulation electrodes did not allow for a very focal stimulation, but it has been shown that maximal current flow is achieved underneath the stimulation electrodes (Miranda et al. 2006). Our electrode positions lie close to the human motion complex (hMT), a region that has been related to the processing of stable (Goebel et al. 1998) and bistable (Muckli et al. 2002; Sterzer et al. 2002, 2003; Rose and Büchel 2005) apparent motion.

Both experiments consisted of a sham condition followed by a stimulation condition. The stimulation frequency was 40 Hz in Experiment 1 and 6 Hz in Experiment 2. For Experiment 1, tACS mean intensity was 0.645 (±0.333) mA prior to the sham condition and 1.023 (±0.620) mA during tACS at 40 Hz. For Experiment 2, tACS mean intensity was 0.421 (±0.225) mA prior to the sham condition and 0.496 (±0.191) mA during tACS stimulation at 6 Hz.

Experiment 3

In order to produce an in-phase stimulation protocol that did not induce an interhemispheric phase difference between the stimulated areas, we had to place one anode and one cathode on each hemisphere. Therefore, four conductive rubber electrodes (3.9 × 3.9 cm, 15.21 cm^2; NeuroConn GmbH, Ilmenau, Germany), which were placed in saline-soaked sponges prior to measurement to ensure optimal conductive characteristics, were attached to the head bilaterally underneath the EEG recording cap over central locations (C3 and C4), and occipital locations (dorsal to O1 and O2; Fig. 2b).

Experiment 3 consisted of two sessions (40 and 6 Hz tACS) on two separate days with three conditions each (sham 1, stimulation, sham 2). The order of the two sessions was balanced across participants. TACS mean intensity in the 40 Hz session was 1.111 (±0.383) mA prior to the first sham condition, 1.230 (±0.351) mA during tACS stimulation, and 1.380 (±0.335) mA prior to the second sham condition. TACS mean intensity in the 6 Hz session was 1.193 (±0.475) mA prior to the first sham condition, 1.397 (±0.392) mA during tACS stimulation,

and 1.437 (±0.324) mA prior to the second sham condition.

Data Analysis

Behavioral Data

The mean duration of horizontal motion perception was defined as the mean time difference between each left button press and the subsequent right button press (for vertical motion perception the mean time difference between the right and subsequent left button press, respectively). Double and triple button presses, as well as the first button press after a double or triple button press were excluded from this analysis. For each participant, the motion dominance index (MDI) was calculated as

$$MDI = \frac{\overline{t_V} - \overline{t_H}}{\overline{t_V} + \overline{t_H}},$$

where $\overline{t_V}$ and $\overline{t_H}$ are the mean durations of vertical and horizontal motion perception. MDI values of 1 would indicate 100 % perceived vertical motion and values of −1 would indicate 100 % perceived horizontal motion. Zero indicates 50 % perceived horizontal and 50 % perceived vertical motion direction.

In addition, we used gamma distributions of the time intervals between switches to visualize the temporal dynamics of the SAM pattern. Gamma distributions were fitted with a maximum likelihood estimator using the MatLab function gamfit.

EEG Data

After data storage, EEG signals were further processed using EEGlab (Version 8.0.3.5b) and Matlab (The Mathworks). An additional finite impulse response (FIR) high-pass filter with a cut-off frequency of 1 Hz and a low-pass filter of 100 Hz (EEGlab, firfilt 1.5.1 plugin by Andreas Widmann) was applied off-line.

For each participant, each of the four EEG recordings (pre SAM/sham, post SAM/sham, pre SAM/tACS, post SAM/tACS) was split into one-second segments by moving a window of one second in steps of 250 ms along the dataset. Segments with muscle and blink artefacts were excluded and the first 100 artefact free segments of each dataset were included in subsequent analyses. Coherence was quantified as Magnitude Squared Coherence (MSC):

$$C_{x,y} = \frac{abs(P_{x,y})^2}{P_{x,x} \cdot P_{y,y}},$$

where $P_{x,y}$ is the cross power spectral density, and $P_{x,x}$ and $P_{y,y}$ are the power spectral densities of the EEG signals in channel x and y. Coherence was calculated utilizing the

MatLab function mscohere. The electrodes P3, P4, O1, and O2 were the electrodes of interest for the coherence analysis. For each participant and EEG condition, coherence was calculated between electrode pairs P3–P4 and O1–O2 for each of 100 segments and then averaged across segments and electrode pairs.

MSC bears the problem that artificial coherences can result from the two sides of one dipolar source. This disadvantage can be avoided by using the imaginary part of the complex-values coherency (Nolte et al. 2004). However, then two signals which have 0° or 360° phase difference will never be considered coherent. Therefore, we decided to use MSC instead of coherency.

Results

Experiment 1: 40 Hz tACS with 180° Phase Difference Between Hemispheres (Anti-phase Stimulation)

As shown in Fig. 3 (left side), the motion dominance index (MDI) increased during tACS as compared to sham stimulation ($t(16) = -2.2$, $P = 0.04$), reflecting a longer total duration of perceived vertical motion.
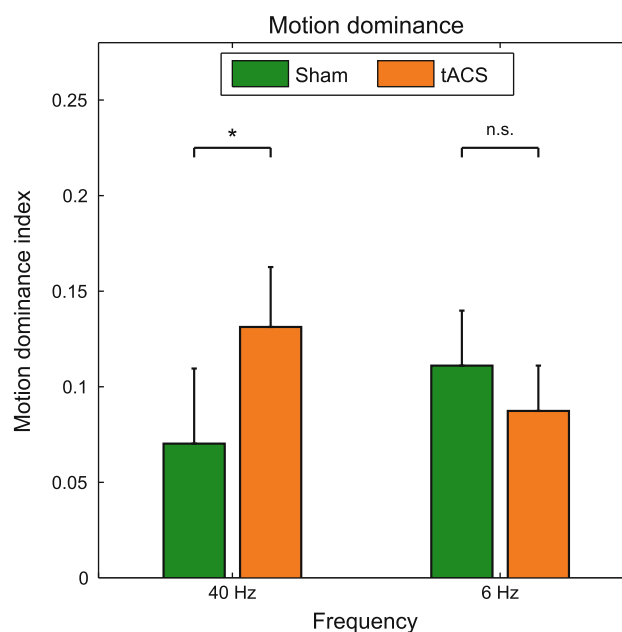

Fig. 3 Effects of tACS on motion dominance. In Experiment 1 (*left side*), the motion dominance index is significantly enhanced during 40 Hz tACS (*orange bar*) as compared to sham stimulation (*green bar*), indicating that 40 Hz tACS results in a longer total duration of perceived vertical motion (*$P < 0.05$). *Error bars* display the standard error of the mean. In Experiment 2 (*right side*), the motion dominance index did not differ significantly between 6 Hz tACS and sham stimulation

We examined the temporal dynamics of our SAM stimulus by assessing the distributions of percept durations separately for perceived horizontal and vertical motion (Fig. 4). Percept durations of both motion directions in the sham and tACS conditions exhibited the typical unimodal distribution with a fast rise and rightward tail representing a gamma distribution (Fig. 4a), as has been described previously for the SAM (Kohler et al. 2008) and other bistable stimuli from different modalities (Pressnitzer and Hupé 2006).

Comparing the gamma distributions of the horizontal and vertical percept durations within each condition at a descriptive level shows higher probability values for relatively short horizontal and long vertical percept durations, with this effect being stronger in the tACS than in the sham condition (Fig. 4b). This imbalance between horizontal and vertical percept durations reflects a bias toward vertical motion perception that is well-known for equidistantly presented SAM displays, and has been related to the cost of interhemispheric transfer, since the vertical bias disappears with lateralized SAM presentation (Gengerelli 1948; Chaudhuri and Glaser 1991). Together, our behavioral results for anti-phase 40 Hz tACS demonstrate an amplification of the usual vertical bias for equidistantly presented SAM displays.

In addition to these behavioral effects, we were interested in the electrophysiological consequences of anti-phase 40 Hz tACS. Therefore, we recorded 3 min of spontaneous EEG before (pre-stimulation) and after (post-stimulation) the combined SAM/tACS versus SAM/sham measurements and calculated the coherence between left and right parietal–occipital electrodes (Fig. 5a, b). Coherence values were submitted to a repeated measures ANOVA with factors condition (sham vs. tACS) and time (pre vs. post). We found a significant main effect of condition ($F_{1,14} = 7.66$, $P = 0.015$). Post hoc t-tests (Bonferroni corrected) revealed an increase of interhemispheric coherence in the gamma range (30–45 Hz) between left and right parietal–occipital electrodes following tACS ($t(14) = -4.32$, $P = 0.004$), but not sham stimulation (Fig. 5c). Although not significant, the interaction between factors condition and time showed at least a trend ($F_{1,14} = 3.27$, $P = 0.09$), which might be indicative of a tACS-induced modulation of ongoing gamma oscillations that outlasted stimulation offset. However, since the interaction only approached significance, this EEG result remains suggestive (Nieuwenhuis et al. 2011).

Moreover, we calculated the coherence between all left/right symmetric electrode pairs in order to further investigate the topographical distribution of the effect. This analysis revealed that the enhancement of the interhemispheric gamma band coherence following tACS stimulation was maximal near the stimulation electrodes over

motion sensitive areas, suggesting a topographical specificity of the increased gamma coherence (Fig. 6).

Importantly, the coherence effect was not only spatially specific, but it was also obtained without a corresponding power effect. As revealed by a repeated measures ANOVA with factors condition (sham vs. tACS) and time (pre vs. post), there was neither a significant main effect of condition ($F_{1,14} = 0.001$; $P = 0.982$) or time ($F_{1,14} = 0.45$, $P = 0.514$), nor a significant interaction condition x time ($F_{1,14} = 2.71$, $P = 0.122$) for the power values. This pattern of results indicates that the enhanced interhemispheric gamma band coherence is due to an increase in phase synchronization of gamma oscillations over parietal–occipital areas.

Experiment 2: 6 Hz tACS with 180° Phase Difference Between Hemispheres (Anti-phase Stimulation)

In order to test whether the effects reported in Experiment 1 are obtained whenever the two hemispheres are stimulated in anti-phase regardless of frequency, we repeated the same experiment with new participants, now applying 6 Hz instead of 40 Hz anti-phase tACS. We chose 6 Hz to test for frequency specificity because EEG activity in the theta frequency range has been characterized as unspecific to perceptual reversals (Nakatani and van Leeuwen 2005; Ehm et al. 2011), so that it is not to be expected that 6 Hz tACS will boost perceptual reversal related mechanisms. Furthermore, this frequency, like 40 Hz, is out of the range where tACS may induce phosphene sensations at the stimulation intensity applied in the present study (Kanai et al. 2008). Accordingly, none of the participants reported any phosphene sensations during 6 or 40 Hz tACS.

In this control experiment, we did not find significant differences between sham and anti-phase 6 Hz tACS for the motion dominance index ($t(12) = 0.947$, $P = 0.362$; Fig. 3, right side). Similar to Experiment 1, the frequency histograms of perceived horizontal and vertical motion durations followed a gamma distribution (Fig. 4c). In contrast to Experiment 1, the difference between the gamma distributions for the horizontal and vertical percept durations did not increase for the tACS condition (Fig. 4d). More importantly, a direct comparison between the behavioral effects (MDI) of 40 Hz anti-phase stimulation from Experiment 1 and 6 Hz anti-phase stimulation by means of a two-way ANOVA with the factors stimulation frequency (40 vs. 6 Hz; between subjects) and condition (sham vs. tACS; within subjects) revealed a significant interaction of stimulation frequency x condition ($F_{1,28} = 4.87$, $P = 0.035$), indicating frequency specificity of the effect of anti-phase tACS on motion dominance during SAM perception. That is, motion dominance showed a significant difference between sham stimulation and tACS for the 40 Hz but not for the 6 Hz stimulation. Coherence spectra did not show any significant
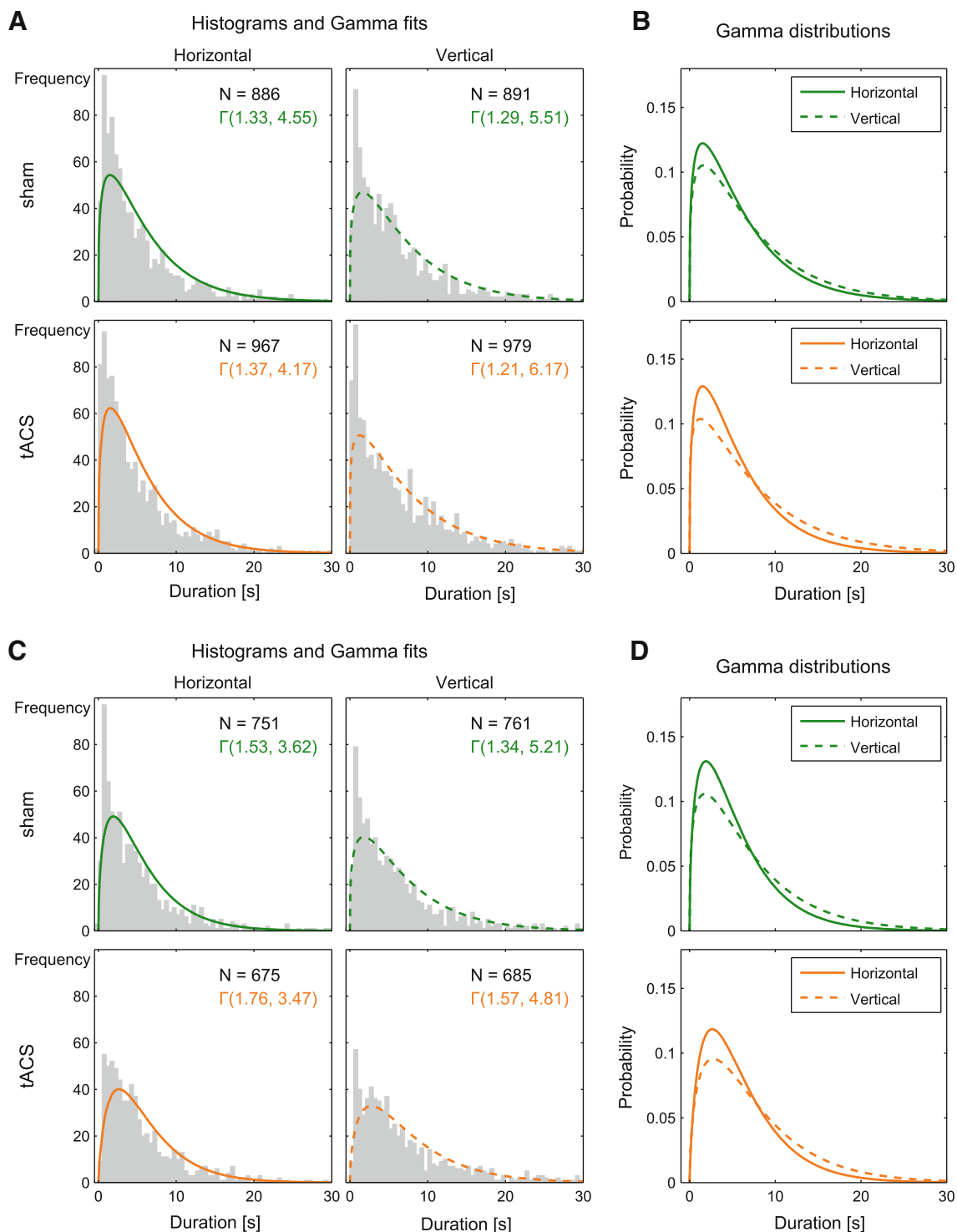
Fig. 4 Distributions of the durations of perceived horizontal and vertical motion integration. **a** Frequency histograms displaying percept durations pooled across observers (*grey*) and gamma distribution fits for perceived horizontal (*solid curves*) and vertical (*dashed curves*) motion in the sham (*top*) and tACS (*bottom*) condition of Experiment 1. *N* indicates the total number of observations across all participants. The numbers above each distribution represent the fitted shape and scale parameters of the gamma fits. **b** Fitted gamma distributions represent the probability density functions of horizontal (*solid curves*) and vertical (*dashed curves*) percept durations for the sham (*top*) and tACS (*bottom*) conditions. **c** Same as "**a**" but for Experiment 2. **d** Same as "**b**" but for Experiment 2
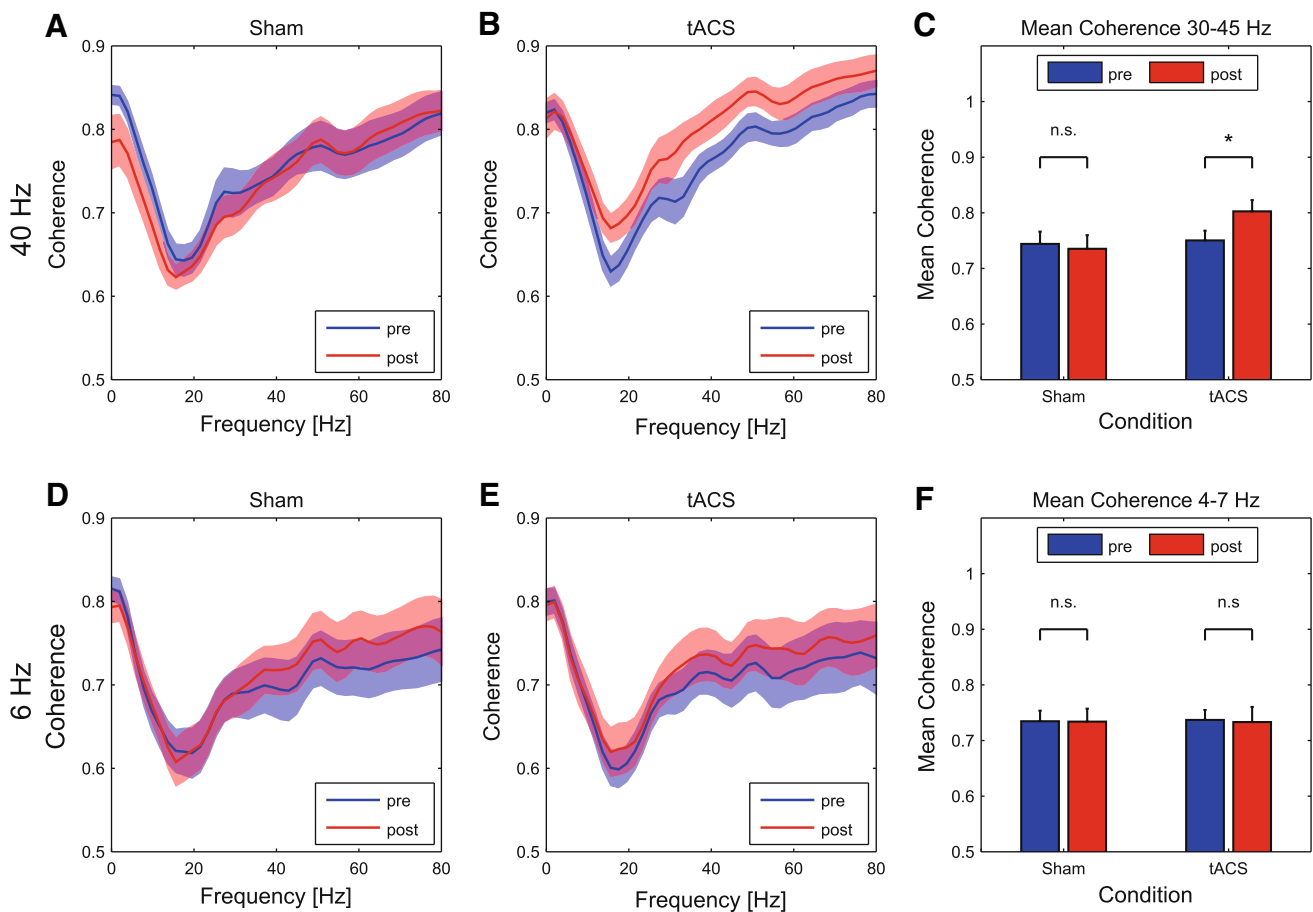
Fig. 5 Effects of tACS on interhemispheric coherence in Experiment 1 (*top*) and Experiment 2 (*bottom*). **a** Coherence spectra before (*blue*) and after (*red*) SAM presentation in the sham condition show no significant difference. The *solid colored lines* represent the mean values for each condition and the shaded regions represent ±1 SE. **b** In the 40 Hz tACS condition (tACS together with SAM presentation), coherence is elevated in the frequency range from roughly 35–55 Hz (including a power line 50 Hz effect) after (*red*) as compared to before (*blue*) stimulation. **c** Coherence within the 30–45 Hz frequency band (excluding the power line 50 Hz effect) shows a significant increase from pre-tACS to post-tACS (*right*), but not from pre-sham to post-sham (*left*). *Error bars* correspond to standard errors of the mean; *$P < 0.05$. Coherence spectra in Experiment 2 do not show any pre/post differences for either the sham condition (**d**) or 6 Hz tACS condition (**e**). Accordingly, statistical analysis of the mean coherence within the theta band (4–7 Hz) does not yield significant differences (**f**)

differences between pre/post EEG measurements—neither for sham stimulation nor for 6 Hz tACS (Fig. 5d–f).

Formal statistical testing of the mean coherence in the theta band (4–7 Hz) by means of a repeated measures ANOVA with the factors condition (sham vs. tACS) and time (pre vs. post) yields no significant results for condition ($F_{1,12} = 0.008$, $P = 0.929$), time ($F_{1,12} = 0.058$, $P = 0.817$) or an interaction condition × time ($F_{1,12} = 0.015$, $P = 0.9$). Moreover, we conducted the same type of ANOVA also for the mean coherence in the gamma band (30–45 Hz) in order to test whether the stimulated area may respond unspecifically with enhanced gamma coherence to varying stimulation frequencies (6 vs. 40 Hz). The ANOVA did not yield any significant results for condition ($F_{1,12} = 0.352$, $P = 0.564$), time ($F_{1,12} = 1.393$, $P = 0.261$) or an interaction condition x time ($F_{1,12} = 0.027$, $P = 0.872$). Thus, this absence of a

coherence effect in the gamma band during 6 Hz tACS supports that the gamma coherence effect of experiment 1 is related to 40 Hz tACS only.

Experiment 3: 40 and 6 Hz tACS with 0° Phase Difference Between Hemispheres (In-phase Stimulation)

Given that our main result of a decreased proportion of horizontal percept durations during 40 Hz tACS is based on anti-phase stimulation of the two hemispheres, one might expect an increase of perceived horizontal motion direction when tACS is applied in-phase. In order to test this possibility, we conducted a third experiment with in-phase tACS at 6 and 40 Hz.
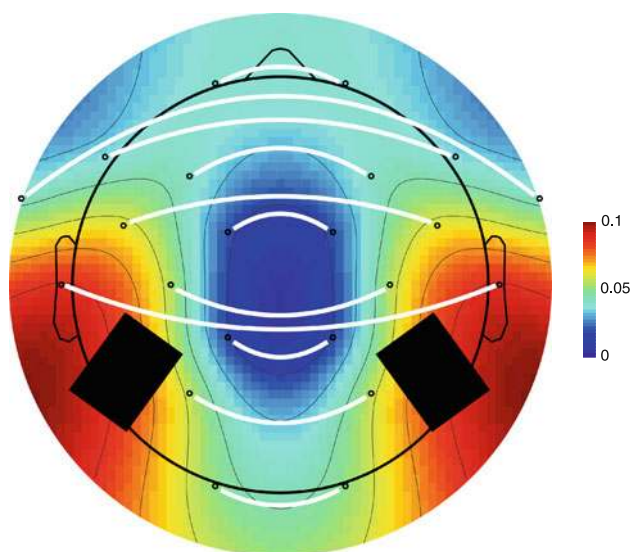
Fig. 6 Topography of the interhemispheric gamma coherence increase (post–pre) following tACS in Experiment 1. Coherence was calculated between the *left/right* electrode pairs as indicated by the *white lines*. The coherence estimates show a well defined maximum near the tACS electrodes (*black patches*). This scalp distribution demonstrates specificity of the coherence effect

Fig. 7 Effects of tACS on motion dominance in Experiment 3. In-phase tACS at 40 Hz (*left side*) and 6 Hz (*right side*) had no significant effect on motion dominance

In this second control experiment, we found no indications of any modulatory tACS effects on motion dominance or coherence—neither for 6 Hz nor for 40 Hz stimulation (Figs. 7, 8). Thus, in-phase stimulation does not seem to have a facilitating effect on interhemispheric communication with regard to perceived horizontal motion of the SAM pattern.

Discussion

This study demonstrates for the first time that tACS in the gamma frequency range affects subjective experience of bistable motion. Furthermore, we provide electrophysiological evidence for a modulation of ongoing gamma oscillations, as reflected in an increase of interhemispheric EEG gamma band coherence by tACS.

An elevation in interhemispheric EEG gamma band coherence (30–50 Hz) was previously reported for perceived horizontal as compared to vertical motion using the SAM display (Rose and Büchel 2005). Our findings of Experiment 1 strongly support a functional role of gamma band coherence in bistable motion perception by demonstrating that driving gamma activity externally enhances interhemispheric coherence. However, our behavioral tACS effect of decreased proportion of horizontal percept durations in Experiment 1 seems to contradict the finding of increased interhemispheric EEG gamma band coherence for perceived horizontal motion (Rose and Büchel 2005), because if 40 Hz tACS enhances interhemispheric gamma band coherence,
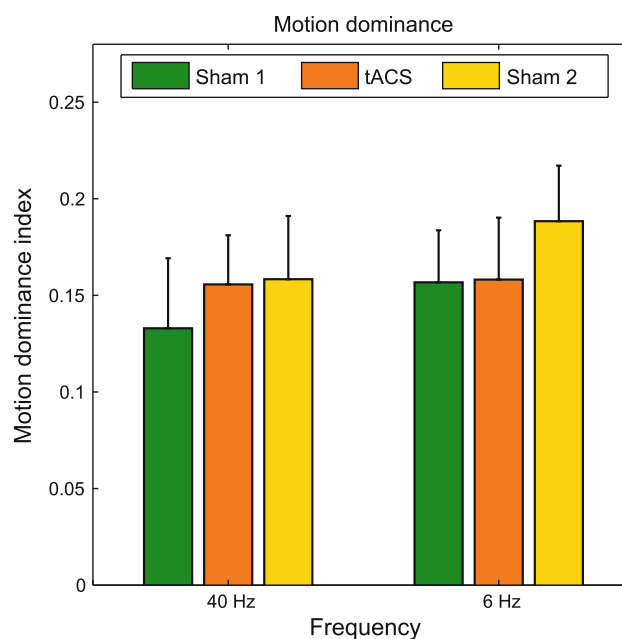
one might expect an increase rather than a decrease of the proportion of perceived horizontal motion. This discrepancy is very likely due to the fact that our bilateral tACS with a 180° phase difference between hemispheres entrains ongoing gamma oscillations of both hemispheres in anti-phase, whereas the study by Rose and Büchel (2005) investigated the coherence of ongoing gamma oscillations between hemispheres and these oscillations are typically in phase (Demiralp et al. 2007). Importantly, coherence is not informative with respect to the phase difference, since two signals with different phases can be highly coherent as long as their phase difference remains constant. Therefore, an increase in interhemispheric coherence can either be due to signals that are in-phase or signals that are in anti-phase. A possible consequence of anti-phase stimulation of the two hemispheres in Experiment 1 could be a functional decoupling of the hemispheres that impairs horizontal motion integration and thereby decreases the proportion of perceived horizontal motion. In contrast, an increase of perceived horizontal motion might require the gamma oscillations of the two visual hemispheres to be coherent and in phase.

This relates to our Experiment 3, in which we used in-phase stimulation of the two hemispheres. However, we found no evidence for a functional role of in-phase 40 Hz stimulation regarding both behavior and coherence. This finding might suggest that—at least for SAM perception—interhemispheric integration can only be disturbed by (anti-phase) 40 Hz tACS, whereas a facilitation of interhemispheric coupling via in-phase stimulation seems to be more difficult. So far, a facilitating effect of
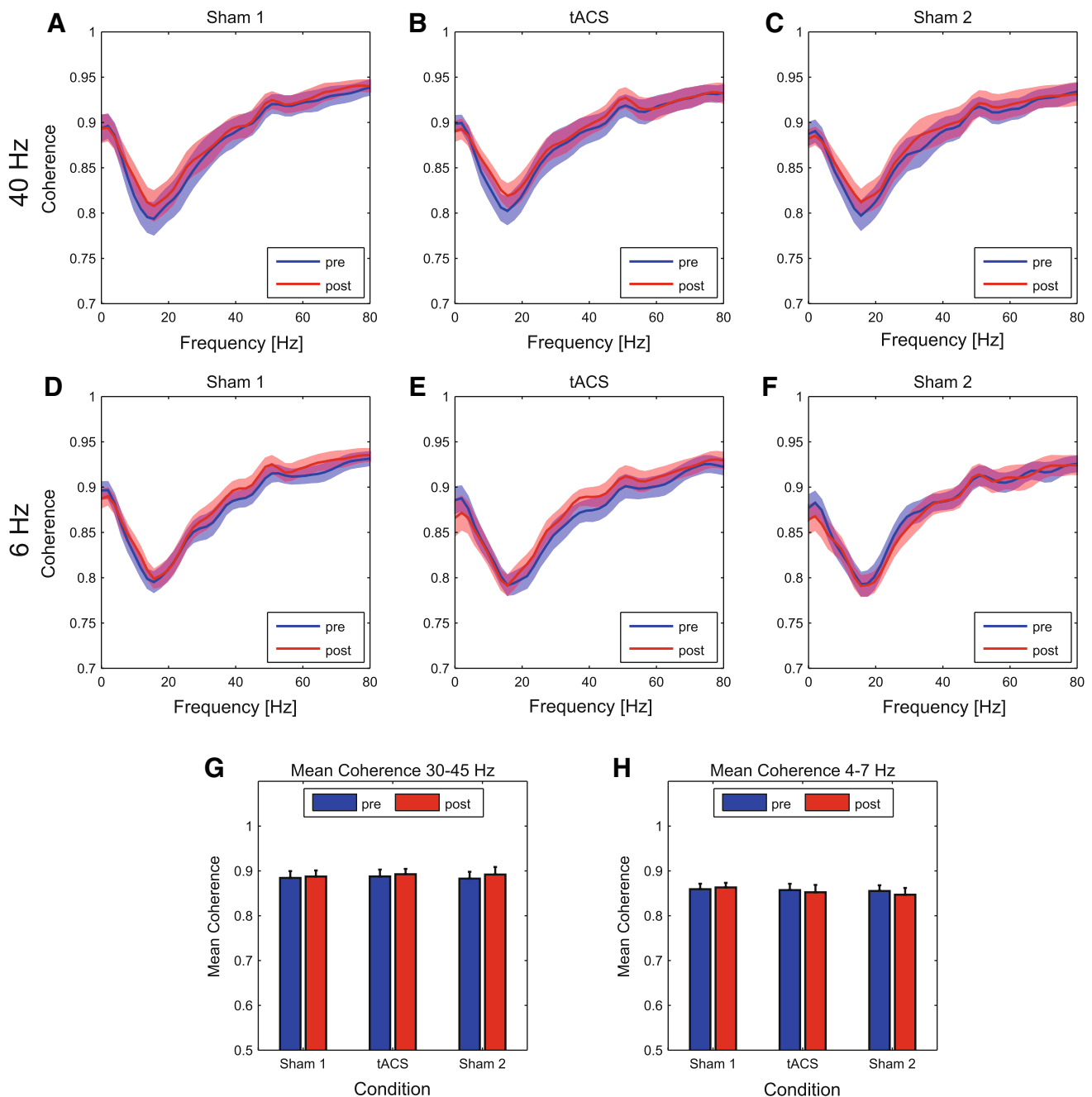
Fig. 8 Effects of tACS on interhemispheric coherence in Experiment 3. Coherence spectra of the spontaneous EEG before (*blue*) and after (*red*) SAM presentation in the sham1 (**a**), tACS (**b**), and sham2 (**c**) condition are very similar, regardless of whether in-phase 40 Hz stimulation was applied or not. The solid colored lines represent the mean values for each condition and the shaded regions represent ± 1 SE. Similarly for the 6 Hz condition, there are no indications of any pre/post differences in the coherence spectra for the sham1 (**d**), tACS (**e**), and sham2 (**f**) condition. Formal statistical testing of the mean coherence in the gamma (**g**) and theta (**h**) range yields no significant results

in-phase tACS on cognitive performance has been reported only for cortical regions within one hemisphere, but not between hemispheres (Polanía et al. 2012). Alternatively, our tACS electrode montage for in-phase stimulation might have been ineffective in coupling the two hemispheres, because the current flows mainly between the anode and cathode within each hemisphere and not between hemispheres (as in the anti-phase stimulation set-up). Future experiments with finite element modeling (Miranda et al. 2006; Neuling et al. 2012a, b) of the tACS-induced current flow in the brain are needed to answer this question.

The effects of 40 Hz anti-phase tACS were frequency specific in that they were not observed with 6 Hz in Experiment 2. However, one possible confound is that stimulation intensity was lower during 6 Hz than 40 Hz anti-phase tACS. Nevertheless, we argue that stimulation intensity is not sufficient to explain the observed effects, because the stimulation intensities in Experiment 3 were even higher and did not lead to significant differences between 6 and 40 Hz in-phase tACS.

Interhemispheric gamma band coherence is mediated via the corpus callosum in the animal (Kiper et al. 1999) and human (Knyazeva et al. 1999) brain, and it breaks down after callosal sectioning (Engel et al. 1991). For the SAM display, it has been shown that the subjective experience of bistable motion can be predicted by the microstructural integrity of those corpus callosum segments that connect the motion sensitive areas of the human MT/V5 complex (Genç et al. 2011). Our results strongly suggest interhemispheric gamma band coherence as the physiological mechanism underlying these structure–function relations in bistable motion perception. This view is in line with a relation between corpus callosum structure and gamma band oscillations that has recently been reported (Zaehle and Herrmann 2011).

There is evidence from functional magnetic resonance imaging (fMRI) that perceptual switches between the two alternative percepts of bistable motion stimuli are mediated by activity changes in the human motion complex (hMT/V5+) in a bottom-up fashion (Castelo-Branco et al. 2002; Muckli et al. 2002). A direct role of extrastriate motion sensitive areas in the processing of bistable apparent motion is supported by our study in that it demonstrates a modulating effect of tACS close to hMT/V5+ on the subjective motion experience of the SAM display. However, other fMRI studies on bistable motion perception reported switch-related activations not only for hMT/V5+ but also in high-level frontal and parietal areas (Sterzer et al. 2002; Sterzer and Kleinschmidt 2007).

Regarding the role of parietal networks in perceptual switches, it has been shown that transient disruption of parietal regions by transcranial magnetic stimulation (TMS) modulates the duration of perceptual states in bistable structure-from-motion perception (Kanai et al. 2010, 2011) and other forms of perceptual bistability (Carmel et al. 2010; Zaretskaya et al. 2010). Although these TMS studies provide evidence for a causal role of parietal cortex in a variety of bistable settings, the underlying neurophysiological mechanisms by which parietal brain regions exert their presumed top-down influence on lower-level areas of the network remain elusive. In this context, our study underscores the usefulness of tACS in providing evidence for the causal role of a neurophysiological mechanism, i.e., brain oscillations, which have been associated previously with the perception of SAM displays (Başar-Eroglu et al. 1996; Müller et al. 1999; Strüber et al. 2000; Strüber and Herrmann 2002).

As pointed out by Thut et al. (2011a), the existing studies on the entrainment of perceptually relevant brain oscillations by tACS are only suggestive of rhythmic entrainment of neural oscillations, because they provide either behavioral (Kanai et al. 2008; Feurra et al. 2011; Laczó et al. 2012) or electrophysiological (Zaehle et al. 2010) evidence for entrainment, whereas only a combination of both would clearly demonstrate entrainment and the behavioral relevance of oscillatory activity. Our study includes both behavioral and electrophysiological effects of tACS. However, we measured EEG offline after stimulation because of the tACS-induced artifacts, whereas online EEG recording would be desirable to unequivocally demonstrate entrainment, as has been reported recently for simultaneous recordings of TMS and EEG (Thut et al. 2011b). Nevertheless, it seems plausible to assume that our EEG effects after tACS result from neurophysiological changes during tACS. In addition, our behavioral effects were recorded during tACS and must have evolved from some neurophysiological change. Therefore, we argue that our findings suggest that we have actually entrained EEG oscillations in the gamma frequency range which in turn modulated behavior.

However, the question arises how tACS can produce EEG effects (increased gamma band coherence) that outlast stimulation offset. In a previous study, we suggested (and modeled) spike timing-dependent plasticity (STDP) as a plausible candidate to explain a tACS-induced increase in EEG alpha power (Zaehle et al. 2010). In the current study, however, we observed a pure coherence effect in the gamma range without a corresponding power increase. Thus, the enhanced gamma coherence between hemispheres most probably reflects an increase in phase synchronization. Interestingly, it has been shown that phase synchronization between two brain regions can induce STDP (Fell and Axmacher 2011). Moreover, an induction of GABAergic STDP has been demonstrated recently (Lamsa et al. 2010). This is important because STDP is predominantly related to excitatory synapses, whereas gamma oscillations are strongly influenced by GABAergic inhibitory interneurons (Whittington et al. 2000). Thus, there is evidence supporting the notion that the increase of gamma coherence during the post-stimulation period might indeed reflect tACS-induced STDP effects that outlasted stimulation offset.

Principally, these putative STDP effects might also be induced by 6 Hz stimulation, since phase synchronization-related STDP has also been reported for theta oscillations (Fell and Axmacher 2011). However, given that theta oscillations are commonly found in frontal brain regions and subcortical structures like the hippocampus (Mitchell

et al. 2008), it seems unlikely that our tACS electrodes over occipital–parietal areas were effective in driving theta generators and related neuroplasticity.

Moreover, our findings give causal support to previous correlative studies in animals (Fries et al. 1997, 2002) and humans (Başar-Eroglu et al. 1996; Keil et al. 1999; Rodriguez et al. 1999; Strüber et al. 2000, 2001; Doesburg et al. 2005; Mathes et al. 2006; Ehm et al. 2011; Hipp et al. 2011) on the role of gamma band oscillations for bistable perception. A similar causal relationship has been demonstrated between beta oscillations (12–30 Hz) and motor behavior by applying either 20 Hz tACS in healthy humans (Pogosyan et al. 2009) or 20 Hz deep-brain stimulation in patients with Parkinson's disease (Kühn et al. 2009). Another causal relationship was demonstrated between slow oscillations and human memory retention by applying slow transcranial oscillatory stimulation during sleep (Marshall et al. 2006). These findings, in combination with ours, suggest that tACS can be a very powerful tool to demonstrate the causal interaction between certain cognitive functions and specific frequencies.

Conclusions

The present study demonstrates that bilateral 40 Hz tACS in anti-phase affects subjective experience of bistable motion. Furthermore, our data provide electrophysiological evidence for an entrainment of gamma oscillations by tACS. Since different frequencies have been associated with different cognitive processes during bistable perception (Başar-Eroglu et al. 1996; Müller et al. 1999; Strüber et al. 2000, 2001; Strüber and Herrmann 2002; Doesburg et al. 2005; Işoğlu-Alkaç and Strüber 2006; Mathes et al. 2006, 2010; Ehm et al. 2011), future studies could apply tACS at different frequencies in order to investigate their proposed functional roles. In addition, tACS could prove useful in improving gamma band related cognitive functions in neuropsychiatric disorders like schizophrenia (Herrmann and Demiralp 2005; Uhlhaas and Singer 2010).

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