The causal role of α -oscillations in feature binding

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The binding problem-how to integrate features into objectsposes a fundamental challenge for the brain. Neural oscillations, especially γ -oscillations, have been proposed as a potential mechanism to solve this problem. However, since γ -oscillations usually reflect local neural activity, how to implement feature binding involving a large-scale brain network remains largely unknown. Here, combining electroencephalogram (EEG) and transcranial alternating current stimulation (tACS), we employed a bistable color-motion binding stimulus to probe the role of neural oscillations in feature binding. Subjects' perception of the stimulus switched between its physical binding and its illusory (active) binding. The active binding has been shown to involve a large-scale network consisting of spatially distant brain areas. α -Oscillations presumably reflect the dynamics of such large-scale networks, especially due to volume conduction effects in EEG. We found that, relative to the physical binding, the α -power decreased during the active binding. Additionally, individual α -power was negatively correlated with the time proportion of the active binding. Subjects' perceptual switch rate between the 2 bindings was positively correlated with their individual α -frequency. Furthermore, applying tACS at individual α -frequency decreased the time proportion of the active binding. Moreover, delivering tACS at different temporal frequencies in the α -band changed subjects' perceptual switch rate through affecting the active binding process. Our findings provide converging evidence for the causal role of α-oscillations in feature binding, especially in active feature binding, thereby uncovering a function of α -oscillations in human cognition.

brain oscillations | individual α -frequency (IAF) | electroencephalogram (EEG) | transcranial alternating current stimulation (tACS) | visual feature binding

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*.

Results

Psychophysical Results. When subjects fixated at the center of the stimulus, the color and motion of the dots in the effect part were perceived as being bound either in the same fashion (active binding) as those in the induction part or in the opposite fashion (physical binding). On average, their perceptual states switched about every 13.640 s (SEM: 1.079). The mean durations of the active binding state and the physical binding state were 16.088 s (SEM: 1.707) and 11.192 s (SEM: 1.332). The former mean duration was significantly longer than the later one [t(17) = 2.254, P = 0.038].

EEG Results. We recorded subject's continuous EEG signals when they performed the behavioral task and obtained the full power spectrum of the EEG signal epochs (100 to 1,100 ms after key press) using fast Fourier transform (FFT). Fig. 24 shows the group-averaged brain topographies of the power difference between the 2 perceptual states in θ - (4 to 7 Hz), α - (7 to 14 Hz), β - (14 to 30 Hz), and γ - (30 to 60 Hz) bands For each band, the power was submitted to a repeated-measures ANOVA with perceptual state (physical binding and active binding) and electrode as within-subject factors For the α -band, we found that the main effects of electrode [F(60, 1,020) = 7.972, P = 0.004] and perceptual state [F(1, 17) = 12.069, P = 0.003] were significant, while the interaction between perceptual state and electrode [F(60, 1,020) = 1.033, P = 0.371] was not significant. For the other 3 bands, the main effects of perceptual state [all F(1, 17) <1.711, P > 0.208] and the interactions between perceptual state and electrode [all F(60, 1,020) < 0.965, P > 0.363] were not significant, and the main effects of electrode [all F(60, 1,020) >3.284, P < 0.033] were significant. It is clear that there was significant α -power difference in the left posterior area (note that the perceptual state changes occurred in the right visual field in Fig. 2 A and B). In this area, we selected 10 electrodes with the largest differences as the region-of-interest (ROI), including P1, P3, P5, P7, Pz, PO3, PO7, POZ, O1, and Oz [all t(17) > 2.597, P < 0.019]. EEG signals from these electrodes were pooled together for further analysis

In this ROI, the power was submitted to a repeated-measures ANOVA with perceptual state (physical binding and active binding) and frequency band (θ -, α -, β -, and γ -bands) as withinsubject factors (Fig. 2 *C* and *D*). The interaction between perceptual state and frequency band was significant [*F*(3, 51) = 3.893, *P* = 0.047]. Both the main effects of frequency band [*F*(3, 51) = 45.911, *P* < 0.001] and perceptual state [*F*(1, 17) = 8.095, *P* = 0.011] were significant. Planned paired *t* tests showed that the α -power during the physical binding state was significantly larger than during the active binding state [*t*(17) = 4.063, *P* = 0.001], but no significant difference was found in the other frequency bands [all *t*(17) < 1.718, *P* > 0.104] (Fig. 2*D*). These findings suggest that α -activity might be important for feature binding, either physical binding or active binding or both.

To further evaluate the role of α -activity in feature binding and perceptual switch, we performed 2 correlation analyses We first calculated the correlation coefficients between the percentage of time subjects perceived the active binding and the individual α -powers (IAPs) during the active and physical binding across individual subjects The correlations were significant and negative (active binding: r = -0.554, P = 0.008, 1-tailed; physical binding: r = -0.472, P = 0.024, 1-tailed) (Fig. 3A). The larger the IAP, the shorter the active binding state. Second, we calculated the correlation coefficient between the individual α -frequency (IAF) and the perceptual switch rate across individual subjects and found that there was a significant positive correlation (r = 0.549, P =0.009, 1-tailed) (Fig. 3B), suggesting that the individual α -peak frequency could predict the perceptual switch rate.

The EEG data analysis performed above was based on the 1,000-ms EEG epochs immediately following key press We also tried to segment the continuous EEG signals during each perceptual state into epochs of 1,000 ms and then perform similar analyses For the power in the ROI (i.e., the left posterior area), we found a significant interaction between perceptual state and frequency band [F(3, 51) = 4.408, P = 0.021]. Both the main effect of frequency [F(3, 51) = 38.423, P < 0.001] and the main effect of perceptual state [F(1, 17) = 8.213, P = 0.011] were significant. Planned paired t tests showed a significant power difference between 2 perceptual states in the α -band [t(17) = 3.152, P = 0.006], but not in the other bands [all t(17) < 1.642, P > 0.119]. We also found significant negative correlations between the percentage of time subjects perceived the active binding and the IAPs during the active and physical binding across individuals (active binding: r = -0.440, P = 0.034, 1-tailed; physical binding: r = -0.498, P =0.018, 1-tailed) and a significant positive correlation between the IAF and the perceptual synth rate (r = 0.507, P = 0.016, 1-tailed) across subjects Taken together, these 2 segmentation methods provide consistent evidence for the critical role of α -activity in



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 \pm SEM: 0.46 \pm 0.06) relative to the sham stimulation (mean \pm SEM: 0.65 \pm 0.05). The difference between the 2 stimulation condition swas significant [t(12) = 3.028,

P = 0.011] (Fig. 4A). 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.

difference in the proportion of the active binding time between the sham stimulation condition (mean \pm SEM: 0.46 \pm 0.05) and the tACS condition (mean \pm SEM: 0.48 \pm 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 syitch rate was significantly faster during tACS at IAF + 2 Hz (mean \pm SEM: 0.103 ± 0.013) than during tACS at IAF – 2 Hz (mean \pm SE: 0.075 ± 0.012 [t(12) = 2.996, P = 0.011] (Fig. 4B). The observed faster perceptual syitch could be due to the shortening of perceptual epochs of the physical binding, the active binding, or both kinds of binding. Fig. 4C 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, subject's 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 syntch rates tACS at a higher frequency led to a faster perceptual svitch 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 stimulu scould 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 \pm 2 Hz modified subject's 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 \pm 1 Hz. Cecere et al. (23) also suggested a similar effective manipulation of the EEG peak α -frequency using tACS at IAF \pm 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 longrange 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 a-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 svitched 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 topdown 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 posterior area (Cz and PO3 in the international 10 to 20 EEG system), respectively. The size of the electrodes was 35 cm². We used a sinusoidal current and set DC offset at 0. The impedance was kept below 10 k Ω . 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

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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 \pm 2 sessions, subjects received continuous tACS at IAF \pm 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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