



Original Articles

Subconscious processing reveals dissociable contextual modulations of visual size perception

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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 (Pooremaeili, 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

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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.

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