The causal role of α-oscillations in feature binding

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specific frequency to individual subjects to examine how the stimulation might modulate their perceptual states. It is noteworthy that, because of volume conduction effects in EEG, even "local" α-oscillations are usually driven by large-scale brain networks. This is why we chose α-oscillations at some electrodes to index the dynamics of large-scale brain networks. We also performed interregional connectivity analyses with the EEG data. The connectivity results are presented in *SI Appendix*.

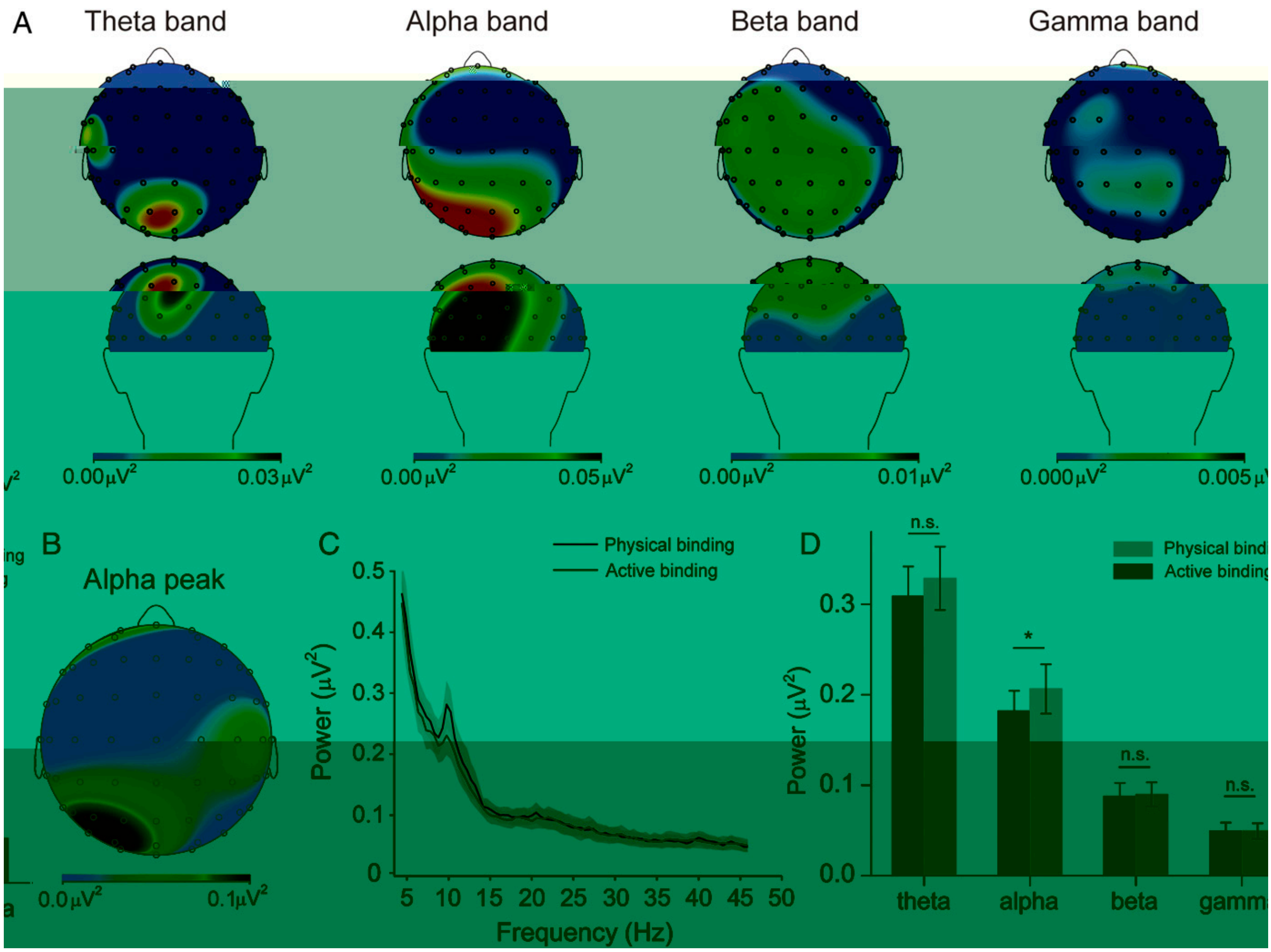

Fig. 2. EEG results. (*A*) Group-averaged brain topographies of power differences in different bands from top and back views. From left to right are topographies in the θ- (4 to 7 Hz), α- (7 to 14 Hz), β- (14 to 30 Hz), and γ- (30 to 60 Hz) bands. (*B*) Group-averaged brain topography of the α-peak power difference. (*C*) Group-averaged FFT power spectra for the physical binding state (light gray line) and the active binding state (dark gray line). The shaded areas represent 1 SEM calculated across subjects. (*D*) Group-averaged powers in the θ-, α-, β-, and γ-bands for the 2 binding states. Error bars represent 1 SEM calculated across subjects; n.s., not significant; *$P < 0.05$.

found that the continuous tACS decreased the proportion of the active binding time (mean ± SEM: 0.46 ± 0.06) relative to the sham stimulation (mean ± SEM: 0.65 ± 0.05). The difference between the 2 stimulation conditions was significant [$t(12) = 3.028$, $P = 0.011$] (Fig. 4*A*). Furthermore, in a control experiment (tACS Exp. 3), we examined whether the tACS effect was specific to the stimulation site. We applied continuous tACS over the right posterior area (PO4) and found that there was no significant

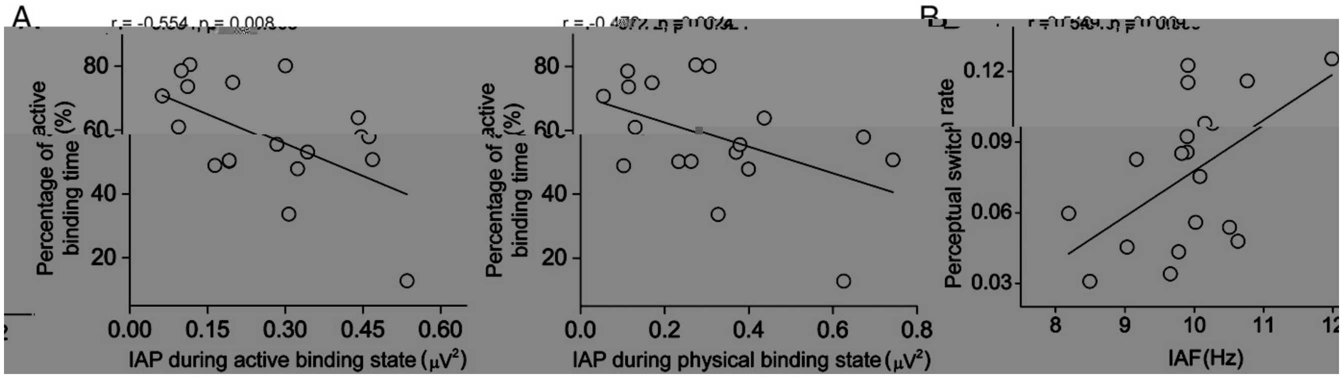

Fig. 3. Results of correlation analyses. (*A*) Correlations between the percentage of time subjects perceived the active binding and the IAPs during the active and physical binding across individual subjects. (*B*) Correlation between the IAF and the perceptual switch rate across individual subjects.

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difference in the proportion of the active binding time between the sham stimulation condition (mean ± SEM: 0.46 ± 0.05) and the tACS condition (mean ± SEM: 0.48 ± 0.05) [$t(11) = 1.244$, $P = 0.240$].

In tACS Exp. 2, subjects received continuous tACS stimulation at 1 of 3 possible frequencies, including IAF, IAF − 2 Hz, and IAF + 2 Hz. We aimed to test whether driving IAF toward slower vs. faster oscillations would result in slower vs. faster perceptual switch, respectively. A 1-way repeated-measures ANOVA on perceptual switch rate showed that the main effect of tACS frequency was significant [$F(2, 24) = 4.351$, $P = 0.024$]. Post hoc paired *t* tests showed that the perceptual switch rate was significantly faster during tACS at IAF + 2 Hz (mean ± SEM: 0.103 ± 0.013) than during tACS at IAF − 2 Hz (mean ± SE: 0.075 ± 0.012) [$t(12) = 2.996$, $P = 0.011$] (Fig. 4*B*). The observed faster perceptual switch could be due to the shortening of perceptual epochs of the physical binding, the active binding, or both kinds of binding. Fig. 4*C* shows the average durations of perceptual epochs of the physical and active binding at the 3 tACS frequencies. One-way repeated-measures ANOVAs showed that the main effect of tACS frequency was significant for the active binding [$F(2, 24) = 3.935$, $P = 0.033$], but not for the physical binding [$F(2, 24) = 1.813$, $P = 0.201$], indicating that tACS mainly acted on the active binding process.

Discussion

Several major findings emerged in this study. First, IAP was negatively correlated with the time proportion of the active binding state. Second, subjects' perceptual switch rate was positively correlated with their IAF. Third, with the entrainment of α-oscillations by tACS, selectively changing α-oscillations could shape subjects' perceptual states of the color-motion binding. On the one hand, applying tACS at IAF could effectively decrease the time proportion of the active binding state. On the other hand, delivering tACS at different temporal frequencies in the α-band could change subjects' perceptual switch rates; tACS at a higher frequency led to a faster perceptual switch through shortening perceptual epochs of the active binding. α-Oscillations are the dominant oscillations in the human brain and are negatively correlated with cortical excitability and task performance. They are traditionally believed to represent idling processes in the brain and were recently viewed as a general inhibition mechanism for cognitive processing (26). Our findings provide strong evidence of the causal role of α-oscillations in feature binding, especially in active feature binding, which significantly advances our understanding of the functions of α-oscillations in human cognition.

In recent years, a growing body of research has suggested that α-activity is closely associated with conscious visual perception (27–29). α-Oscillations have been demonstrated to be able to dictate the resolution of conscious visual updating (24), to determine whether a visual stimulus could be perceived or not (30), to predict the stability of subjects' bistable perception (31), and to determine the perceived motion-direction changes when subjects were facing continuously moving objects (32). Here, we used a bistable color-motion binding stimulus and found that α-oscillations could trigger the switches between the two perceptual states and determine the dominant perceptual state, adding further evidence that α-band oscillations play a key role in visual perception and visual consciousness.

The decrease in the time proportion of the active binding state by applying tACS at IAF suggests that tACS might enhance IAP effectively, which is in line with previous studies (22, 33, 34). For example, Zaehle et al. (34) found that delivering tACS at subject's IAF could enhance α-power in human EEG. Additionally, the α-power increase induced by tACS could last for at least half an hour (33). Our finding that tACS at IAF ± 2 Hz modified subjects' perceptual switch rates indicates that tACS might interfere with the peak frequency of the α-band, which is also consistent with previous studies (23–25). Combining magnetoencephalography and tACS, Minami and Amano (25) demonstrated that the peak α-frequency was changed according to the target frequency for parieto-occipital tACS at IAF ± 1 Hz. Cecere et al. (23) also suggested a similar effective manipulation of the EEG peak α-frequency using tACS at IAF ± 2 Hz.

There has been a long, intense debate about the role of neural oscillations in the binding problem (12, 35–37). Some electrophysiological studies found that synchronized neuronal firing in the γ-band (∼40 Hz) in monkey (14), cat (13), and human brains (15, 37, 38) was responsible for feature binding. However, this view has been challenged by some research groups (39, 40). Here, we found that α-band activities causally affected feature binding (active feature binding more profoundly). Some kinds of feature binding (e.g., the active binding here) require interactions among various brain areas (8, 9, 41). γ-Oscillations are typically restricted to monosynaptic connections and intraareal interactions (42), whereas α-oscillations are associated with long-range integrations and could provide a dynamic link among distributed visual areas (43, 44). Therefore, α-band activities might be necessary for feature binding requiring large-scale brain networks. Furthermore, γ-band synchronization modulates input gain and mediates feedforward connections (45, 46), whereas reentrant feedback influences are mediated by α-band activities (11, 19, 42). Accumulating evidence suggests that feature binding requires reentrant processing (7, 9), which further underscores the importance of α-oscillations in feature binding.

We observed that the α-power decreased during the active feature binding. In our recent fMRI study (9), using the same visual stimulus, we found that the active feature binding required

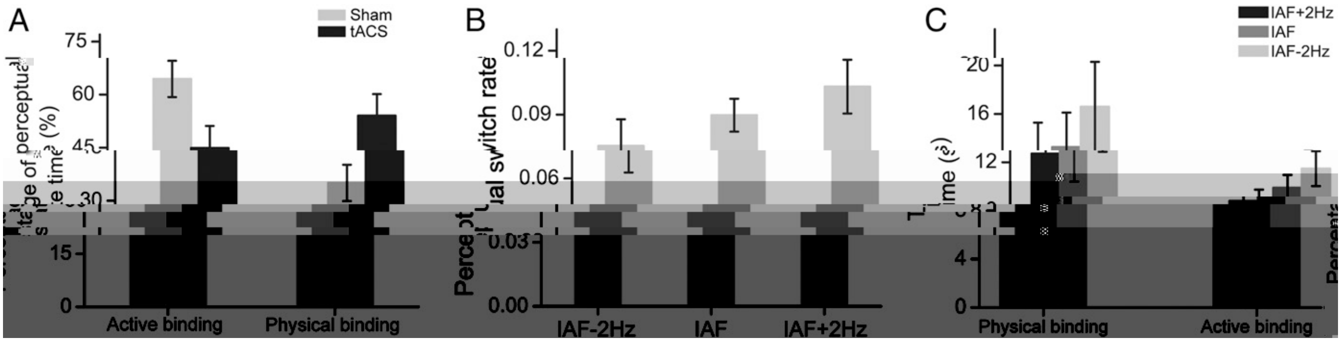

Fig. 4. Results of tACS experiments. (*A*) Percentages of perceptual state time for the physical and active binding in the sham stimulation condition and the tACS condition. (*B*) Perceptual switch rates under tACS at IAF, IAF − 2 Hz, and IAF + 2 Hz. (*C*) Averaged durations of perceptual epochs for the physical and active binding at the 3 tACS frequencies. Error bars represent 1 SEM calculated across subjects.

increased feedback connections from V4 and V5 to V2 and decreased feedforward connections from V2 to V4 and V5, whereas the physical binding relied on increased feedforward connections (also see ref. 47). In other words, when subjects switched to the active binding state, the representation of feedback connections was recruited and became more activated. Previous works found that α-band activities were essential in feedback processing (11) and were weaker when there were top-down or feedback influences (48, 49). Consistent with these findings, we found that the lower α-power accompanied the active binding, relative to the physical binding. This finding is also in line with Jensen et al.'s hypothesis (50) that α-band activity could control information flow dynamically. They argue that α-band activity reflects how many active representations could be processed simultaneously. If α-power increases or decreases, it means that fewer or more representations could be processed in one α-cycle. Notably, decreased α-activity is usually associated with a concurrent increase in interareal α-band phase synchrony (51, 52), which might be essential for the active binding.

We also found that α-oscillations could determine the perceptual switch rate between the 2 states, through affecting the active binding process specifically. Even though the perceptual switch rate was much lower than the individual α-frequency, there was a strong correlation between the individual α-frequency and the perceptual switch rate, indicating that α-band oscillations might serve as a basic temporal unit for feature binding. Temporal structure is one of the most important dimensions in visual information processing and timing is believed to be a fundamental function of α-band oscillations (53). With magnetoencephalography, Wutz et al. (54) found that there was a strong correlation between individual α-frequency and the temporal resolution of perception. They also found that the cycle of α-oscillations was the fundamental unit of temporal integration in visual perception. Minami and Amano (25) found that tACS could elongate or shorten the temporal window of motion-induced spatial conflict (i.e., an illusion involving motion and shape integration). α-Oscillations were also found to be an underlying mechanism of multisensory integration (23, 55). For example, Cecere et al. (23) showed that delivering tACS in the α-band over occipital regions could causally modulate the temporal window of visual–auditory integration. These findings provide converging evidence that α-band oscillations, serving as a temporal unit, could determine the integration of features, even from different sensory modalities.

It might be argued that our findings with α-oscillations can be simply explained by different attention levels during the 2 bindings. We have several reasons against this explanation. First, in the tACS experiments, we found that, when delivering tACS at different temporal frequencies in the α-band, subjects' perceptual switch rates changed correspondingly. To our best knowledge, no evidence has been found to show that attention is associated with α-frequency. Second, previous work found that attention could enhance γ-oscillations and synchrony in both humans and monkeys (56–58). However, we failed to find any significant difference in γ-oscillations and synchrony between the 2 bindings (Fig. 2*D* and *SI Appendix*, Figs. S1 and S2). Third, in our previous work (9), we did a whole-brain scan when subjects viewed the 2 bindings. A group analysis did not find any brain area (V1–V5 and posterior parietal cortex) showing differential responses to the 2 bindings. The dynamic causal modeling analysis also failed to find any significant difference in modulatory connectivity from the posterior parietal cortex (a key brain area in human attention network) to V2, V4, and V5 between the 2 bindings.

In conclusion, our findings here provide insights into not only the neural mechanisms of feature binding but also the functions of brain oscillations. We demonstrate that α-oscillations could determine the way of color-motion binding and that tACS is an effective approach to shaping feature binding. Our findings suggest that α-activity is an important neural substrate for feature binding, especially for active feature binding.

Materials and Methods

Subjects. Eighteen subjects (10 female, 19 to 27 y old) participated in the EEG experiment. Of the 18 subjects, 13 (6 female, 19 to 25 y old) also participated in tACS Exps. 1 and 2. Twelve subjects (9 female, 19 to 25 y old) participated in tACS Exp. 3 (3 new subjects and 9 of the subjects who had already taken part in tACS Exps. 1 and 2). In total, we recruited 21 subjects in this study. All subjects were naïve to the purpose of the study. They were right-handed, reported normal or corrected-to-normal vision, and had no known neurological or visual disorders. They each gave written informed consent before participating. Our experimental procedures were approved by the Human Subject Review Committee of Peking University.

Apparatus. Visual stimuli were displayed on Sony Trinitron monitors (model: MultiScan G520; resolution: 1,024 × 768; refresh rate: 100 Hz). Before the experiments, the monitors were calibrated with a MINOLTA CS-100A Chroma Meter. The viewing distance was 60 cm. During the experiments, we used a head and chin rest to stabilize subjects' head position.

Stimuli. Two stimuli were used in this study (Fig. 1). Each of them contained 2 sheets of random dots, 1 sheet moving up and the other moving down [sheet size: 29° × 26.5°; dot diameter: 0.11°; dot speed: 3°/s; dot luminance: 15 cd/m^2; dot density: $5/(°)^2$]. Both stimuli were able to induce color-motion misbinding in the right peripheral area. On both sheets of these 2 stimuli, dots in the right peripheral area (6° × 26.5°, the effect part) and those in the rest area (23° × 26.5°, the induction part) were rendered with different colors, either red [CIE (1,931): $x = 0.614$, $y = 0.344$] or green [CIE (1,931): $x = 0.289$, $y = 0.593$]. For 1 stimulus, on the upward-moving sheet, dots in the effect and induction parts were red and green, respectively. On the downward-moving sheet, dots in the effect and induction parts were green and red, respectively. For the other stimulus, on the upward-moving sheet, dots in the effect and induction parts were green and red, respectively. On the downward-moving sheet, dots in the effect and induction parts were red and green, respectively. Subjects knew how the stimuli were designed and knew that the dot motion directions in the induction and effect parts were opposite.

EEG Experiment. The EEG experiment consisted of 16 blocks, 8 blocks for each of the 2 stimuli. At the beginning of a block, a white dot was presented at the center of the screen and subjects were instructed to fixate on the dot throughout the block. Six seconds later, 1 of the 2 visual stimuli was presented for 180 s. Subjects were asked to press 1 of 2 keys to indicate their perceptual state, either the physical binding state or the active binding state. Meanwhile, continuous EEG was recorded from 64 sintered Ag/AgCl electrodes positioned according to the extended international 10 to 20 EEG system. Vertical electrooculogram was recorded from an electrode placed above the right eye. Horizontal EOG was recorded from an electrode placed at the outer canthus of the left eye. Electrode impedance was kept below 5 kΩ. EEG was amplified with a gain of 500 K, band pass-filtered at 0.05 to 100 Hz, and digitized at a sampling rate of 1,000 Hz. The signals from these electrodes were referenced online to the tip of the nose and were rereferenced offline to the average of the 2 mastoids.

Offline EEG data analysis was perfor(e)-269(EE)-415.5(a)09(pl22.7(n-273.4(w)17.3(as)-257 posterior area (Cz and PO3 in the international 10 to 20 EEG system), respectively. The size of the electrodes was 35 cm^2. We used a sinusoidal current and set DC offset at 0. The impedance was kept below 10 kΩ. The intensity of the current was initially set at 2 mA. We asked subjects to report any perception of tACS-induced phosphenes throughout the experiments. For participants reporting perception of phosphenes, the intensity was lowered in 0.1-mA steps until no phosphene was perceived. In our study, the mean stimulation intensity was 1.43 mA.

In tACS Exp. 1, subjects underwent 2 experimental sessions (the IAF session and the sham session) spaced 40-min apart from each other to avoid any carryover effect from the preceding session (33). In each session, they performed 6 blocks of the behavioral task (same as that in the EEG experiment) while receiving continuous tACS at PO3 at IAF Hz or receiving sham stimulation. The sham session was identical to the IAF session except that we kept the stimulator off during the "stimulation" period.

tACS Exp. 2 was very similar to tACS Exp. 1 except that it had 4 experimental sessions: The IAF session, the IAF − 2 session, the IAF + 2 session, and the sham session. In the IAF ± 2 sessions, subjects received continuous tACS at IAF ± 2 Hz, respectively. tACS Exp. 3 served as a control experiment for tACS Exp. 1. These 2 experiments were identical except that tACS was delivered over the right posterior area (PO4) in tACS Exp. 3. In all of the tACS experiments, the session order was randomized across subjects.

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