Size-contrast illusion induced by unconscious context

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The present study examined whether the Ebbinghaus illusion can be induced by surrounding contexts that are suppressed from conscious perception. We employed continuous flash suppression to render the contextual stimuli invisible. The surrounding contexts were presented to one eye and the masking stimulus was presented to the other eye, followed by the presentation of the two center test stimuli to both eyes. The illusory size effect was observed even when the inducers were rendered invisible, although the effect was weak—approximately one third the strength of that induced by visible contexts. The effects induced by both visible and invisible contexts decayed with equal speed as the interstimulus interval between the inducer and test stimuli increased. Moreover, interocular transfer of illusory size effect did not occur when the inducers were suppressed from awareness. These results suggest that the size-contrast effect in the Ebbinghaus illusion is mediated in V1, and the monocular pathway in V1 is involved in the unconscious effect.

Introduction

The visual system actively estimates characteristics of the external world using various cues in the environment. Consequently, visual perception depends not only on the features of objects but also on surrounding contexts. For example, the perceived size of objects is influenced by the size of surrounding contextual objects; a center circle appears to be larger than its physical size when the surrounding circles are small, and smaller when the surrounding circles are large (the Ebbinghaus illusion). Such visual illusions occur automatically, without attention to the contextual stimuli. However, little is known about whether visual illusions occur even without conscious awareness. Recent studies have shown that the brightness contrast illusion occurs even when inducers are rendered invisible (Harris, Schwarzkopf, Song, Barhrami, & Rees, 2011) but illusory contours do not (Harris et al., 2011; Moor, Wagemans, van Ee, & de-Wit, 2016). In this context, it is unknown whether size illusions occur without the conscious processing of contexts. The present study examined the Ebbinghaus illusion under the suppression of conscious perception of surrounding contexts.

We used a technique derived from binocular rivalry—that is, continuous flash suppression (CFS; Tsuchiya & Koch, 2005)—to render inducers invisible. When a stimulus is presented to one eye in a period during which high-contrast and dynamic masking images are presented to the other eye, the stimulus is continuously suppressed from conscious perception. Binocular rivalry may be mediated by interactions between binocular neurons at several levels in the visual processing pathway (Leopold & Logothetis, 1996). Information of a perceptually suppressed stimulus would be processed by monocular neurons in the early visual pathway. If an illusion occurs even when inducers are rendered invisible by CFS, we can infer that the illusion is mediated in V1 or in the earlier pathway.

Several studies have suggested that the contextual effect in the Ebbinghaus illusion is mediated in V1. The functionally defined V1 surface area representing the central visual field is correlated with strength of the Ebbinghaus illusion (Schwarzkopf, Song, & Rees, 2011; Schwarzkopf & Rees, 2013). The Ebbinghaus illusion is weaker when inducers are presented to one eye and test stimuli are presented to the other eye, suggesting that the monocular pathway in the early visual areas is involved in this illusion (Song, Schwarzkopf, & Rees, 2011). If the Ebbinghaus illusion is mediated in V1, the effect can be observed even when inducers are suppressed.

In the present study, we measured the Ebbinghaus illusion under the conditions that surrounding inducers were (a) suppressed, (b) visible, and (c) not presented. The inducer was presented separately from the center test stimuli. This temporally separate paradigm was used in Jaeger and Pollack (1977), in which the illusion occurred but was weaker than in the normal Ebbinghaus illusion. We tested several interstimulus intervals

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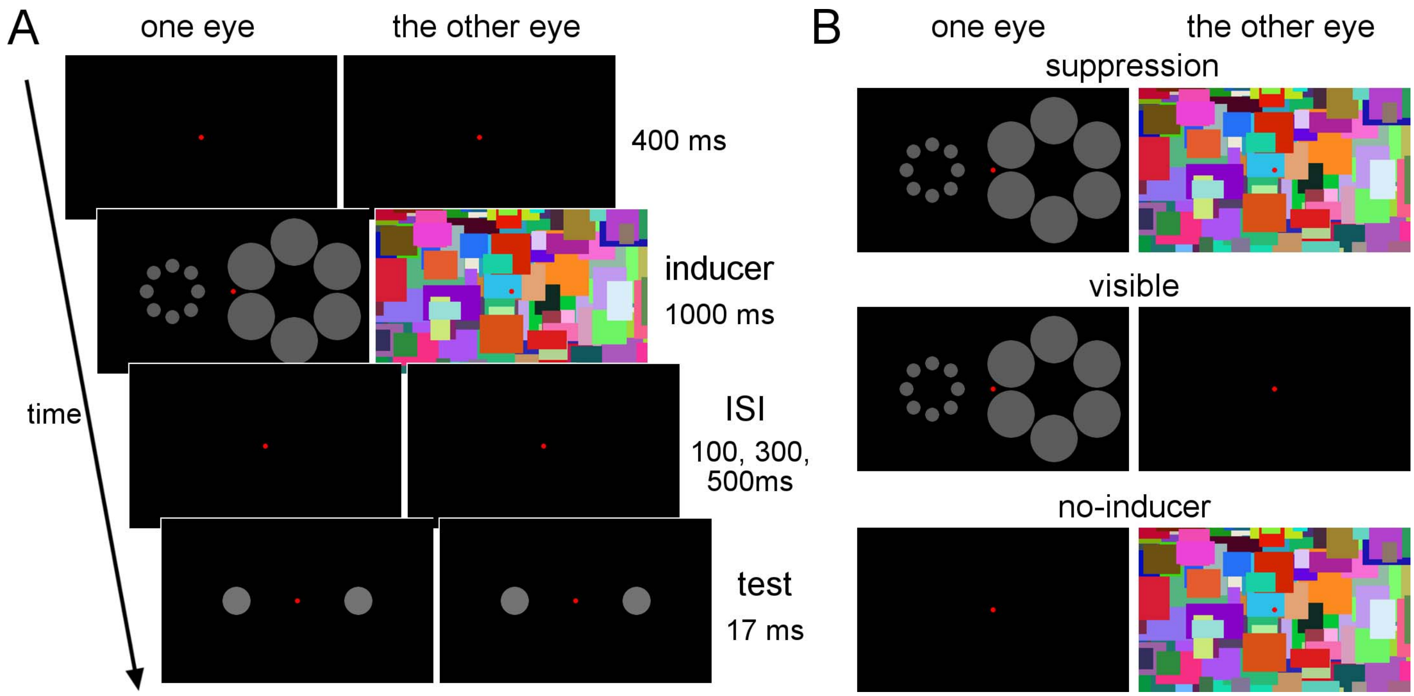

Figure 1. Design of the experiment. (A) Trial sequence. After a 400-ms presentation of the fixation, the inducers were presented to one eye and the mask was presented to the other eye for 1,000 ms. After the ISI, the test stimuli were presented for 17 ms. Participants judged which circle was larger. (B) The three inducer conditions. The suppression condition was the same as that described above. In the visible condition, the inducers were presented to one eye and only the fixation was presented to the other eye. In the no-inducer condition, only the fixation was presented to one eye and the mask was presented to the other eye.

(ISI) between the inducer and test stimuli to examine decay time of the illusion. If the size-contrast effect decays as the ISI increases, it would be due to perceptual shifts rather than response biases. We examined the decay time to confirm that effects induced by both visible and suppressed surrounding contexts were perceptual shifts.

Experiment 1

Methods

Participants

Eighteen participants (20–29 years old) took part in the experiment. All participants had normal or corrected-to-normal vision, and were naive to the purpose of the experiment. The experiment was performed in accordance with the Declaration of Helsinki, and informed consent was obtained from all participants.

Stimuli

Two-dimensional visual stimuli were presented on a 24-in. CRT display (800 × 600 pixel resolution, with a refresh rate of 60 Hz), at a viewing distance of 65 cm. The Ebbinghaus illusion stimulus was presented on a uniform black background (0.1 cd/m^2). The test stimuli (i.e., center circles in the Ebbinghaus illusion stimulus) consisted of two gray circles (12.3 cd/m^2). The center of the test stimuli was located at 1.23° left and right from the fixation. Inducer stimuli (5.2 cd/m^2) consisted of two types. Small inducers consisted of eight gray circles (0.31° in diameter), the centers of which were located at 1° from the center of the test stimulus. Large inducers consisted of six gray circles (0.97° in diameter) that were located at 1° from the test stimulus. Mondrian images (21.6° in width and 24.8° in height) were used as a mask, which consisted of randomly generated squares of random colors. Sixty different patterns were presented at a rate of approximately 20 Hz. The stimuli were separately presented to the left and right eye, with a circular polarizing filter.

Procedure

A red fixation circle (0.09° in diameter, 25.8 cd/m^2) always appeared at the center of the screen during a trial (Figure 1A). The participants were instructed to look at the fixation. After 400 ms, the inducers were presented to one eye and the mask stimulus was presented to the other eye, for 1,000 ms. After an ISI, the test stimuli were presented for 17 ms. We used three different ISIs (100, 300, and 500 ms) to examine the decay time of the illusion. Participants were required to judge which of the test stimuli was larger. The size of one of the test stimuli (reference stimulus) was constant (0.62° in diameter), while the size of the other (comparison stimulus) varied as follows: –0.088°, –0.044°, 0°, 0.044°, 0.088°, 0.132°, and 0.176°, relative to the reference stimulus. The reference stimulus was always presented at the side of the small inducer. In half of participants, the inducer stimuli were presented to the left eye, and in the other half, they were presented to the right eye.

In the condition mentioned above, the inducers were suppressed and rendered invisible by the Mondrian mask (suppression condition). The experiment also included two control conditions (Figure 1B). In the visible condition, after the presentation of the fixation for 400 ms, the inducers were presented to one eye and only the fixation was presented to the other eye, such that the participants could perceive the inducers. In the no-inducer condition, only the fixation was presented to one eye and the Mondrian mask was presented to the other eye, such that no illusion would occur.

Nine sessions (3 Inducer conditions × 3 ISI conditions) were conducted with a short break. A session consisted of five blocks, and each block included 14 trials in which the seven trials with differing size of the comparison stimulus were repeated twice. Further, in half of these 14 trials, the small inducer was presented at the left of the fixation, and in the other half, it was presented at the right of the fixation. Trials were randomly presented. The order of the inducer and ISI conditions was counterbalanced across participants.

We asked whether participants perceived the inducer stimuli during the suppression condition. The data of four participants reporting that they perceived an image other than the Mondrian squares in the suppression condition were rejected from the analysis.

Results

The proportion of trials in which the comparison stimulus appeared larger than the reference stimulus was plotted against the size of the comparison stimulus relative to the reference stimulus. When the ISI between the inducer and test stimuli was 100 ms, the curve largely shifted rightward in the visible condition relative to the no-inducer condition (Figure 2), indicating that the perceived size of the circle decreased when surrounded by the large inducers. The curve in the suppression condition also shifted rightward, although the shift was smaller than that in the visible condition.

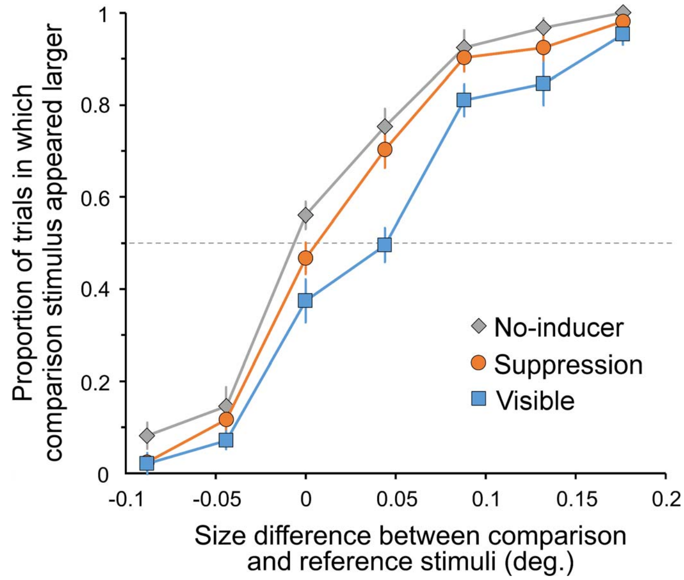

Figure 2. Average proportion of trials in which the comparison stimulus appeared larger than the reference stimulus. On the horizontal axis, negative values indicate that the comparison stimulus was smaller than the reference stimulus, and positive values indicate that the comparison stimulus was larger. The data in the 100-ms ISI condition have been presented. Error bars indicate the standard error.

To estimate a point of subjective equality (PSE), we calculated the 50% point by fitting a cumulative normal distribution function to individual participants' data using the maximum likelihood estimation. As seen in Figure 3A, PSE shifted in the positive direction not only in the visible condition but also in the suppression condition relative to the no-inducer condition (positive PSE values indicate reduction in the perceived size of the circle surrounded by the large inducer). PSE in both visible and suppression conditions decreased as the ISI increased. PSE in the visible condition was still large when the ISI was 500 ms, but that in the suppression condition was similar to the PSE in the no-inducer condition. In the 100-ms ISI condition, PSE in the visible condition was significantly greater than those in the no-inducer (one-tailed t test, $t[13] = 6.07$, $p < 0.001$) and suppression conditions, $t(13) = 4.16$, $p < 0.001$. PSE in the suppression condition was also significantly greater than that in the no-inducer condition, $t(13) = 4.23$, $p < 0.001$. The p values were adjusted by the Bonferroni-Holm method for comparison between the inducer conditions. In the 300-ms ISI condition, PSE in the visible condition was significantly greater than those in the no-inducer, $t(13) = 4.96$, $p < 0.001$, and suppression conditions, $t(13) = 3.15$, $p < 0.01$. PSE in the suppression condition was also significantly greater than that in the no-inducer condition, $t(13) = 2.08$, $p < 0.05$. In the 500-ms ISI condition, PSE in the visible condition was significantly greater than those in the no-

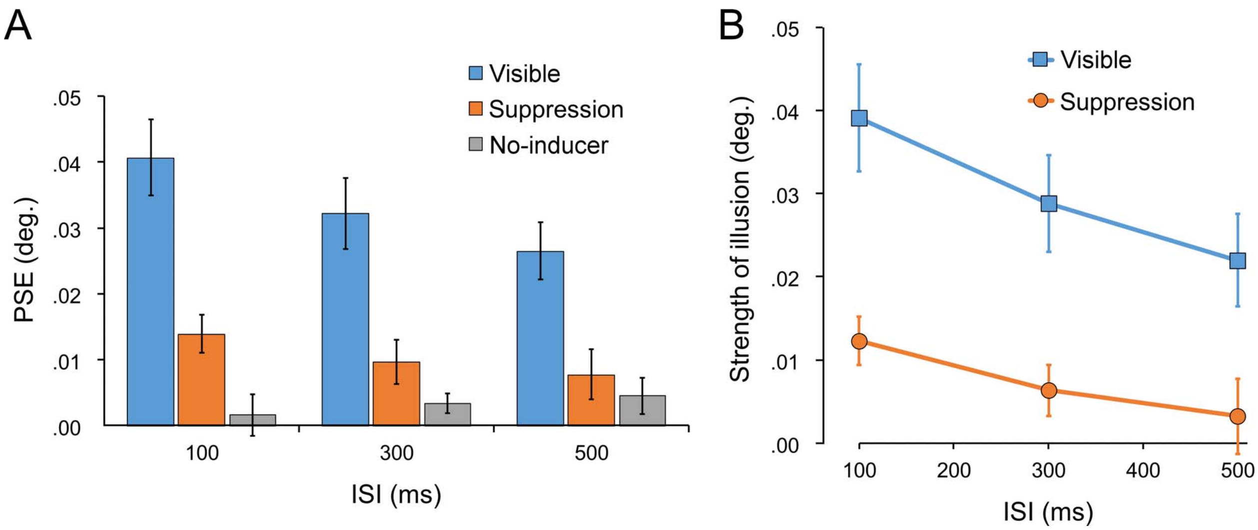

Figure 3. PSE and strength of the Ebbinghaus illusion. (A) PSE in all the nine conditions (3 Inducer conditions × 3 ISI conditions). Positive PSE values mean that perceived size of the circle surrounded by the large inducer decreased. (B) Strength of illusion as a function of the ISI. Error bars indicate the standard error.

inducer, $t(13) = 3.95$, $p < 0.01$, and suppression conditions, $t(13) = 3.40$, $p < 0.01$. However, PSE in the suppression condition was not greater than that in the no-inducer condition, $t(13) = 0.71$, $p = 0.25$.

To examine the decay time of the illusion, we plotted the strength of the illusion in the visible and suppression conditions against the ISI (Figure 3B). The strength of the illusion was calculated by subtracting the PSE in the no-inducer condition from that in the visible or suppression condition. A straight line was fitted to each participant's data. The slopes of the straight lines were not different between the visible and suppression conditions (one-tailed t test, $t[13] = 1.26$, $p = 0.12$), and they were less than zero (visible: $t[13] = 2.29$, $p < 0.05$; suppression: $t[13] = 2.51$, $p < 0.05$). The p values were adjusted by the Bonferroni-Holm method.

Experiment 2

In Experiment 1, to verify that the inducer stimuli were suppressed from awareness during the presentation of the CFS mask, we asked the participants whether they perceived the inducer stimuli only at the end of trials. However, this is not a sensitive measurement of awareness. It is possible that the size-contrast effect observed in the suppression condition was caused by partial awareness of the inducers. In Experiment 2, we repeated the experiment, using more sensitive awareness measurement to verify that the inducers are completely suppressed. We asked participants to report awareness of the inducers and to judge the position of the large inducer on every trial. Not only a subjective report but also an objective test is necessary to confirm that a stimulus is completely suppressed from awareness (Yang, Brascamp, Kang, & Blake, 2014). Moreover, we also measured eye dominance by using breaking CFS before the experiment to present the inducers to the nondominant eye.

Methods

Participants and stimuli

Thirteen participants (19–24 years old) took part in the experiment. All participants had normal or corrected-to-normal vision, and were naive to the purpose of the experiment.

The stimuli were the same as Experiment 1.

Procedure

The methods in Experiment 2 were basically the same as Experiment 1. We required the participants to answer the additional questions regarding visibility of the inducers on every trial and conducted the eye dominance measurement.

Before the main experiment, eye dominance was measured using the modified paradigm from Yang, Blake, and McDonald (2010). A fixation point was presented at the center of the screen. After 400 ms, a square (2° in width and 2° in height) was presented to one eye and the mask stimulus to the other eye. The square was randomly presented 1.5° to the left or right of the fixation. The contrast of the square increased from 30% to 100% over 7 s. Participants were asked to answer the position of the square (left or right) as soon as they perceived it. After the contrast of the square

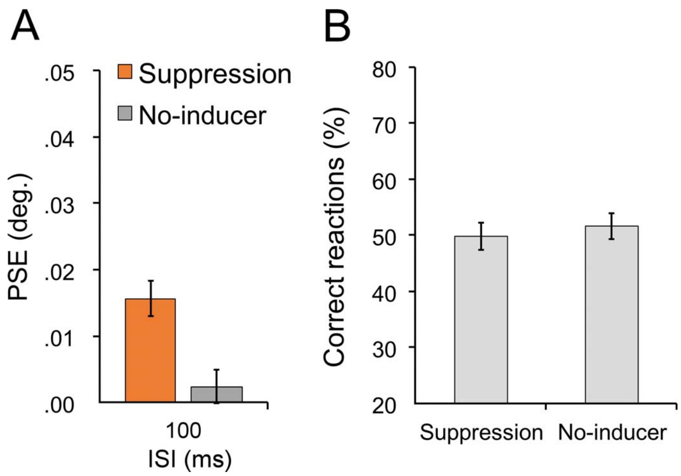

Figure 4. Results in Experiment 2. (A) PSE in the suppression and no-inducer conditions. Positive values indicate that perceived size of the circle surrounded by the large inducer decreased. (B) Percentage of correct reactions to the question about large inducer's position. Error bars indicate the standard error.

reached 100%, it remained at full contrast until participants responded. In 10 trials, the mask stimulus was presented to the left eye, and in other 10 trials, it was presented to the right eye. The trials were randomly conducted. We determined the dominant eye as the eye in which the mean time it took to detect the square was shorter. In the main experiment, the inducer stimulus was presented to the nondominant eye and the CFS mask was presented to the dominant eye.

In the main experiment, participants were asked whether they perceived the inducer stimuli on every trial. Moreover, they were required to judge in which of the sides (left or right) the large inducer was presented on every trial. On half of the trials, the large inducer was presented at the left of the fixation, and on the other half, it was presented at the right. Percentage of correct reactions to the question would be 50% if participants do not perceive the inducers in the suppression condition, and they should also be 50% in the no-inducer condition since the inducer stimuli were not presented. Participants answered them after the judgment about size of the test stimuli. The data of three participants reporting that they subjectively perceived the inducer stimuli even once were rejected from the analysis.

The suppression and no-inducer conditions in the 100-ms ISI condition were conducted.

Results

Percentage of correct reactions to the question regarding inducer's position was at chance level (Figure 4B). Percentage of the correct reactions was not significantly larger than 50% in the suppression (one-tailed t test, $t[9] = -0.06$, $p = 0.52$) and no-inducer conditions, $t(9) = 0.68$, $p = 0.26$. To estimate PSE, we calculated the 50% point by fitting a cumulative normal distribution function to individual participants' data. Similar to Experiment 1, PSE in the suppression condition shifted in the positive direction relative to the no-inducer condition (Figure 4A). PSE in the suppression condition was significantly greater than that in the no-inducer condition (one-tailed t-test, $t[9] = 11.69$, $p < 0.001$).

Experiment 3

In Experiment 1 and Experiment 2, the size-contrast illusion was observed even when the inducers were rendered invisible by CFS, but the effect was weak, approximately one third the strength of that induced by visible contexts. These results suggest that the monocular pathway in V1 is involved in the unconscious effect (see Discussion for details). To test further this idea, we examined interocular transfer of the contextual effect in Experiment 3. The inducers were presented to one eye and the test stimuli were presented to the opposite eye. If the size-contrast effect induced by the unconscious inducers is mediated in the monocular cells, interocular transfer would occur only when the inducers are visible but not when they are suppressed by CFS.

Methods

Participants and stimuli

Thirteen participants (19–24 years old) took part in the experiment. All participants had normal or corrected-to-normal vision, and were naive to the purpose of the experiment.

The stimuli were the same as Experiment 1 and Experiment 2.

Procedure

The methods in Experiment 3 were the same as Experiment 2, except for the presentation of the test stimuli. In Experiment 1 and Experiment 2, the test stimuli were presented to both eye. In Experiment 3, they were presented to only the opposite eye from that to which the inducers were presented. The test stimuli were presented for 33 ms.

Participants were asked whether they perceived the inducer stimuli and were required to judge in which of the sides the large inducer was presented on every trial. The data of three participants reporting that they

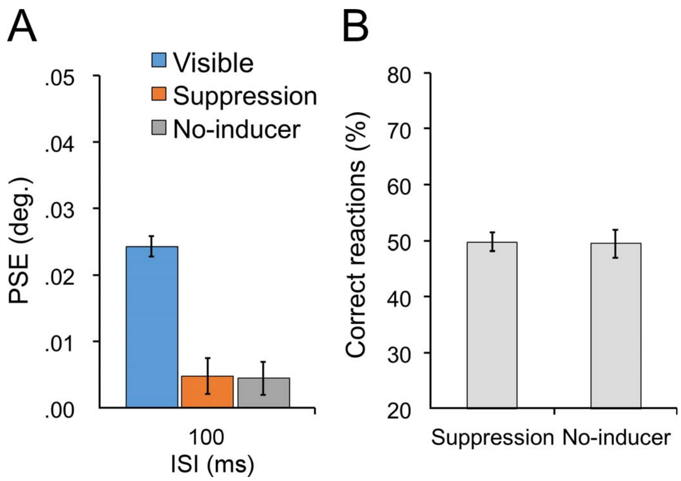

Figure 5. Results in Experiment 3. (A) PSE in the visible, suppression, and no-inducer conditions. Positive values indicate that perceived size of the circle surrounded by the large inducer decreased. (B) Percentage of correct reactions to the question about large inducer's position. Error bars indicate the standard error.

subjectively perceived the inducer stimuli even once were rejected from the analysis.

The visible, suppression, and no-inducer conditions in 100 ms-ISI condition were conducted. Before the experiment, eye dominance was measured and the CFS mask was presented to the dominant eye in the main experiment.

Results

PSE in the visible condition shifted in the positive direction relative to the no-inducer condition (Figure 5A). However, PSE in the suppression condition was not different from that in the no-inducer condition. PSE in the visible condition was significantly greater than those in the suppression (one-tailed *t*-test, $t[9] = 3.57$, $p < 0.01$) and no-inducer conditions ($t[9] = 3.29$, $p < 0.01$). PSE in the suppression condition was not greater than that in the no-inducer condition ($t[9] = 0.05$, $p = 0.48$). The p values were adjusted by the Bonferroni-Holm method for comparison between the inducer conditions. Percentage of correct reactions to the question regarding inducer's position was at chance level (Figure 5B). Percentage of the correct reactions was not significantly larger than 50% in the suppression (one-tailed *t*-test, $t[9] = -0.17$, $p = 0.57$) and the no-inducer conditions ($t[9] = -0.23$, $p = 0.59$).

The strength of the illusion was calculated by subtracting the PSE in the no-inducer condition from that in the visible or suppression condition. The strength of the illusion in the visible condition was approximately 50% of that in the 100 ms-ISI condition in Experiment 1 in which the test stimulus was presented to both eyes. The strength of the illusion in the visible condition in Experiment 3 was significantly smaller than that in the 100 ms-ISI condition in Experiment 1 (two-tailed *t*-test: $t[22] = 2.10$, $p < 0.05$).

Experiment 4

In the above three experiments, the inducer and test stimuli were separately presented with an ISI unlike the normal Ebbinghaus illusion. The size-contrast effect was observed even in this paradigm; however, it is possible that the neural mechanism is distinct from that in the conventional Ebbinghaus illusion. Adaptation-like processes might be involved in the effect under the successive presentation paradigm. In Experiment 4, we tested whether similar results to those in Experiment 1 and Experiment 2 could be observed even when the inducer and test stimuli were simultaneously presented.

Methods

Participants and stimuli

Eleven participants (20–26 years old) took part in the experiment. All participants had normal or corrected-to-normal vision, and were naive to the purpose of the experiment.

The stimuli were the same as the above three experiments.

Procedure

The methods in Experiment 4 were the same as Experiment 2, except for the timing of the presentation of the stimuli.

After the presentation of the fixation, the Mondrian mask was presented to the dominant eye and only the fixation was presented to the nondominant eye. After 500 ms, the Mondrian mask and the test stimuli were presented to the dominant eye and the inducer and test stimuli were presented to the nondominant eye for 200 ms in the suppression condition, such that the participants perceived the test stimuli on Mondrian images. In the visible condition, the test stimuli were presented to the dominant eye and the inducer and test stimuli were presented to the nondominant eye for 200 ms. In the no-inducer condition, the Mondrian mask and the test stimuli were presented to the dominant eye and the test stimuli were presented to the nondominant eye for 200 ms.

Participants were asked whether they perceived the inducer stimuli and were required to judge in which of the sides the large inducer was presented on every trial.

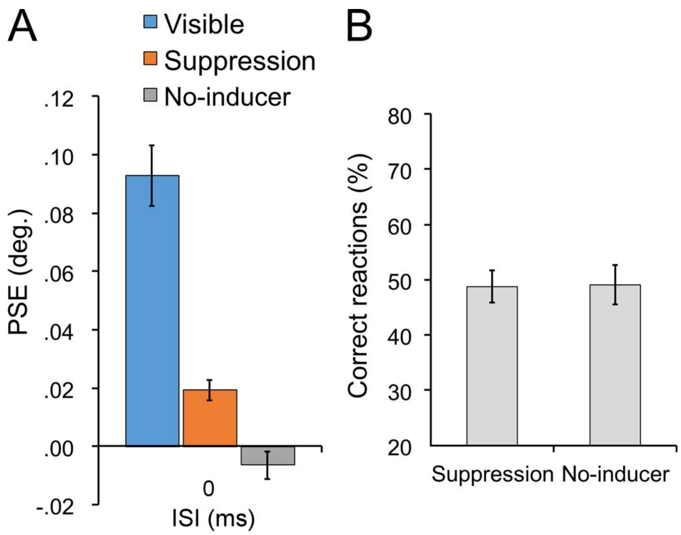

Figure 6. Results in Experiment 4. (A) PSE in the visible, suppression, and no-inducer conditions in the zero-ISI condition. Positive values indicate that perceived size of the circle surrounded by the large inducer decreased. (B) Percentage of correct reactions to the question about large inducer's position. Error bars indicate the standard error.

The data of a participant reporting that they subjectively perceived the inducer stimuli even once were rejected from the analysis.

Results

Similar to Experiment 1, PSE in the visible and suppression conditions shifted in the positive direction relative to the no-inducer condition (Figure 6A). PSE in the visible condition was significantly greater than those in the suppression (one-tailed t-test: $t[9] = 7.30$, $p < 0.001$) and no-inducer conditions ($t[9] = 7.75$, $p < 0.001$). PSE in the suppression condition was also significantly greater than that in the no-inducer condition ($t[9] = 7.90$, $p < 0.001$). The p values were adjusted by the Bonferroni-Holm method for comparison between the inducer conditions. Percentage of correct reactions to the question regarding inducer's position was at chance level (Figure 6B). Percentage of the correct reactions was not significantly larger than 50% in the suppression ($t[9] = -0.42$, $p = 0.66$) and the no-inducer conditions ($t[9] = -0.26$, $p = 0.60$).

The strength of the illusion was calculated by subtracting the PSE in the no-inducer condition from that in the visible or suppression condition. The strength of the illusion in the suppression condition was one fourth of that in the visible condition: 0.025° in the suppression condition and 0.100° in the visible condition. The strength of the illusion in the zero-ISI condition was larger than those in the 100 ms-ISI conditions in Experiment 1. The strength of the illusion in the visible condition in Experiment 4 was significantly larger than that in the 100 ms-ISI condition in Experiment 1 (two-tailed t-test: $t[22] = 4.57$, $p < 0.001$). The strength of the illusion in the suppression condition in Experiment 4 was significantly larger than that in the 100 ms-ISI condition in Experiment 1 (two-tailed t-test: $t[22] = 3.05$, $p < 0.01$).

Discussion

In the present study, we showed that the Ebbinghaus illusion occurs even when inducers were rendered invisible by CFS. The strength of the illusion induced by invisible contextual stimuli was weak, approximately one third the strength of that induced by visible contexts. Further, the illusory size effect induced by both visible and invisible contexts decayed with equal speed as the ISI between the inducer and test stimuli increased from 100 ms to 500 ms, suggesting that the mechanism of the illusion induced by invisible contexts might be similar to that induced by visible contexts and that both effects are due to perceptual shifts rather than response or decisional biases. The unconscious size-contrast effect was observed even when the more rigorous check confirmed that inducers were completely suppressed. The results indicate that the effect induced by suppressed contextual stimuli is not caused by partial awareness of inducers.

CFS is likely to disrupt the processing of stimuli rendered invisible in the high-level visual areas due to interocular suppression in binocular cells. The proportion of neurons that show activities reflecting conscious perception during binocular rivalry increase in the higher areas (Leopold & Logothetis, 1996; Sheinberg & Logothetis, 1997), where binocular cells are dominant (Zeki, 1978; Maunsell & van Essen, 1983). Further, fMRI studies have shown that neural responses in the higher areas reflect perceived stimuli during binocular rivalry (Tong, Nakayama, Vaughan, & Kanwisher, 1998) and CFS (Fang & He, 2005; Hesselmann & Malach, 2011). These findings suggest that suppressed stimuli are no longer processed in the higher visual cortex. In contrast, only a small proportion of neurons in V1 show activities reflecting perceived stimuli (Leopold & Logothetis, 1996). Additionally, fMRI responses in V1 are not modulated by conscious perception (Watanabe et al., 2011). Although another study has shown that fMRI signals in V1 are modulated by conscious awareness (Yuval-Greenberg & Heeger, 2013), the modulation effect is smaller than that in the higher areas (Sterzer, Stein, Ludwig, Rothkirch, & Hesselmann, 2014). These results suggest that although interocular suppression occurs, perceptually suppressed stimuli might be still processed in V1.

Thus, the processing of suppressed stimuli would be presumably mediated by the monocular cells in V1.

Several studies have already suggested that the contextual effect in the Ebbinghaus illusion is mediated in the early visual cortex. The functionally defined V1 surface area representing the central visual field is correlated with strength of the Ebbinghaus illusion (Schwarzkopf et al., 2011; Schwarzkopf & Rees, 2013). The Ebbinghaus illusion was weaker when inducers are presented to one eye and test stimuli are presented to the other eye, suggesting that the monocular pathway in V1 is involved in this illusion (Song et al., 2011). The present results are consistent with those of previous studies, since the illusory size effect was observed even when inducers were rendered invisible by CFS. These results suggest that the Ebbinghaus illusion is mediated in V1. Moreover, the weaker strength of the illusion induced by suppressed contexts supports the involvement of V1 in this illusion, because monocular cells, which might mediate the unconscious effect, are partial in V1. In our experiment, only monocular cells could receive the inducers in the suppression condition, while monocular and binocular cells could receive them in the visible condition. The strength of the illusion in the suppression condition relative to that in the visible condition would be approximately 20%–30%, predicted from the distribution of ocular dominance in V1 (Hubel & Wiesel, 1968; Kiorpes, Kiper, O'Keefe, Cavanaugh, & Movshon, 1998). This is consistent with the result revealed in our study.

As discussed above, the results in Experiments 1 and 2 suggest that the size-contrast effect induced by suppressed inducers is mediated by the monocular pathway in V1. To test further this idea, we examined interocular transfer of the illusion in Experiment 3. When inducers were presented to one eye and test stimuli were presented only to the opposite eye, the size-contrast effect occurred in the visible condition but not at all in the suppressed condition. No interocular transfer in the suppressed condition suggests that inducers suppressed by CFS stimulate only monocular cells. The results support the idea that the unconscious size-contrast effect is processed in monocular cells of V1. The effect induced by visible contexts was weaker when inducer and test stimuli were presented to different eyes than when test stimuli were presented to both eyes; the strength of the effect under the dichoptic presentation was approximately 50% of that under the binocular presentation. The partial interocular transfer in the visible condition is consistent with the previous results (Song et al., 2011). This also suggests that monocular pathway in V1 is involved in the Ebbinghaus illusion.

The present study demonstrated that the processing of consciously perceived stimuli is influenced by suppressed stimuli. The results imply that binocular neurons representing the perceptually dominant stimuli can be influenced by suppressed stimuli. Stimuli suppressed by binocular rivalry or CFS have been found to be still processed in the brain. The amygdala (Pasley, Mayes, & Schultz, 2004; Williams, Morris, McGlone, Abbott, & Mattingley, 2004; Troiani & Schultz, 2013) and the superior temporal sulcus (Jiang & He, 2006) were activated by suppressed emotional face stimuli. Category information of suppressed object stimuli were represented in fMRI activity patterns in the high-level ventral visual areas (Sterzer, Haynes, & Rees, 2008) and in the lateral occipital cortex (Hesselmann & Malach, 2011). The influence of suppressed stimuli on processing in the binocular pathway of V1 might be the underlying mechanism of the unconscious size contrast effect shown in our study.

In the first three experiments, unlike the normal Ebbinghaus illusion, the inducer and test stimuli were separately presented with an ISI. It was to examine temporal decay of the effect and to avoid visual clutter or attentional interference caused by the Mondrian mask. However, it is possible that the mechanism of the illusory size effect under the successive presentation paradigm is distinct from that in the conventional Ebbinghaus illusion. Adaptation-like processes might be involved in the effect under the successive presentation. We tested whether similar results to those under the successive presentation could be observed when inducer and test stimuli were simultaneously presented in Experiment 4, and confirmed that the unconscious size-contrast effect was observed even in the conventional Ebbinghaus illusion. The unconscious effect was one fourth the strength of the effect induced by visible contexts. The ratio was similar to that in Experiment 1, suggesting that size-contrast effects under the successive and simultaneous presentation paradigms might share the mechanism.

However, it is still possible that adaptation-like processes are involved in the effect under the successive presentation, which might be like size aftereffects rather than size-contrast effects. It has been reported that low-level aftereffects, such as orientation (Kanai, Tsuchiya, & Verstraten, 2006) and motion (Maruya, Watanabe, & Watanabe, 2008), are weakened but not eliminated, while higher level aftereffects, such as complex motion (Maruya et al., 2008) and face (Amihai, Deouell, & Bentin, 2011; Stein & Sterzer, 2011), are abolished completely when adapter stimuli are suppressed by CFS. A recent study has shown that size aftereffects do not occur without awareness of adapters, and suggests that relatively higher level visual processing is involved in size aftereffects (Laycock, Sherman, Sperandio, & Chouinard, 2017). This finding leads us to conclude that effects under the successive presentation in our study are different from typical size aftereffects, because they occurred even without awareness of

inducers. These results suggest that distinct mechanisms underlie size-contrast effects in the Ebbinghaus illusion and size aftereffects. Laycock et al. (2017) argued that size aftereffects may require recurrent signals from higher visual areas. Size-contrast effects in the Ebbinghaus illusion might be mediated by a feedforward mechanism in V1.

Keywords: size perception, *Ebbinghaus illusion*, *consciousness*, *continuous flash suppression*

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