Original Articles

# Subconscious processing reveals dissociable contextual modulations of visual size perception

Lihong Chen[a,b,c], Congying Qiao[a], Ying Wang[b,c], Yi Jiang[b,c,*]

[a] Research Center of Brain and Cognitive Neuroscience, Liaoning Normal University, Dalian, PR China
[b] State Key Laboratory of Brain and Cognitive Science, CAS Center for Excellence in Brain Science and Intelligence Technology, Institute of Psychology, Chinese Academy of Sciences, Beijing, PR China
[c] Department of Psychology, University of Chinese Academy of Sciences, Beijing, PR China

## ARTICLE INFO

## ABSTRACT

Visual size perception is highly context-dependent. In a series of experiments reported here, we demonstrated that the contextual modulation of visual size processing could occur independent of conscious awareness. Specifically, the Ebbinghaus illusion, which is mediated by lateral connections within the early visual processing stream, persisted even when the surrounding inducers were rendered invisible. Moreover, when the central target was initially interocularly suppressed, the identical target emerged from suppression faster when surrounded by small relative to large inducers, with the suppression time difference well predicted by the strength of the illusion. By contrast, there were no such subconscious contextual modulation effects associated with the Ponzo illusion, which largely relies on feedback projections to the early visual cortices. These results indicate that contextual information can modulate visual size perception without conscious awareness, and the dissociated modulation effects further suggest that subconscious contextual modulation takes place in the early visual processing stream and is largely independent of high-level feedback influences.

## 1. Introduction

Accurately perceiving the size of visual objects is fundamental to our daily activities. Visual size perception does not only rely on the estimation of the object itself, but also depends on its surrounding context. For instance, an object would be perceived larger when surrounded by small items than when the identical object is surrounded by large items (i.e., the Ebbinghaus illusion). Similarly, an object would appear larger when placed at an apparently far location compared to the same object placed at an apparently near location (i.e., the Ponzo illusion).

Recent studies have revealed that contextual-dependent size perception relates, directly or indirectly, to the anatomical and functional properties of the primary visual cortex (V1). For instance, the magnitudes of the Ebbinghaus illusion and the Ponzo illusion are both found to be negatively correlated with the surface area of V1 (Schwarzkopf, Song, & Rees, 2011). Visual objects that are perceived larger due to depth cues (Fang, Boyaci, Kersten, & Murray, 2008; Murray, Boyaci, & Kersten, 2006) or through size adaptation (Pooresmaeili, Arrighi, Biagi, & Morrone, 2013) activate larger areas of V1. Afterimages, even induced by the same retinal image, can be perceived to be different in size

and elicit different retinotopic activities in V1 (Sperandio, Chouinard, & Goodale, 2012).

More interestingly, the Ebbinghaus illusion effect has also been observed among several other species, including the bottlenose dolphin (Murayama, Usui, Takeda, Kato, & Maejima, 2012), the redtail splitfin fish (Sovrano, Albertazzi, & Salva, 2015), and 4-day-old domestic chicks (Salva, Rugani, Cavazzana, Regolin, & Vallortigara, 2013). These animals experience the Ebbinghaus illusion in the same way as humans do, that is, they perceive the circle surrounded by large inducers to be smaller than the physically identical circle surrounded by small inducers. In avian species including chicks, major visual processing including size perception is carried out by the tectofugal pathway which projects from the retina to the optic tectum (homolog of the superior colliculus), to the nucleus rotundus of the thalamus (homolog of the pulvinar complex), and to the entopallium in the telencephalon (Hodos, Macko, & Bessette, 1984; Hodos, Weiss, & Bessette, 1986; Macko & Hodos, 1984). This raises an intriguing question that the neural mechanism crucial for perceiving the Ebbinghaus illusion might be located in the midbrain (Salva et al., 2013).

Because the early visual processing stream including human V1 and avian subcortical areas makes crucial contribution to the emergence of

---

the Ebbinghaus illusion, it is reasonable to postulate that the contextual modulation of surrounding inducers on the central target (as in the Ebbinghaus illusion) would have evolutionary significance and might take place automatically and even in the absence of awareness. In particular, we conjectured that in the Ebbinghaus illusion, the contextual modulation effect could still be observed even when the central target or the surrounding inducers were rendered invisible. To test these assumptions, we firstly investigated the potency of the central target of the Ebbinghaus configuration to emerge from suppression utilizing *continuous flash suppression* (CFS; Tsuchiya & Koch, 2005), a variant of binocular rivalry in which the target is monocularly presented and suppressed from awareness for quite a long time by simultaneously presenting high contrast dynamic patterns to the other eye (Jiang & He, 2006; Stein & Peelen, 2015). A previous study has demonstrated that stimuli with large physical size (i.e., occupying a wider horizontal region) break from suppression faster than stimuli with small physical size (Jiang, Costello, & He, 2007). If the contextual modulation of visual size processing could occur subconsciously, targets surrounded by small inducers would take a shorter time (termed as suppression time) to break from suppression compared with those surrounded by large inducers (Jiang et al., 2007; Stein, Reeder, & Peelen, 2016; Yang, Zald, & Blake, 2007). Furthermore, we rendered the surrounding inducers invisible with the techniques of CFS and *backward masking*, and measured the perceived target size using the method of adjustment. By this means, we could directly evaluate the Ebbinghaus illusion in subconscious settings and compare its illusion strength with that in a conscious contextual condition.

Finally, to further explore the limits and the neural loci of subconscious contextual modulation of visual size processing, we adopted another size illusion, that is, the Ponzo illusion. Although the perception of the Ebbinghaus illusion and that of the Ponzo illusion both engage V1, it has been suggested that the Ebbinghaus illusion largely relies on horizontal connections within V1 while the Ponzo illusion mainly relies on feedback projections from higher visual areas to V1 (Fang et al., 2008; Schwarzkopf et al., 2011). When the target and its surrounding context are dichoptically presented, the magnitude of the Ebbinghaus illusion is significantly reduced whereas the Ponzo illusion is less affected (Song, Schwarzkopf, & Rees, 2011). Moreover, compared with simultaneous presentation, successive presentation of the surrounding context and the target diminishes or even eliminates the Ebbinghaus illusion (Cooper & Weintraub, 1970; Jaeger & Pollack, 1977) but not the Ponzo illusion (Shen et al., 2015). The aforementioned evidence suggests that the contextual modulation of visual size processing in the Ponzo illusion, compared with that in the Ebbinghaus illusion, emerges at a relatively late processing stage and involves high-level feedback mechanisms. If subconscious modulation occurs primarily within the early visual processing stream, the contextual modulation effect would not be observed when the context or the target in the Ponzo configuration is rendered invisible. Conversely, if high-level feedback mechanisms are engaged in subconscious processing, the contextual modulation effect would be expected for the Ponzo illusion in the absence of awareness.

## 2. Method

### 2.1. Participants

A total of 136 participants (age ranged between 19 and 29 years with a mean of 22.7 years) took part in the study.[1] Seventeen (7 male) participated in Experiments 1a and 1b, sixteen (6 male) participated in Experiment 1c, twenty-four (10 male) participated in Experiment 2a, twenty (11 male) participated in Experiment 2b, twenty (10 male)

participated in Experiment 3, twenty (9 male) participated in Experiment 4, and another twenty (9 male) participated in Experiment 5 (one participant also took part in Experiment 3). All participants had normal or corrected-to-normal vision and gave written, informed consent in accordance with procedures and protocols approved by the institutional review boards of Institute of Psychology, Chinese Academy of Sciences and Liaoning Normal University. They were naive to the purpose of the experiments.

### 2.2. Stimuli

Stimuli were generated with MATLAB (Mathworks, Natick, MA) and presented on a CRT monitor (1280 × 1024 or 1024 × 768 at 60 Hz) using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). The Ebbinghaus configuration (4.8° × 4.8° or 2.6° × 2.6°) was composed of a central target (a circle or an irregular shape, 1.1° × 1.1°) surrounded by four large (1.7° × 1.7°) or small (0.6° × 0.6°) circles. The Ponzo configuration (7.7° × 9.1° or 4.0° × 9.8°) was made up of a pair of two converging or parallel lines and one target bar (1.1° × 0.2°). The CFS display consisted of high-contrast, colored noise patterns that changed at a rate of 10 Hz. In the experiments using CFS displays (Experiments 1b, 2a, 2b, 4b and 5), the images presented to the two eyes were displayed side by side on the screen and fused using a mirror stereoscope. A fusion frame with a fixation point was also presented to each eye at the beginning of each trial to facilitate stable convergence of the two images. All stimuli were presented at a viewing distance of 60 cm against a gray background.

### 2.3. Procedure

#### 2.3.1. Experiment 1: Contextual modulations of visible and invisible targets in the Ebbinghaus configuration

In Experiment 1a, the Ebbinghaus configuration (Fig. 1A) was presented in the left visual field, and the comparative figure was presented in the right visual field. The shape of the comparative figure corresponded with the target type in each trial, and its initial size varied randomly from 0.9° to 1.4° in steps of 0.06°. Observers were instructed to adjust the size of the comparative figure by pressing keys until it looked identical to the target. There was no time limit for the observers to perform the task. The two types of central targets (a circle or an irregular shape) were comparable in size and area. There was a total of 132 trials with 33 trials per condition.

In Experiment 1b, a dynamic noise pattern (1.3° × 1.3°) was presented to one eye of the observer at full contrast, and the target surrounded by four inducers was simultaneously presented to the other eye at the corresponding location of the noise pattern. At the very beginning of each trial, observers perceived the noise pattern and were unaware of the target. The contrast of the target was ramped up gradually from 0% to 100% within 1 s starting from the onset of the noise pattern and then remained constant until the observer made a button-press response to indicate the target's shape or until 10 s elapsed without response (Fig. 1B). The illusory configuration and the noise pattern were randomly switched across eyes in each trial. There was a total of 160 trials with 40 trials per condition.

In Experiment 1c, the target was blended into the dynamic noise (Fig. 1C) and its contrast was ramped up gradually at a rate of 16.7% increment per second so that response time would be in the same range as the suppression time in Experiment 1b. Observers viewed the stimuli without the mirror stereoscope, and performed exactly the same task as that in Experiment 1b. There was a total of 160 trials with 40 trials per condition.

Previous studies have demonstrated that the illusion strength varies with the similarity of the shapes of the central target and its surrounding inducers (Coren & Miller, 1974; Rose & Bressan, 2002). Therefore, we expected that the illusion strength of the circle target would be larger than that of the irregular target in Experiment 1a. The

---

[1] For each of the experiments, we sought to collect data from 16 to 24 participants, according to the standard of a typical psychophysical study.
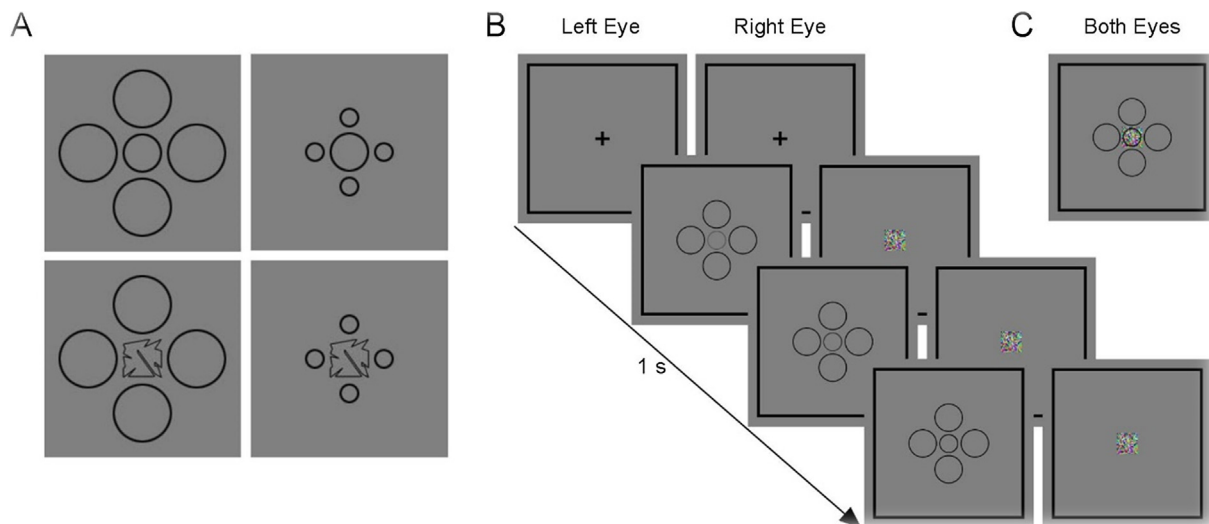
**Fig. 1.** Stimuli and experimental design. (A) Examples of the Ebbinghaus configurations as used in Experiment 1. (B) A typical trial in Experiment 1b and (C) the corresponding control condition in Experiment 1c.

inclusion of the target with an irregular shape in the Ebbinghaus configuration was also to provide a control condition for Experiment 1b to rule out the possibility that the contextual modulation of the invisible target, if observed, was simply due to the presence of the visible large vs. small inducers alone (which were identical for the circle and the irregular targets).

### 2.3.2. Experiment 2: Ebbinghaus illusion with invisible inducers using CFS masking

A dynamic Mondrian pattern (5.7° × 5.7°) was presented to the dominant eye and the target was presented to both eyes. Following a period of 0.2 s, four surrounding inducers were presented to the non-dominant eye at the corresponding location of the Mondrian pattern and their contrast was ramped up from 0% to 30% within 0.3 s. After the simultaneous disappearance of the Mondrian pattern and the illusory configuration, a comparative figure whose size ranged from 0.9° to 1.4° in steps of 0.06° was presented in the lower visual field (2.8° from the frame center; see Fig. 2A). In Experiment 2a, observers were asked to adjust the size of the comparative figure to match that of the target without time limit, and then to judge whether they had seen anything else except the Mondrian pattern and the target at the end of each trial. To further confirm the invisibility of the surrounding inducers, a separate objective two-alternative forced-choice (2AFC) task was used (a total of 200 trials with 50 trials per condition). The stimuli and procedure were similar to the main experiment, except that the comparative figures were not presented. The observers had to guess whether the surrounding inducers were large or small in reference to the central target even though they could not see the inducers. To rule out the potential influence of regression to the mean on the observed effect (Shanks, 2017) and further check the invisibility of surrounding inducers trial by trial, we conducted Experiment 2b, during which the size adjustment task and the 2AFC size discrimination task were performed sequentially for each trial. There was a total of 80 trials with 20 trials per condition for both Experiments 2a and 2b.

### 2.3.3. Experiment 3: Ebbinghaus illusion with invisible inducers using backward masking

The typical Ebbinghaus configuration (a circle surrounded by four large or small circles) with noise on it was presented for 33 ms. Then the surrounding inducers were replaced by a black-and-white random-noise mask (4.8° × 4.8°) for 100 ms. Following the simultaneous disappearance of the mask and the target, a comparative circle whose diameter ranged from 0.9° to 1.4° in steps of 0.06° was presented in the

lower visual field (8.5° from the screen center; see Fig. 2B). Observers were required to adjust the size of the comparative circle to match that of the target without time limit, and then performed a 2AFC task to indicate whether the surrounding inducers were large or small at the end of each trial. There was a total of 40 trials with 20 trials per condition.

### 2.3.4. Experiment 4: Contextual modulations of visible and invisible targets in the Ponzo configuration

In Experiment 4a, the Ponzo configuration (Fig. 3A) was presented at the center of the screen. The comparative bar was presented on the right side of the illusory configuration (8.5° from screen center), and its initial length varied from 0.9° to 1.4° in steps of 0.06°. To exclude the potential confounding influence of the physical location of the target bar on the monitor, we used two converging conditions, that is, converging upward and converging downward. Thus, the location of the target near the apex in the converging upward context corresponded to that far from the apex in the converging downward context, and vice versa. Observers were instructed to adjust the length of the comparative bar by pressing keys to match that of the target bar without time limit. There was a total of 132 trials with 22 trials per condition.

In Experiment 4b, two standard dynamic noise patterns were presented to one eye at full contrast, and the target simultaneously surrounded by two converging or parallel lines was presented to the other eye at one of the locations of the noise patterns. At the very beginning of each trial, observers perceived the noise patch and were unaware of the target. The contrast of the target was ramped up gradually from 0% to 60% (70% for one observer) within 1 s and then remained constant until the observer made a button-press response to indicate the location of the target or until 10 s passed without response (Fig. 3B). Throughout the whole experiment, observers were required to keep their eyes fixed at the fixation point. There was a total of 240 trials with 40 trials per condition.

### 2.3.5. Experiment 5: Ponzo illusion with invisible inducers using CFS masking

A dynamic Mondrian pattern (10.2° × 10.2°) was presented to the dominant eye and the target bar was presented to both eyes for 0.2 s (Fig. 3C). Thereafter, one of the three contexts was presented to the nondominant eye at the corresponding location of the Mondrian pattern and its contrast was ramped up from 0% to 30% within 0.3 s. After the simultaneous disappearance of the Mondrian pattern and the illusory configuration, a comparative bar whose length ranged from 0.9° to 1.4°
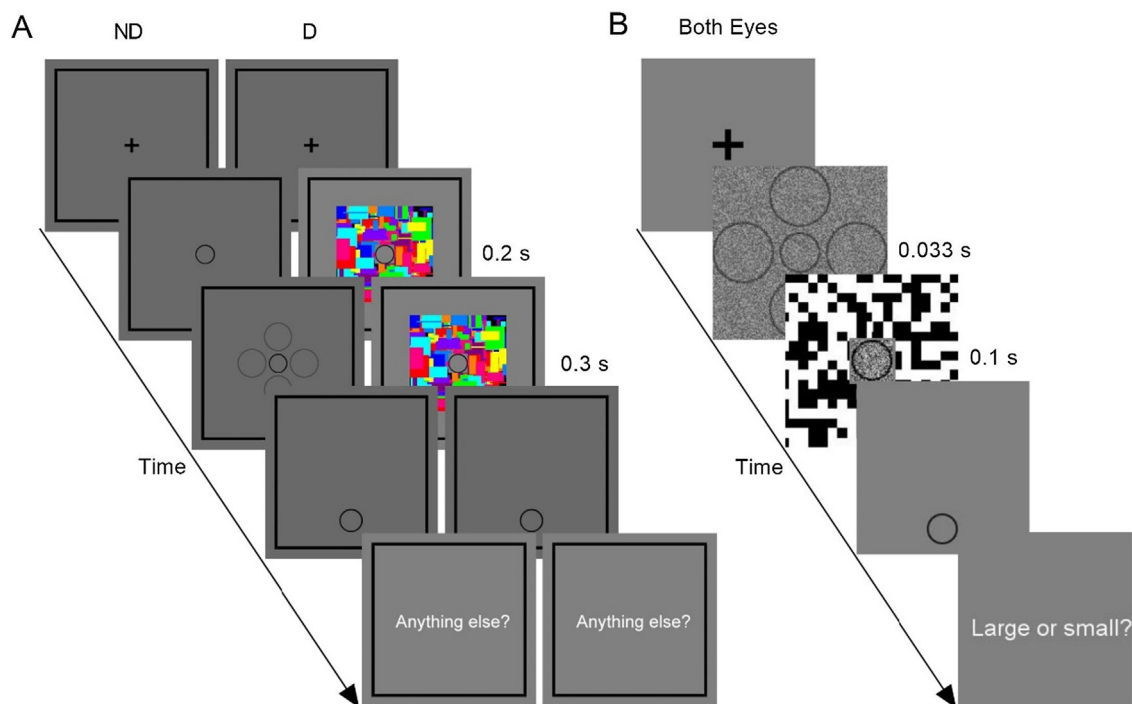
**Fig. 2.** Schematic representation of the experimental procedures in Experiments 2 and 3. (A) In Experiment 2, the dynamic Mondrian pattern was presented to the dominant eye and the surrounding inducers were presented to the nondominant eye. (B) In Experiment 3, the illusory configuration with noise on it was presented binocularly, followed by a mask of black-and-white random noise.

in steps of 0.06° was presented in the lower visual field (4.8° from the frame center). Observers were asked to adjust the length of the comparative bar to match that of the target bar without time limit, and then to identify which one of the three contexts was presented during the CFS phase at the end of each trial. There was a total of 120 trials with 20 trials per condition.

## 3. Results

To draw definite conclusions about the viability of the null hypothesis, we calculated Jeffrey-Zellner-Siow Bayes factor (BF) with Cauchy distribution (scale r = 1) to denote the likelihood of the null ($H_0$) over the alternative ($H_1$) hypothesis (Moors, Boelens, van Overwalle, & Wagemans, 2016; Rouder, Speckman, Sun, Morey, & Iverson, 2009; Vadillo, Konstantinidis, & Shanks, 2016). We used $BF_{10}$ to report evidence in favor of the alternative hypothesis.

### 3.1. Experiment 1: Contextual modulations of visible and invisible targets in the Ebbinghaus configuration

In Experiment 1a, the perceived size of the central target was calculated by the formula: $\frac{\text{perceived size - physical size}}{\text{physical size}} \times 100\%$, and the illusion effect was measured as the disparity of the perceived sizes of the targets
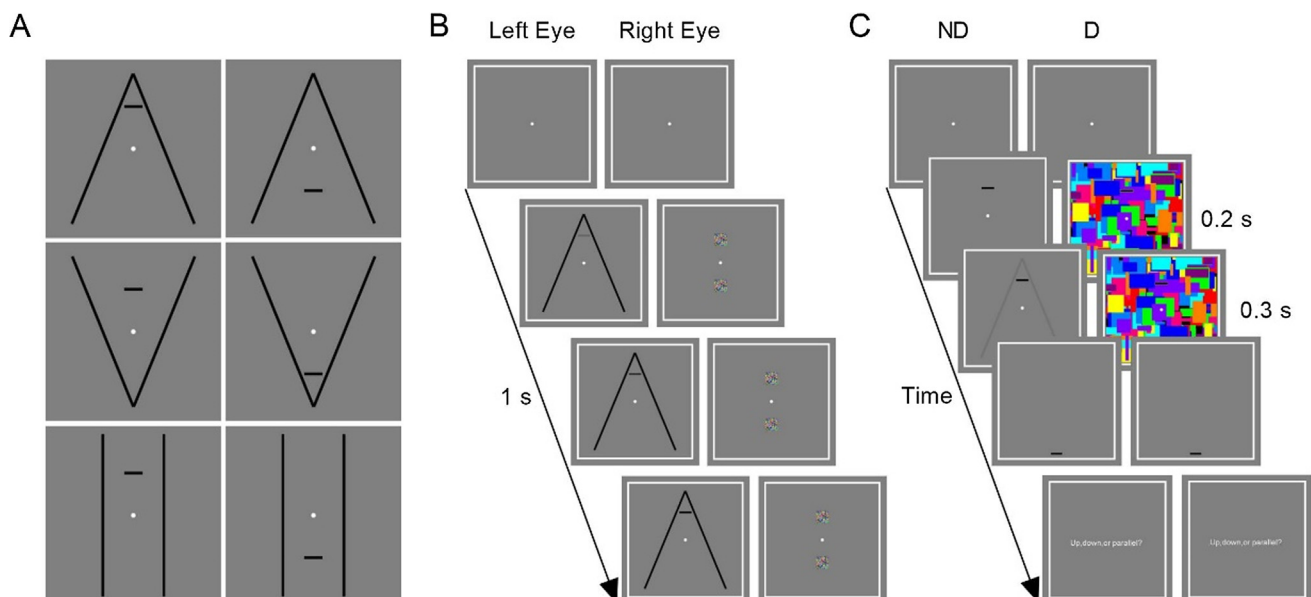


**Fig. 3.** Stimuli and experimental design. (A) Examples of the Ponzo configurations as used in Experiments 4 and 5. A typical trial in Experiments 4b (B) and 5 (C).
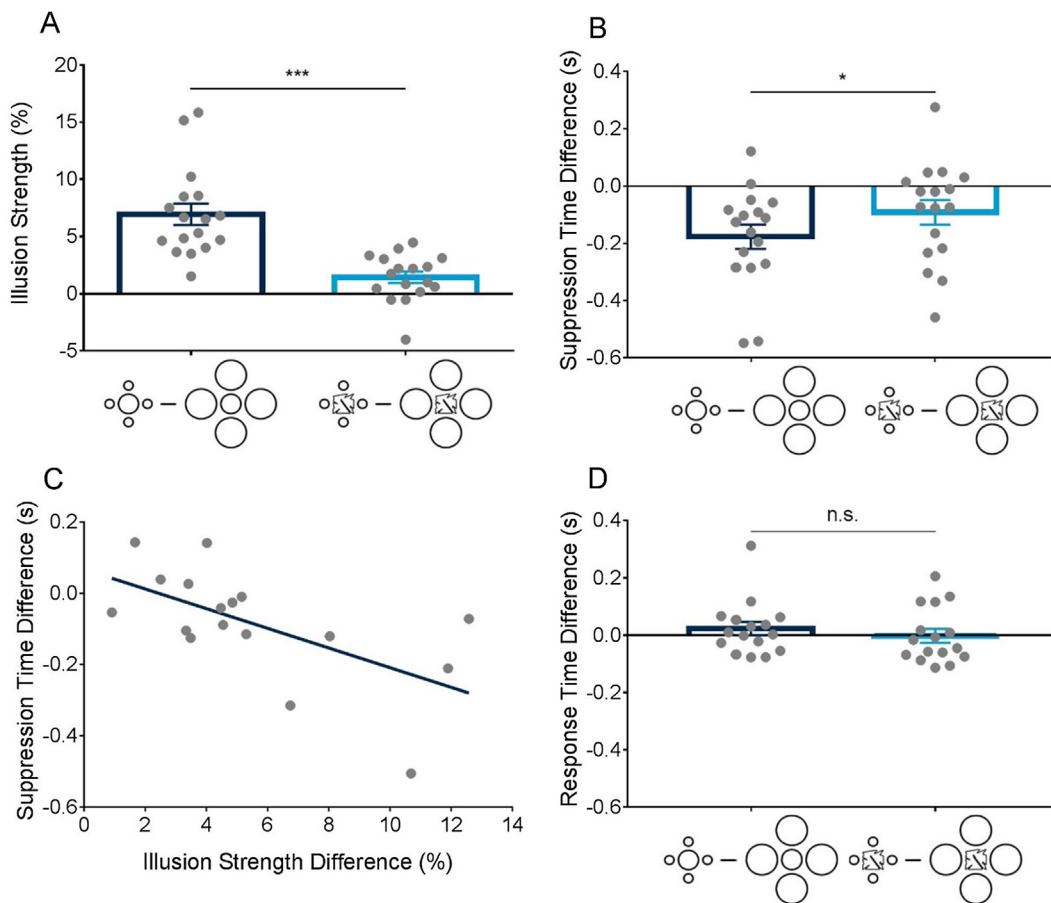
**Fig. 4.** Results from Experiment 1. (A) The illusion strength, (B) the suppression time difference, (C) the correlation between the illusion strength difference and the corresponding suppression time difference, and (D) the response time difference when the target was blended into the noise pattern. Error bars denote one standard error of the mean (*SEM*). Asterisks (*) indicate significance levels of * $p < .05$, and *** $p < .001$.

surrounded by small and large inducers. Repeated-measures ANOVA showed that both the main effects of Target Type (circle vs. irregular shape, $F(1,16) = 37.45$, $p < .001$, $\eta_p^2 = .70$) and Size of Inducers (large vs. small, $F(1,16) = 44.29$, $p < .001$, $\eta_p^2 = .74$) and the interaction between the two variables ($F(1,16) = 43.73$, $p < .001$, $\eta_p^2 = .73$) were significant. The illusion magnitudes were significant for both the circle ($M = 6.93\%$, 95% confidence interval (CI) = [4.94%, 8.93%], $t(16) = 7.36$, $p < .001$, $d = 1.79$, $BF_{10} = 14019.38$) and the irregular ($M = 1.43\%$, 95% CI = [0.37%, 2.49%], $t(16) = 2.87$, $p = .011$, $d = 0.70$, $BF_{10} = 4.40$) targets. Moreover, the illusion strength was significantly larger for the circle than for the irregular targets (mean difference = 5.50%, 95% CI = [3.74%, 7.27%], $t(16) = 6.61$, $p < .001$, $d = 1.60$, $BF_{10} = 4140.83$; see Fig. 4A).

In Experiment 1b, incorrect responses and extreme values outside ± 3 standard deviations of the mean were excluded from further analyses (1.4% of all trials). Repeated-measures ANOVA demonstrated significant main effects of Target Type ($F(1,16) = 6.20$, $p = .024$, $\eta_p^2 = .28$) and Size of Inducers ($F(1,16) = 12.58$, $p = .003$, $\eta_p^2 = .440$), as well as significant interaction between the two variables ($F(1,16) = 5.01$, $p = .040$, $\eta_p^2 = .24$). The apparently large target (surrounded by small inducers) took less time to gain dominance against the dynamic noise compared with the apparently small target (surrounded by large inducers) for both the circle (mean difference = −0.18 s, 95% CI = [−0.27, −0.09], $t(16) = −4.19$, $p = .001$, $d = 1.02$, $BF_{10} = 52.69$) and the irregular (mean difference = −0.09 s, 95% CI = [−0.18, −0.002], $t(16) = −2.17$, $p = .046$, $d = 0.53$, $BF_{10} = 1.33$) targets (see Fig. 4B). Furthermore, the disparity of the suppression times for the targets surrounded by small and large inducers was significantly larger for the circle target than for the irregular

target (mean difference = −0.08 s, 95% CI = [−0.17, −0.005], $t(16) = −2.24$, $p = .040$, $d = 0.54$, $BF_{10} = 1.49$), suggesting that the suppression time effect observed with the circle target to a large extent reflects the difference of the perceived sizes of the invisible targets rather than the simple presence of the large vs. small inducers alone.

Notably, by subtracting out the potential influences purely from the visible inducers (large vs. small inducers with the irregular target), the suppression time disparity of the identical circle targets with different perceived sizes in Experiment 1b significantly correlated with the corresponding illusion strength difference obtained in Experiment 1a ($r(17) = −0.61$, $p = .010$, $BF_{10} = 6.33$; see Fig. 4C). In other words, the suppression time difference can be well predicted by the perceived Ebbinghaus illusion strength across participants. The stronger the perceived Ebbinghaus illusion strength (the perceived size difference between the apparently large vs. small targets), the larger the suppression time difference between the two identical targets respectively surrounded by small and large inducers.

In Experiment 1c, we tested whether the results obtained in Experiment 1b could be explained simply by different recognition speeds or different response criteria corresponding to the different perceived sizes of the target. Repeated-measures ANOVA showed that neither the main effect of Size of Inducers ($F(1,15) = 0.47$, $p > .250$, $\eta_p^2 = .03$) nor the interaction of Target Type and Sizes of Inducers ($F(1,15) = 0.44$, $p > .250$, $\eta_p^2 = .03$, $BF_{10} = 0.22$) was significant. The response times for the targets surrounded by small and large inducers were not significantly different (circle target: $t(15) = 0.95$, $p > .250$, $d = 0.24$, $BF_{10} = 0.29$; irregular target: $t(15) = −0.11$, $p > .250$, $d = 0.03$, $BF_{10} = 0.19$), and the disparity of the response times was not different between the circle and irregular targets ($t(15) = 0.67$,

$p > .250$, $d = 0.17$, $BF_{10} = 0.23$; see Fig. 4D). These results confirmed that the significant disparity of the suppression times observed in Experiment 1b was not due to different recognition speeds or response criteria.

### 3.2. Experiment 2: Ebbinghaus illusion with invisible inducers using CFS masking

In Experiment 2a, the observers reported that they did not perceive the surrounding inducers in 88.4% trials with the circle target, and in 85.7% trials with the irregular target. The number of unperceived trials in these two conditions was comparable (mean difference = 2.71%, 95% CI = [−1.90%, 7.31%], $t(23) = 1.21$, $p = .236$, $d = 0.25$). When we analyzed only these unperceived trials, repeated-measures ANOVA demonstrated a significant interaction between Target Type and Size of Inducers ($F(1,23) = 12.74$, $p = .002$, $\eta_p^2 = .36$). When the target was a circle, the illusion effect was significant ($M = 1.42\%$, 95% CI = [0.56%, 2.28%], $t(23) = 3.42$, $p = .002$, $d = 0.70$, $BF_{10} = 15.28$). However, when the target was an irregular shape, the illusion effect was not evident ($M = −0.27\%$, 95% CI = [−0.89%, 0.36%], $t(23) = −0.89$, $p > .250$, $d = 0.18$, $BF_{10} = 0.23$). Notably, the illusion magnitude of the circle target was significantly larger than that of the irregular target (mean difference = 1.69%, 95% CI = [0.71%, 2.67%], $t(23) = 3.57$, $p = .002$, $d = 0.73$, $BF_{10} = 21.11$; see Fig. 5A). Sixteen of the observers were enrolled in the 2AFC task. Results showed that the accuracy of identification was at chance level ($M = 50.03\%$, 95% CI = [48.10%, 51.97%], $BF_{10} = 0.19$). Since the exclusion of the perceived trials in Experiment 2a would potentially bring in the effect of regression to the mean (Shanks, 2017), we further conducted Experiment 2b.

In Experiment 2b, repeated-measures ANOVA demonstrated a significant interaction between Target Type and Size of Inducers ($F(1,19) = 8.63$, $p = .008$, $\eta_p^2 = .31$). When the target was a circle, the illusion effect was significant ($M = 0.78\%$, 95% CI = [0.17%, 1.38%], $t(19) = 2.68$, $p = .015$, $d = 0.60$, $BF_{10} = 3.24$), and it was significantly reduced compared to the visible condition in Experiment 1a ($F(1,35) = 44.71$, $p < .001$, $\eta_p^2 = .56$). However, when the target was an irregular shape, the illusion effect was not evident ($M = −0.61\%$, 95% CI = [−1.62%, 0.41%], $t(19) = −1.25$, $p = 0.226$, $d = 0.28$, $BF_{10} = 0.35$). Notably, the illusion magnitude of the circle target was significantly larger than that of the irregular target (mean difference = 1.38%, 95% CI = [0.40%, 2.37%], $t(19) = 2.94$, $p = .008$, $d = 0.66$, $BF_{10} = 5.26$; see Fig. 5B). Results of the 2AFC task showed that the accuracy of discrimination was at chance level ($M = 49.00\%$, 95% CI = [46.50%, 51.50%], $BF_{10} = 0.24$). Considering the narrow confidence interval and the Bayes factor favoring the null hypothesis in the 2AFC task, as well as all trials being included in the analysis, the significant Ebbinghaus illusion effect observed in Experiment 2b was unlikely accounted for by the regression-to-the-mean effect. Still, the optimal method to assess observers' awareness is to combine the subjective (Experiment 2a) and the objective (Experiment 2b) measurements (Shanks, 2017).

### 3.3. Experiment 3: Ebbinghaus illusion with invisible inducers using backward masking

Paired-sample $t$ test showed that the illusion effect was significant for the circle target ($M = 1.81\%$, 95% CI = [0.55%, 3.07%], $t$
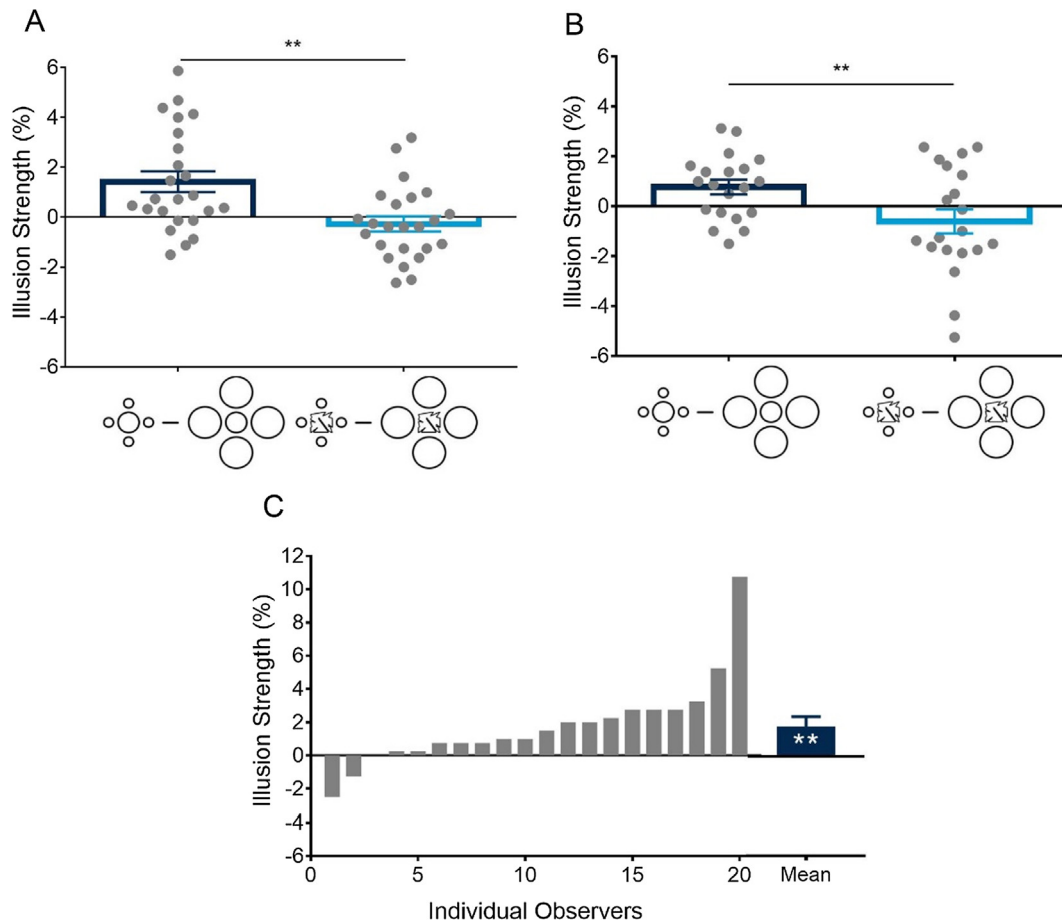


**Fig. 5.** Results from Experiments 2a (A), 2b (B) and 3 (C). Note that only the circle target was adopted in Experiment 3. Error bars denote one standard error of the mean (*SEM*). Asterisks (*) indicate the significance level of ** $p < .01$.

(19) = 3.01, $p$ = .007, $d$ = 0.67, $BF_{10}$ = 6.07; see Fig. 5C). Again, the illusion magnitude of the circle target was significantly reduced compared with the visible condition in Experiment 1a ($F(1,35)$ = 22.27, $p$ < .001, $\eta_p^2$ = .39), but was comparable to the illusion magnitude of the circle target obtained in Experiment 2b ($F(1,38)$ = 2.42, $p$ = .128, $\eta_p^2$ = .06). Furthermore, results of the 2AFC task showed that the accuracy of discrimination was at chance level ($M$ = 49.38%, 95% CI = [46.03%, 52.72%], $BF_{10}$ = 0.18).

### 3.4. Experiment 4: Contextual modulations of visible and invisible targets in the Ponzo configuration

In Experiment 4a, the perceived size of the target in the parallel-line context was subtracted from that of the corresponding target in the converging-line contexts, and the Ponzo illusion effect was measured as the disparity of the perceived lengths of the targets located near and far from the apex. The results revealed a significant main effect of Context ($F(1,19)$ = 5.48, $p$ = .030, $\eta_p^2$ = .22), as well as a significant interaction between Context and Target Location ($F(1,19)$ = 95.07, $p$ < .001, $\eta_p^2$ = .83). Paired-sample t tests showed that, in the converging-line contexts, the target presented near the apex was perceived significantly longer than the same target presented far from the apex (converging upward: mean difference = 4.05%, 95% CI = [2.83%, 5.27%], $t(19)$ = 6.95, $p$ < .001, $d$ = 1.56, $BF_{10}$ = 16976.4; converging downward: mean difference = 3.67%, 95% CI = [2.14%, 5.19%], $t(19)$ = 5.04, $p$ < .001, $d$ = 1.13, $BF_{10}$ = 394.8; see Fig. 6A). The illusion strength in the two converging-line contexts was comparable (mean difference = 0.39%, 95% CI = [−1.82%, 2.59%], $t(19)$ = 0.37, $p$ > .250, $d$ = 0.08, $BF_{10}$ = 0.18), and their mean illusion effect was significant (M = 3.86%, 95% CI = [3.03%, 4.69%], $t(19)$ = 9.75, $p$ < .001, $d$ = 2.18, $BF_{10}$ = 1.98×10⁶). The main effect of Target

Location was not significant ($F(1,19)$ = 0.14, $p$ > .250, $\eta_p^2$ = .01). The mean magnitude of the Ponzo illusion in the converging-line contexts was in between the magnitudes of the Ebbinghaus illusion with the circle target ($F(1,35)$ = 10.12, $p$ = .003, $\eta_p^2$ = .22) and that with the irregular target ($F(1,35)$ = 14.89, $p$ < .001, $\eta_p^2$ = .30; see Fig. 6B).

In Experiment 4b, incorrect responses and extreme values outside ± 3 standard deviations of the mean were excluded from further analyses (1.7% of all trials). The main effect of Context was significant ($F(1,19)$ = 9.47, $p$ = .006, $\eta_p^2$ = .33). The interaction between Context and Target Location was not significant ($F(1,19)$ = 1.18, $p$ > .250, $\eta_p^2$ = .06, $BF_{10}$ = 0.30). Suppression times of the targets at the upper and the lower locations were not different in each of the converging-line contexts (converging upward: mean difference = 0.003 s, 95% CI = [−0.24, 0.25], $t(19)$ = 0.03, $p$ > .250, $d$ = 0.006, $BF_{10}$ = 0.17; converging downward: mean difference = 0.18 s, 95% CI = [−0.07, 0.43], $t(19)$ = 1.51, $p$ = .149, $d$ = 0.34, $BF_{10}$ = 0.48; see Fig. 6C). The mean suppression time of the target near the apex in the converging-line contexts was comparable to that far from the apex (mean difference = −0.09 s, 95% CI = [−0.26, 0.08], $t(19)$ = −1.08, $p$ > .250, $d$ = 0.24, $BF_{10}$ = 0.30). The main effect of Target Location was not significant ($F(1,19)$ = 1.11, $p$ > .250, $\eta_p^2$ = .06).

### 3.5. Experiment 5: Ponzo illusion with invisible inducers using CFS masking

In Experiment 5, the accuracy of context identification was at chance level ($M$ = 33.38%, 95% CI = [32.03%, 34.72%], $BF_{10}$ = 0.17). Repeated-measures ANOVA demonstrated that neither the main effects of Context ($F(1,19)$ = 0.02, $p$ > .250, $\eta_p^2$ = 0.001) and Target Location ($F(1,19)$ = 0.05, $p$ > .250, $\eta_p^2$ = 0.002) nor the interaction between the two variables ($F(1,19)$ = 0.16, $p$ > .250, $\eta_p^2$ = 0.01, $BF_{10}$ = 0.16) was significant. Paired-sample t tests revealed that the
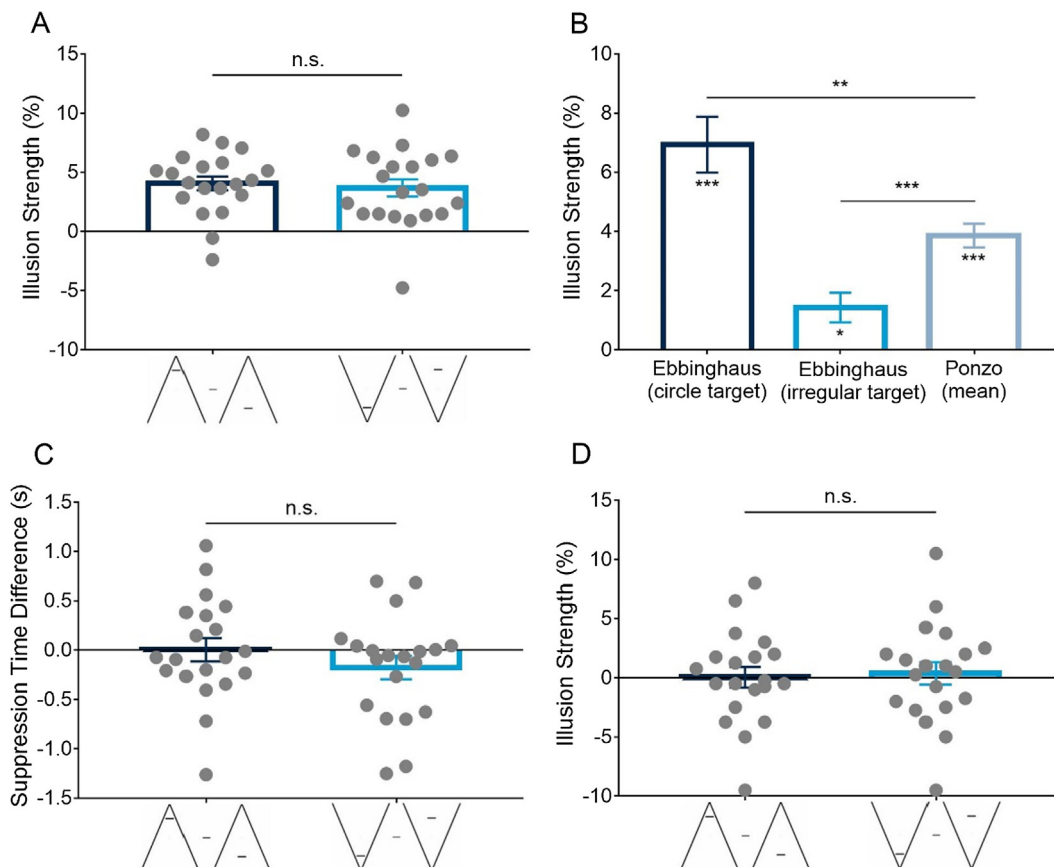


**Fig. 6.** Results from Experiments 4a (A), 4b (C) and 5 (D). (B) Comparison of illusion strength between the Ebbinghaus illusion (Experiment 1a) and the Ponzo illusion (Experiment 4a). Error bars denote one standard error of the mean (*SEM*). Asterisks (*) indicate significance levels of * p < .05, and *** p < .001.

perceived sizes of the targets presented at the upper and the lower locations were not different in the converging-line contexts (converging upward: mean difference = 0.04%, 95% CI = [−1.80%, 1.88%], $t$(19) = 0.04, $p$ > .250, $d$ = 0.01, $BF_{10}$ = 0.17; converging downward: mean difference = −0.36%, 95% CI = [−2.36%, 1.63%], $t$(19) = −0.38, $p$ > .250, $d$ = 0.09, $BF_{10}$ = 0.18; see Fig. 6D). There was no significant illusion effect in the subconscious converging-line contexts ($M$ = 0.20%, 95% CI = [−0.86%, 1.26%], $t$(19) = 0.40, $p$ > .250, $d$ = 0.09, $BF_{10}$ = 0.18).

## 4. Discussion

Contextual modulation of visual size processing correlates with both human V1 and avian subcortical areas, suggesting that it would have evolutionary significance and might take place without consciousness. Here we probed this issue using the Ebbinghaus illusion in conjunction with two masking techniques. We selectively rendered the central target of the illusory configuration invisible with CFS, and found that the suppressed target gained access into awareness more quickly when surrounded by small relative to large inducers (Experiment 1). Furthermore, when the surrounding inducers were rendered invisible through CFS (Experiment 2) and backward masking (Experiment 3), we found significant illusion effects under both masking methods. These results provide compelling evidence that contextual information can modulate visual size processing without awareness of the surrounding inducers or the central target.

Two main cognitive theories have been proposed to explain the Ebbinghaus illusion. One is the size contrast theory (Massaro & Anderson, 1971). According to this account, surrounding inducers serve as a standard for the size estimation of the central target. The size contrast theory requires high-level inferential mechanism to be involved. The other view is the contour interaction theory (Jaeger, 1978), in which contextual contours that are adjacent to the central target perceptually attract the edges of the target and induce size overestimation, whereas contextual contours that are relatively far from the target perceptually repel the edges of the target and induce size underestimation. Jaeger and Klahs (2015) found that increasing the number of small inducers along the perimeter of large inducers reduced the perceived size of the central target, suggesting that the Ebbinghaus illusion results from the contour interaction. Song et al. (2011) have also found that the Ebbinghaus illusion strength is significantly reduced when the surrounding inducers and the central target are presented to different eyes. Further, when the surrounding inducers and the central target were sequentially presented to different eyes with the surrounding inducers being rendered invisible, the Ebbinghaus illusion effect disappeared (Nakashima & Sugita, 2018). Along these lines, the current study further demonstrates that the Ebbinghaus illusion effect persists even when the central target or its surrounding inducers are rendered invisible. Our findings, together with these previous studies, support the account that low-level contour interaction robustly contributes to the emergence of the Ebbinghaus illusion, which might take place prior to awareness of the illusory configuration. On the other side, the significant magnitude reduction of the Ebbinghaus illusion from conscious processing to the subconscious processing suggests that the Ebbinghaus illusion might be a multilevel course encompassing both high-level (e.g., cognitive) and low-level (e.g., perceptual) processing.

For the Ponzo illusion, the subconscious contextual modulation effect vanished when we rendered the target bar (Experiment 4b) or the surrounding context (Experiment 5) invisible with CFS, even though the visible Ponzo configuration produced robust size illusion effect (Experiment 4a). It has been proposed that, different from the Ebbinghaus illusion, the Ponzo illusion is largely mediated by feedback projections from higher visual areas to V1. Therefore, our study suggests that subconscious contextual modulation of visual size processing occurs at relatively early visual processing stages and is largely independent of high-level feedback influences.

Note that recent studies have demonstrated that the subconscious contextual modulation of visual processing can also take effect on some other low-level visual properties, including orientation (Clifford & Harris, 2005; Hayashi & Murakami, 2015; Mareschal & Clifford, 2012; Pearson & Clifford, 2005) and brightness (Harris, Schwarzkopf, Song, Bahrami, & Rees, 2011). The magnitude of tilt illusion correlates with the effective connectivity from peripheral to foveal V1 (Song, et al., 2013) as well as the surface area of V1 (Song, Schwarzkopf, & Rees, 2013). Context-dependent brightness perception correlates with neural activity in V1 (Boyaci, Fang, Murray, & Kersten, 2007). By contrast, the subconscious contextual modulation effect is not observed for visual processing that involves relatively higher-level inferential mechanisms, such as the Kanizsa-type illusory contours (Banica & Schwarzkopf, 2016; Harris et al., 2011; Sobel & Blake, 2003; but see Fahrenfort, van Leeuwen, Olivers, & Hogendoorn, 2017). Kanizsa contour processing relies on the lateral occipital area and feedback projections from higher visual areas to V1/V2 (Wokke, Vandenbroucke, Scholte, & Lamme, 2013). In line with these observations, the current study further reveals that subconscious contextual modulation can also take effect on visual size processing in the Ebbinghaus illusion but not in the Ponzo illusion which is largely mediated by feedback influences from higher visual areas to V1. Thus, all the converging evidence lends support to the notion that subconscious contextual modulation takes place at relatively early visual processing stage without high-level feedback influences being directly involved. Yet the exact neural mechanisms underlying subconscious contextual modulation remain to be delineated by future neurophysiological investigations.

In summary, the current study provides evidence that contextual information can modulate visual size processing without awareness of the surrounding inducers or the central target, and that such modulation occurs in the early visual processing stream independent of feedback influences. Our findings extend the understanding of subconscious contextual modulation, and further underscore the contour interaction account in explaining the Ebbinghaus illusion.

## Author contributions

L. Chen and Y. Jiang conceived, developed, and designed the study. L. Chen and C. Qiao collected the data. L. Chen analyzed the data and drafted the manuscript under the supervision of Y. Jiang. Y. Jiang and Y. Wang provided critical revisions. All authors approved the final version of the manuscript for submission.

## Declaration of conflicting interests

The authors declared no conflicts of interest with respect to the authorship or the publication of this article.

## Funding

## References

Banica, T., & Schwarzkopf, D. S. (2016). Induction of Kanizsa contours requires awareness of the inducing context. PLoS ONE, 11(8), e0161177.
Boyaci, H., Fang, F., Murray, S. O., & Kersten, D. (2007). Responses to lightness variations in early human visual cortex. Current Biology, 17(11), 989–993.
Brainard, D. H. (1997). The psychophysics toolbox. Spatial Vision, 10, 433–436.
Clifford, C. W., & Harris, J. A. (2005). Contextual modulation outside of awareness. Current Biology, 15(6), 574–578.

Cooper, L. A., & Weintraub, D. J. (1970). Delboeuf-type circle illusions: Interactions among luminance, temporal characteristics, and inducing-figure variations. *Journal of Experimental Psychology, 85*(1), 75–82.

Coren, S., & Miller, J. (1974). Size contrast as a function of figural similarity. *Perception & Psychophysics, 16*(2), 355–357.

Fahrenfort, J. J., van Leeuwen, J., Olivers, C. N., & Hogendoorn, H. (2017). Perceptual integration without conscious access. *Proceedings of the National Academy of Sciences, USA, 114*(14), 3744–3749.

Fang, F., Boyaci, H., Kersten, D., & Murray, S. O. (2008). Attention-dependent representation of a size illusion in human V1. *Current Biology, 18*(21), 1707–1712.

Harris, J. J., Schwarzkopf, D. S., Song, C., Bahrami, B., & Rees, G. (2011). Contextual illusions reveal the limit of unconscious visual processing. *Psychological Science, 22*(3), 399–405.

Hayashi, D., & Murakami, I. (2015). Facilitation of contrast detection by flankers without perceived orientation. *Journal of Vision, 15*(15), 15.

Hodos, W., Macko, K. A., & Bessette, B. B. (1984). Near-field acuity changes after visual system lesions in pigeons II. Telencephalon. *Behavioural Brain Research, 13*(1), 15–30.

Hodos, W., Weiss, S. R., & Bessette, B. B. (1986). Size-threshold changes after lesions of the visual telencephalon in pigeons. *Behavioural Brain Research, 21*(3), 203–214.

Jaeger, T. (1978). Ebbinghaus illusions: Size contrast or contour interaction phenomena? *Perception & Psychophysics, 24*(4), 337–342.

Jaeger, T., & Klahs, K. (2015). The Ebbinghaus illusion: New contextual effects and theoretical considerations. *Perceptual and Motor Skills, 120*(1), 177–182.

Jaeger, T., & Pollack, R. H. (1977). Effect of contrast level and temporal order on the Ebbinghaus illusion. *Perception & Psychophysics, 21*(1), 83–87.

Jiang, Y., Costello, P., & He, S. (2007). Processing of invisible stimuli: Advantage of upright faces and recognizable words in overcoming interocular suppression. *Psychological Science, 18*(4), 349–355.

Jiang, Y., & He, S. (2006). Cortical responses to invisible faces: Dissociating subsystems for facial-information processing. *Current Biology, 16*(20), 2023–2029.

Macko, K. A., & Hodos, W. (1984). Near-field acuity after visual system lesions in pigeons I. Thalamus. *Behavioural Brain Research, 13*(1), 1–14.

Mareschal, I., & Clifford, C. W. (2012). Dynamics of unconscious contextual effects in orientation processing. *Proceedings of the National Academy of Sciences, USA, 109*(19), 7553–7558.

Massaro, D. W., & Anderson, N. H. (1971). Judgmental model of the Ebbinghaus illusion. *Journal of Experimental Psychology, 89*(1), 147–151.

Moors, P., Boelens, D., van Overwalle, J., & Wagemans, J. (2016). Scene integration without awareness: No conclusive evidence for processing scene congruency during continuous flash suppression. *Psychological Science, 27*(7), 945–956.

Murayama, T., Usui, A., Takeda, E., Kato, K., & Maejima, K. (2012). Relative size discrimination and perception of the Ebbinghaus illusion in a bottlenose dolphin (Tursiops truncatus). *Aquatic Mammals, 38*(4), 333–342.

Murray, S. O., Boyaci, H., & Kersten, D. (2006). The representation of perceived angular size in human primary visual cortex. *Nature Neuroscience, 9*(3), 429–434.

Nakashima, Y., & Sugita, Y. (2018). Size-contrast illusion induced by unconscious context. *Journal of Vision, 18*(3), 16.

Pearson, J., & Clifford, C. W. (2005). Suppressed patterns alter vision during binocular rivalry. *Current Biology, 15*(23), 2142–2148.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*(4), 437–442.

Pooresmaeili, A., Arrighi, R., Biagi, L., & Morrone, M. C. (2013). Blood oxygen level-dependent activation of the primary visual cortex predicts size adaptation illusion. *The Journal of Neuroscience, 33*(40), 15999–16008.

Rose, D., & Bressan, P. (2002). Going round in circles: Shape effects in the Ebbinghaus illusion. *Spatial Vision, 15*(2), 191–203.

Rouder, J. N., Speckman, P. L., Sun, D., Morey, R. D., & Iverson, G. (2009). Bayesian t tests for accepting and rejecting the null hypothesis. *Psychonomic Bulletin & Review, 16*(2), 225–237.

Salva, O. R., Rugani, R., Cavazzana, A., Regolin, L., & Vallortigara, G. (2013). Perception of the Ebbinghaus illusion in four-day-old domestic chicks (Gallus gallus). *Animal Cognition, 16*(6), 895–906.

Schwarzkopf, D. S., Song, C., & Rees, G. (2011). The surface area of human V1 predicts the subjective experience of object size. *Nature Neuroscience, 14*(1), 28–30.

Shanks, D. R. (2017). Regressive research: The pitfalls of post hoc data selection in the study of unconscious mental processes. *Psychonomic Bulletin & Review, 24*(3), 752–775.

Shen, M., Xu, H., Zhang, H., Shui, R., Zhang, M., & Zhou, J. (2015). The working memory Ponzo illusion: Involuntary integration of visuospatial information stored in visual working memory. *Cognition, 141*, 26–35.

Sobel, K. V., & Blake, R. (2003). Subjective contours and binocular rivalry suppression. *Vision Research, 43*(14), 1533–1540.

Song, C., Schwarzkopf, D. S., Lutti, A., Li, B., Kanai, R., & Rees, G. (2013). Effective connectivity within human primary visual cortex predicts interindividual diversity in illusory perception. *Journal of Neuroscience, 33*(48), 18781–18791.

Song, C., Schwarzkopf, D. S., & Rees, G. (2011). Interocular induction of illusory size perception. *BMC Neuroscience, 12*(1), 27.

Song, C., Schwarzkopf, D. S., & Rees, G. (2013). Variability in visual cortex size reflects tradeoff between local orientation sensitivity and global orientation modulation. *Nature Communications, 4*, 2201.

Sovrano, V. A., Albertazzi, L., & Salva, O. R. (2015). The Ebbinghaus illusion in a fish (Xenotoca eiseni). *Animal Cognition, 18*(2), 533–542.

Sperandio, I., Chouinard, P. A., & Goodale, M. A. (2012). Retinotopic activity in V1 reflects the perceived and not the retinal size of an afterimage. *Nature Neuroscience, 15*(4), 540–542.

Stein, T., & Peelen, M. V. (2015). Content-specific expectations enhance stimulus detectability by increasing perceptual sensitivity. *Journal of Experimental Psychology: General, 144*(6), 1089–1104.

Stein, T., Reeder, R. R., & Peelen, M. V. (2016). Privileged access to awareness for faces and objects of expertise. *Journal of Experimental Psychology: Human Perception and Performance, 42*(6), 788–798.

Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience, 8*(8), 1096–1101.

Vadillo, M. A., Konstantinidis, E., & Shanks, D. R. (2016). Underpowered samples, false negatives, and unconscious learning. *Psychonomic Bulletin & Review, 23*(1), 87–102.

Wokke, M. E., Vandenbroucke, A. R., Scholte, H. S., & Lamme, V. A. (2013). Confuse your illusion: Feedback to early visual cortex contributes to perceptual completion. *Psychological Science, 24*(1), 63–71.

Yang, E., Zald, D. H., & Blake, R. (2007). Fearful expressions gain preferential access to awareness during continuous flash suppression. *Emotion, 7*(4), 882–886.