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# **Distinct Contributions of Alpha and Beta Oscillations to Context-Dependent Visual Size Perception**

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**Abstract** Previous studies have proposed two cognitive mechanisms responsible for the Ebbinghaus illusion effect, i.e., contour interaction and size contrast. However, the neural underpinnings of these two mechanisms are largely unexplored. The present study introduced binocular depth to the Ebbinghaus illusion configuration and made the central target appear either in front of or behind the surrounding inducers in order to disturb size contrast instead of contour interaction. The results showed that the illusion effect, though persisted, was significantly reduced under the binocular depth conditions. Notably, the target with a larger perceived size reduced early alpha-band power (8-13 Hz, 0-100 ms after stimulus onset) at centroparietal sites irrespective of the relative depth of the target and the inducers, with the parietal alpha power negatively correlated with the illusion effect. Moreover, the target with a larger perceived size increased the occipito-parietal beta-band power (14-25 Hz, 200-300 ms after stimulus onset) under the nodepth condition, and the beta power was positively correlated with the illusion effect when the depth conditions were subtracted from the no-depth condition. The findings provided neurophysiological evidence in favor of the two cognitive mechanisms of the Ebbinghaus illusion by revealing

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that early alpha power is associated with low-level contour interaction and late beta power is linked to high-level size contrast, supporting the claim that neural oscillations at distinct frequency bands dynamically support different aspects of visual processing.

**Keywords** Binocular depth · Ebbinghaus illusion · Alpha oscillation · Beta oscillation · EEG

#### Introduction

Human visual size perception is not always a faithful reflection of the physical world, but is highly context-dependent. For instance, an object looks larger when surrounded by several small items than by large ones, termed the Ebbinghaus illusion. Visual illusions provide a unique window into the mechanisms responsible for our conscious experience of the visual world.

The Ebbinghaus illusion has been accounted for by two cognitive mechanisms. One is low-level contour interaction [1-3], which is a sensory interaction at the level of contours or features that causes perceptual distortion of a figure when surrounded by other figures [4]. Local circuits within the primary visual cortex (V1) have been suggested to be associated with contour interaction [5–7]. The other is high-level size contrast [8-10], which relies on cognitive size comparisons of the central target and surrounding inducers and results in a perceptual accentuation of their size differences. Size contrast has been suggested to require feedback connections from higher visual areas [11]. In particular, the Ebbinghaus illusion is linked to feedback projections from the right parietal cortex to the occipital region [12]. Though these two theories are supported by numerous psychophysical studies, the underlying neural mechanisms are largely unexplored.

To probe this issue, by using the stereoscopic presentation of the Ebbinghaus illusion and the electroencephalogram (EEG) technique, the present study investigated the illusory change in stimulus extent as a function of the relative depth positions of the central target and surrounding inducers and its underlying neural mechanisms. The relative depth position of the central circle was manipulated by varying the horizontal disparity of the inducers while keeping the disparity of the central circle fixed. Previous studies have found that separating the target stimulus in depth from the surrounding context significantly reduces the size illusion magnitude [13-15], which is due to that the depth separation would disturb size contrast instead of contour interaction.

Neural oscillations have been suggested to contribute to both depth and size perception. For example, occipital steady-state visually evoked potentials (SSVEP) were larger when stimuli flickering at 8 Hz were viewed at far distances compared to stimuli with identical retinal sizes viewed at near distances in both a real-world setup and a virtual reality environment [16]. A three-dimensional object generated by dynamic random-dot stereograms elicited greater alpha- and beta-band powers at frontal and occipital sites [17]. Both correlated and anticorrelated random-dot stereograms created a diminishment of beta power (13–30 Hz), and the anticorrelated condition also increased alpha power (8-12 Hz) at an occipital site [18]. Resting alpha activity in the occipital and temporal cortex predicted an object's perceived size, and temporal alpha power was also associated with the Ebbinghaus illusion strength [19]. Therefore, we predicted that alpha and beta oscillations would contribute to the generation of the Ebbinghaus illusion.

#### **Materials and Methods**

#### **Participants**

Thirty right-handed healthy volunteers (16 males, mean age = 23.3 years) gave their written consent to participate in this study and received monetary compensation for their participation. Twenty-two participated in Experiment 1, 5 of them also joined in Experiment 2, and 21 of them took part in Experiment 4 [i.e., the event-related potential (ERP) experiment]. Another 8 joined in Experiment 3. Each of them reported no history of neurological or psychiatric disorders and had normal or corrected-to-normal vision. The study was approved by the institutional review board of the Institute of Psychology, Chinese Academy of Sciences, and complied with the tenets of the Declaration of Helsinki.

#### **Stimuli and Procedure**

Stimuli were configured as described below using the MAT-LAB software package (The MathWorks Inc., Natick, USA) and displayed on a 20-inch cathode ray tube (CRT) monitor  $(1,024 \times 768 \text{ at } 100 \text{ Hz})$  using the Psychophysics Toolbox [20, 21]. The images presented to the two eyes were displayed side-by-side on the monitor and perceptually fused using a stereoscope mirror, which presented the left and right halves of the screen separately to the left and right eyes (Fig. 1). Binocular disparity was manipulated by shifting the surrounding circles horizontally without changing their physical sizes. A central fixation  $(1.08^{\circ} \times 1.08^{\circ})$  was presented to each eye at the beginning of each trial to facilitate stable convergence of the two eyes' images. Prior to the start of experiments, participants performed a series of assessments to ensure a stable fusion of the stimuli presented to the two eyes. The viewing distance was 60 cm.

In Experiment 1 (Fig. 2A), two black fixations were respectively presented at the centers of left and right visual fields for 0.5 to 0.9 s, followed by two black circle targets (diameter =  $1.44^{\circ}$ ), each of which was surrounded by four large (diameter =  $2.17^{\circ}$ ) or small circles (diameter =  $0.72^{\circ}$ ). The relative horizontal disparity of the target was 0°, but that of the inducers was  $-0.3^{\circ}$ ,  $0.3^{\circ}$  or  $0^{\circ}$ , thus the target was perceived as in front of (3 cm), behind (3 cm), or at the same depth plane as the inducers (corresponding to crossed, uncrossed, and zero disparities, respectively). The observers' first task was to judge the perceived location of the target relative to the surrounding inducers by key press. Immediately after the key press, a comparison circle whose initial size was selected randomly across trials with a uniform distribution between 1.08° and 1.80° was presented below the target (10.83° from the center of the target). The observers' second task was to adjust the size of the comparison circle to match that of the target in an unspeeded manner. There were 132 trials in total with 22 repetitions for each condition (size of inducers: small or large; relative depth of the target: crossed, uncrossed, and zero).

In Experiment 2 (Fig. 2B), the stimuli were the same and the procedure was similar to those in Experiment 1. The illusory configuration that was presented to one eye in Experiment 1 was presented at the screen center in Experiment 2. The observers binocularly viewed the stimuli without a stereoscope mirror and were required to perform the sizematching task only.

In Experiment 3 (Fig. 2C), the procedure and the tasks used were the same as in Experiment 1, except that the horizontal disparities of the four inducers were different from each other ( $0.2^{\circ}$  to  $0.5^{\circ}$ ,  $-0.5^{\circ}$  to  $-0.2^{\circ}$ , or  $-0.5^{\circ}$  to  $0.5^{\circ}$ ). Specifically, the four inducers were displayed at separate planes, and none of them were at the same plane as the target. The four inducers were either all in front of or behind



the target, or two of them in front of and another two behind the target. The observers were required to perform the depth discrimination task and size-matching task in succession.

In Experiment 4 (i.e., the ERP experiment; Fig. 2D), the observers viewed the stimuli *via* a stereoscope mirror. On each trial, two fixation crosses were presented to opposite eyes for 500 ms, followed by two illusory configurations displayed for 500 ms, then two fixation crosses remained on the screen until a response was made. The observers were asked to judge the location of the target relative to surrounding inducers. Each trial was followed by an inter-trial interval of 200 ms. There were 720 trials in total with 120 repetitions for each condition.

#### **EEG Data Recording**

Participants were seated in a comfortable chair in a silent, electrical-shielded, and temperature-controlled room. Continuous EEG data were recorded from 64 scalp electrodes embedded in a NeuroScan Quick-Cap (Neuroscan, Charlotte, USA). Electrodes were placed according to the international 10–20 system. Four bipolar facial electrodes, positioned on the outer canthi of each eye and in the inferior and superior areas of the left eye orbit, monitored horizontal and vertical eye movements, respectively. Sensor impedances were kept below 10 k $\Omega$ . EEG was continuously recorded at a rate of 250 Hz using the midpoint of CZ and CPZ as reference. The signal was amplified and acquired using NeuroScan Synamps 2 amplifiers and acquisition software. The signal was band-pass filtered online at 0.01–100 Hz.

#### **EEG Data Analysis**

EEG data were analyzed offline with EEGLAB v2023.0 [22]. The data were re-referenced to the average of left and right mastoid sites and were filtered with the default EEGLAB filter (pop\_eegfiltnew) excluding activity below 1 Hz and above 40 Hz in succession. The preprocessed data was cut into 1500 ms segments covering 500 ms before and 1000 ms after the onset of illusory configuration and was baseline corrected by subtracting the pre-stimulus data (-500 ms to 0 ms). The data were visually inspected to reject trials with artifacts (e.g., muscle artifacts), and independent component analysis (ICA) was computed (i.e., EEGLAB implementation of the infomax ICA algorithm). The IClabel algorithm [23] was used to categorize the Brain, Muscle, Eye, Heart, Channel Noise, and others based on their spatial topography. Independent components that were classified as muscle, eyes, heart, or channel noise by the IClabel algorithm with a probability higher than 80% were discarded.

EEG data were transformed into the time-frequency domain using the method of fast Fourier transformation (FFT). The event-related spectral perturbation (ERSP) after the onset of the illusory figure was baseline corrected by subtracting the pre-stimulus power (-200 ms to 0 ms). For each participant, alpha and beta amplitudes were respectively defined as the mean power in the alpha (8–13 Hz)



Fig. 2 Experimental procedures. In Experiment 1 (A), stimuli were dichoptically presented *via* a stereoscope mirror, and observers were required to sequentially perform depth discrimination and size-matching tasks. In Experiment 2 (B), stimuli were binocularly presented at the screen center. In Experiment 3 (C), stimuli were simultaneously

and beta (14–25 Hz) range, expressed in normalized power  $[10*\log_{10}(\mu V)^2]$ .

#### Results

#### **Experiment 1: Depth Cue Decreases Size Illusion Effect**

The average accuracy of depth discrimination was 98.6% (SD = 2.1%). The illusion effect was measured as the difference in the perceived sizes of the central target surrounded by small and large inducers relative to its physical size (%).

The results of repeated-measures analysis of variance (ANOVA) showed that both the main effects of depth ( $F_{(2, 42)} = 49.97$ , P < 0.001,  $\eta_p^2 = 0.71$ ) and size

presented to separate eyes, with the four surrounding inducers presented at different depths. In Experiment 4 (**D**), stimuli were dichoptically presented for 0.5 s, and observers had to perform the depth discrimination task only.

of inducers ( $F_{(1, 21)} = 14.04$ , P = 0.001,  $\eta_p^2 = 0.40$ ) and their interaction ( $F_{(2, 42)} = 11.10$ , P < 0.001,  $\eta_p^2 = 0.35$ ) were significant. Further analysis demonstrated that the illusion effect was significant for zero disparity ( $t_{(21)} =$ 5.01, P < 0.001, d = 1.07) and uncrossed disparity ( $t_{(21)} =$ 2.92, P = 0.008, d = 0.62), but not for crossed disparity ( $t_{(21)} = 1.32$ , P = 0.200, d = 0.28) condition. Moreover, the illusion effect under the condition of zero disparity was significantly larger than the conditions of crossed and uncrossed disparity (crossed:  $t_{(21)} = 4.58$ ,  $P_b < 0.001$ , d =0.98; uncrossed:  $t_{(21)} = 3.24$ ,  $P_b = 0.007$ , d = 0.69; all P-values Bonferroni corrected; Fig. 3A), but there was no significant difference between the conditions of crossed and uncrossed disparity ( $t_{(21)} = -1.34$ ,  $P_b = 0.563$ , d =0.29).





Fig. 3 Behavioral results. The illusion strength under each of the three conditions in Experiment 1 (A) and the corresponding three conditions without a stereoscope mirror in Experiment 2 (B), as well as the comparison of the illusion effect across Experiments 1,

2, and 3 (C). The perceived size of the target as a function of target depth in Experiment 3 (D). Error bars represent the SEM. \*P < 0.05, \*\*P < 0.01, and \*\*\*P < 0.001, two-tailed *t*-test (N = 22, 5, and 8 for Experiments 1 to 3, respectively).

# Experiment 2: Effect of Physical Offset of Surrounding Inducers

The main effect of the size of inducers was significant  $(F_{(1, 4)} = 37.95, P = 0.004, \eta_p^2 = 0.91)$ . Further analysis showed that the illusion effect was significant under each of the three disparity conditions (crossed:  $t_{(4)} = 4.53, P = 0.011, d = 2.02$ ; zero:  $t_{(4)} = 4.08, P = 0.015, d = 1.83$ ; uncrossed:  $t_{(4)} = 13.94, P < 0.001, d = 6.23$ ; Fig. 3B). The main effect of disparity ( $F_{(2, 8)} = 0.73, P = 0.513, \eta_p^2 = 0.15$ ) and their interaction ( $F_{(2, 8)} = 2.48, P = 0.145, \eta_p^2 = 0.38$ ) were not significant.

We performed repeated-measures ANOVA between Experiments 1 and 2, and found that the main effect of the experiment was significant ( $F_{(1, 4)} = 20.45$ , P = 0.011,  $\eta_p^2 = 0.84$ ), suggesting that the illusion effect was significantly larger in Experiment 2 than that in Experiment 1. The main effect of depth was not significant ( $F_{(2, 8)} =$ 0.31, P = 0.741,  $\eta_p^2 = 0.07$ ). A significant interaction was observed between experiment and depth ( $F_{(2, 8)} = 11.33$ , P =0.005,  $\eta_p^2 = 0.74$ ). Further analysis revealed that the illusion effect in Experiment 2 was significantly larger than in Experiment 1 under both crossed ( $t_{(4)} = 4.60$ , P = 0.010, d =2.06; Fig. 3C) and uncrossed ( $t_{(4)} = 5.79$ , P = 0.004, d = 2.59) disparity condition, but not under zero disparity condition ( $t_{(4)} = -0.14$ , P = 0.897, d = 0.06), suggesting that the reduction of the illusion effect under depth conditions in Experiment 1 was not caused by physical offset of the surrounding inducers.

#### **Experiment 3: Size-Distance Constant Effect**

The main effect of depth was significant ( $F_{(2, 14)} = 48.44$ , P < 0.001,  $\eta_p^2 = 0.87$ ), but the main effect of the size of inducers ( $F_{(1, 7)} = 1.38$ , P = 0.278,  $\eta_p^2 = 0.17$ ) and their interaction ( $F_{(2, 14)} = 0.47$ , P = 0.636,  $\eta_p^2 = 0.06$ ) were not significant. *Post hoc* analysis demonstrated that the perceived size of the target presented at the far plane was larger than at the middle ( $t_{(7)} = 3.30$ ,  $P_b = 0.016$ , d = 1.17; Fig. 3D) and near ( $t_{(7)} = 9.68$ ,  $P_b < 0.001$ , d = 3.42) planes, and the target presented at the middle plane looked larger than at the near plane ( $t_{(7)} = 6.38$ ,  $P_b < 0.001$ , d = 2.26). The perceived size of the target was significantly smaller than its physical size at the near ( $t_{(7)} = -3.65$ , P = 0.008, d = 1.29) and middle ( $t_{(7)} = -2.67$ , P = 0.032, d = 0.94) plane, but not at the far plane ( $t_{(7)} = -1.25$ , P = 0.252, d = 0.44). However, the illusion effect failed to reach significance under each of the three depth conditions (P > 0.26; Fig. 3C).

# Experiment 4: Neural Oscillations Underlying the Ebbinghaus Illusion

The average accuracy of depth judgment was 96.7% (SD = 5.9%).

We compared the amplitude of the N1 peak (100–250 ms) between crossed and zero, uncrossed and zero, as well as crossed and uncrossed disparity conditions. The results showed that crossed and uncrossed disparity conditions

showed a significantly larger N1 peak at parietal and occipital electrodes (P < 0.05, false discovery rate (FDR) corrected) compared to zero disparity (crossed: P7, P4, P6, P8, P07, P05, P03, P0Z, P04, P06, P08, O1, OZ, O2; uncrossed: CP6, P7, P5, P3, P2, P4, P6, P8, P07, P05, P03, P0Z, P04, P06, P08, O1, OZ, O2; Fig. 4A, B). However, a significant difference between crossed and uncrossed disparities was not observed in N1 amplitude.

The target surrounded by large inducers induced a larger N1 amplitude (100–250 ms) in contrast to the same target surrounded by small inducers at electrode CP6 (P <0.05, FDR corrected; Fig. 5A, B). In the meantime, the target surrounded by large inducers induced a larger P2 amplitude than the same target surrounded by small inducers at parietal and occipital electrodes (P3, P4, PO7, PO5, PO3, POZ, PO4, O1, OZ, O2; P <0.05, FDR corrected; Fig. 5C, D).

Under the three depth conditions, the target with a large perceived size elicited decreased alpha power (8–13 Hz) in the early time window (0–100 ms) at right centroparietal electrodes (FC4, C4, C6, CP2, and CP4; Fig. 6A) compared to the same target with small perceived size (P < 0.01, uncorrected). Moreover, a negative correlation was observed between the mean alpha power at electrodes CP2 and CP4 and the behavioral illusion effect ( $r_{(63)} = -0.24$ , P = 0.055; Fig. 6B).

Under the zero-disparity condition, the target with large perceived size produced increased beta power (14–25 Hz) in the late time window (200–300 ms) at parietal and occipital electrodes (T7, C5, CP5, P5, P3, PO3, POZ; Fig. 6C) relative to the same target with small perceived size (P < 0.01, uncorrected). Notably, the mean beta power at the occipitoparietal electrodes (P3, PO3, POZ) was positively correlated with the behavioral illusion effect when the horizontal



Fig. 4 ERP results of binocular disparity. Topography of horizontal disparity effect on N1 peak (A) and the mean amplitude averaged across parietal and occipital electrodes (P7, P4, P6, P8, P07, P05, P03, P0Z, P04, P06, P08, O1, OZ, O2; panel B). The pink dots

indicate the electrodes with a significant horizontal disparity effect (crossed vs zero or uncrossed vs zero, P < 0.05, two-tailed *t*-test, FDR corrected).

Fig. 5 ERP results of size of inducers. Topography of size of inducers (large vs small) on N1 peak averaged across three depth conditions (A), and the wave at electrode CP6 as a function of size of inducers (B). Topography of size of inducers on the P2 peak averaged across three depth conditions (C) and the mean wave of parietal and occipital electrodes (P3, P4, PO7, PO5, PO3, POZ, PO4, O1, OZ, O2) as a function of size of inducers (D). The pink dots indicate the electrodes with significant comparisons (P < 0.05, two-tailed *t*-test, FDR corrected).



disparity was subtracted from the zero-disparity condition  $(r_{(21)} = 0.44, P = 0.048; \text{Fig. 6D}).$ 

It has been suggested that the EEG signal contains both evoked (phase-locked) and induced (nonphase-locked) activity [24]. To obtain the induced responses, we subtracted the average ERP waveform from each single-trial EEG epoch before performing a time-frequency analysis [25]. Similar patterns of results were observed for the induced activity. In particular, a significant negative correlation was observed between the mean alpha power (0–100 ms) at electrodes CP2 and CP4 and behavioral illusion effect ( $r_{(63)} = -0.25$ , P = 0.048), and the mean beta power (200–300 ms) at occipito-parietal electrodes (P3, PO3, POZ) was positively correlated with the behavioral illusion effect when the horizontal-disparity was subtracted from the zero-disparity condition ( $r_{(21)} = 0.42$ , P = 0.058).

### Discussion

By using the technique of EEG and a stereoscope mirror, we investigated the neurophysiological correlates that underlie the two cognitive mechanisms responsible for the production of the Ebbinghaus illusion. By varying the horizontal disparities of the surrounding inducers of the Ebbinghaus configuration but leaving the retinal location of the central target unchanged, participants perceived the central target as in front of, behind, or at the same depth plane of the surrounding inducers. Making the central target appear at a different depth from the inducers interfered with the size contrast rather than the contour interaction. The behavioral results showed that when the central target was presented at a different depth plane from the surrounding inducers (i.e., horizontal-disparity condition), the size illusion magnitude was significantly reduced compared with when they were presented at the same depth plane (zero-disparity condition), and the illusion magnitudes were comparable when the target appeared in front of and behind the surrounding inducers. The EEG results revealed that the effect of physical offset of inducers was manifested by larger N1 amplitude at occipito-parietal sites, and the effect of physical size of surrounding inducers (large vs small) was demonstrated by larger N1 and P2 amplitudes at posterior occipito-parietal sites. Moreover, the illusion effect under the depth conditions, in which contour interaction was preserved or even strengthened, was associated with decreased alpha power in the early time window at centroparietal sites, and a negative correlation was observed between the perceived illusion effect and the parietal alpha power. The illusion effect under the zero-disparity condition was associated with increased beta power in a relatively late time window at occipito-parietal sites, and the beta power was positively correlated with

Fig. 6 Results of time-frequency analysis. Topography of illusion effect on alpha power (8-13 Hz) in the early time window (0-100 ms) for the three depth conditions (A), and the correlation of alpha power at parietal electrodes (CP2 and CP4) and behavioral illusion effect (B). Topography of illusion effect on beta power (14-25 Hz) in the late time window (200-300 ms) for the zero disparity condition (C), and the correlation of beta power at parietal electrodes (P3, PO3, POZ) and the behavioral illusion effect with the horizontaldisparity condition subtracted from the zero-disparity condition (D). The pink dots indicate the electrodes with significant comparisons (P < 0.01, twotailed *t*-test, uncorrected).



the behavioral illusion effect when the horizontal-disparity was subtracted from the zero-disparity condition. Consistent patterns of results were observed when phase-locked activity was subtracted from the EEG signal. The findings suggest that induced alpha and beta oscillations were linked to contour interaction and size contrast, respectively.

#### Two Components of the Ebbinghaus Illusion Effect

The contributions of low-level contour interaction and high-level size contrast to the production of the Ebbinghaus illusion have been supported by substantial behavioral evidence. For instance, the illusion effect varies as a function of the shape similarity of the central target and surrounding inducers [26–29] and as a function of the lightness contrast of the surrounding inducers relative to the background [30, 31]. Song, Schwarzkopf, and Rees [5] presented the central target and surrounding inducers to opposite eyes, and found that the Ebbinghaus illusion persisted during the dichoptic presentation, but it was significantly reduced compared with when they were presented to the same eye. The present study resonates well with previous studies by showing that when a binocular depth cue was introduced to make the target appear at a different plane from the surrounding inducers, which interfered with the size contrast instead of the contour interaction, the illusion effect was still observed, but it was significantly reduced compared with when they were presented at the same depth plane. Moreover, when the four inducers were presented at different depth planes from each other, the illusion effect disappeared, suggesting that the size contrast is more dominant than the contour interaction on the generation of the illusion.

Neural correlates underlying these two cognitive mechanisms have been suggested from brain imaging studies. For instance, the local architecture of V1 as demonstrated by the surface area, can predict inter-individual variability in the susceptibility of the Ebbinghaus illusion [6]. Both the feedforward and feedback connections between occipital and temporal regions are correlated with the Ebbinghaus illusion effect [32], and the bidirectional connections between the right V1 and parietal cortex are also predictive of the Ebbinghaus illusion [12, 33]. Moreover, intrinsic alpha activity in the left superior temporal gyrus positively correlates with the Ebbinghaus illusion strength when a red Ebbinghaus configuration is presented on a green background to selectively target the parvocellular visual pathway [19]. The above evidence suggests that both local circuits in the early visual cortex and bidirectional connections between the occipital cortex and higher visual regions contribute to the production of the Ebbinghaus illusion. By presenting the central target and the surrounding inducers at different depth planes to disturb the size contrast but leaving the contour interaction largely intact, the current study revealed that task-related beta and alpha oscillations at parietal sites were respectively associated with high-level size contrast and lowlevel contour interaction. In particular, early alpha power negatively correlated with the illusion effect across the three depth conditions, and relatively late beta power positively correlated with the illusion effect when the depth condition was subtracted from the no-depth condition. The above findings suggest that both inter-regional neural connections and intraregional neural oscillations mutually contribute to human conscious experience.

#### **Functional Role of Alpha Power in Cognitive Processes**

It is widely believed that alpha oscillations are the most prevailing rhythms in electrophysiological recordings, and are associated with distinct aspects of visual processing. Converging evidence supports the functional inhibition role of alpha power in cognitive processing [34–39]. For instance, in a task where participants could anticipate the strength and the exact timing of distracters, alpha power in the occipitotemporal areas is increased prior to strong compared to weak distracter onsets [40], suggesting that alpha power is linked to distracter suppression. A non-invasive brain stimulation study reveals that transcranial alternating current stimulation (tACS) over the left posterior parietal cortex at individual alpha frequency elicits a leftward lateralization of occipito-parietal alpha power and a leftward bias in visuospatial attention in a spatial cueing task [41]. Alpha oscillations have also been involved in perception, including stimulus detection [42], perceptual and temporal discrimination [43–45], as well as illusory perception [46]. Furthermore, alpha power in V1 also contributes to surround suppression [47]. In line with previous findings, the current study further showed that alpha oscillations are associated with the contour interaction mechanism of visual size illusion. The above findings suggest that alpha oscillations are far from a unitary phenomenon and might reflect a number of distinct neural processes, and thus might play multiple functional roles in perceptual and cognitive processes. The independent components of alpha oscillations might be generated in different regions of the brain and different cognitive demands [48], thereby discussions of alpha oscillations must take into account the anatomical and behavioral contexts [49].

#### **Beta Power Involves in High-Level Visual Processing**

Converging studies indicate the role of beta-band activity in high-level visual processing, particularly as a result of its relation to attentional processes [50]. For example, it synchronizes in the selection of relevant rule ensemble [51, 52] and can predict cooperative choices in decision making [53] and the percept of ambiguous audiovisual stimulus [54]. In addition, beta oscillations in the fronto-parietal attentional network are involved in a series of attentional tasks, such as attentional blink [55, 56], attentional shifts [57], as well as spatial and feature-based attention [58]. The prefrontal cortex of monkeys exhibits an increase in beta oscillatory bursts that track the maintenance of a stimulus representation in a delayed matched-to-sample task [59]. Remarkably, it synchronizes during top-down attention instead of bottom-up attention [60]. In a visual search task, beta-frequency transcranial magnetic stimulation (TMS) to the superior precentral sulcus and intraparietal sulcus decreases search accuracy during conjunction search which engages top-down attention [61]. Consistent with the above evidence, our results showed that posterior beta power was linked to the high-level size contrast mechanism which might require top-down attention. Moreover, beta-band activity is positively correlated with behavior performance [62–66], and attentional deficits in elderly subjects are characterized by low behavioral performance and decreased beta power [63, 67]. Furthermore, using frequency-specific alternating current stimulation, beta frequency stimulation can decrease the phosphene threshold in the occipital cortex [68]. The present study further revealed a positive correlation between the beta power and the high-level component of the Ebbinghaus illusion, which is an index of context sensitivity of visual size perception. The aforementioned findings suggest that beta oscillations predict the performance of both target sensitivity and context sensitivity, possibly via top-down modulations.

Moreover, the current study revealed that the time window of alpha power associated with low-level contour interaction was earlier than that of the beta power linked to high-level size contrast. This is consistent with the literature which suggests that contour interaction relies on local circuits in V1 and size contrast requires feedback projections. The nonsignificant correlations of early alpha power and relatively late beta power under each of and across the three depth conditions (P > 0.11) further suggest that contour interaction and size contrast are distinct and mutually independent mechanisms.

Taken together, our results demonstrate neurophysiological correlates of the Ebbinghaus illusion by revealing that early alpha power is associated with low-level contour interaction while relatively late beta power is linked to high-level size contrast, thus supporting the notion that neural oscillations at distinct frequency bands dynamically support different aspects of visual processing.

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**Conflict of interest** The authors declare that there are no conflicts of interest.

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