Low-spatial-frequency bias in context-dependent visual size perception

Lihong Chen
Research Center of Brain and Cognitive Neuroscience, Liaoning Normal University, Dalian, People's Republic of China

Congying Qiao
Research Center of Brain and Cognitive Neuroscience, Liaoning Normal University, Dalian, People's Republic of China

Yi Jiang
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, People's Republic of China
Department of Psychology, University of Chinese Academy of Sciences, Beijing, People's Republic of China

Spatial frequency (SF) information is essential for visual perception. By combining a sensitization procedure and the Ebbinghaus illusion, we investigated the effect of SF bias in context-dependent visual size perception. During the sensitization phase, participants were repeatedly presented with low- or high-pass filtered faces or gratings and were asked to discriminate the gender or the orientation of them, respectively. Immediately following the sensitization phase, the Ebbinghaus illusion strength was measured. The results showed that the illusion strength was significantly larger when the prior sensitized images were low-pass filtered relative to when they were high-pass filtered. Moreover, this SF bias was independent of low-level features and the specific content of the filtered images. Our findings extend the understanding of SF bias induced by sensitization in visual domain, and suggest that the processing of context-dependent visual size information is likely to involve magnocellular projections from subcortical areas via low SF channel.

Introduction

Fast and efficient processing of object size information is crucial to rapid fight-or-flight response. A large object is more likely to be a threat (i.e., a predator) and requires fast reaction, and a small object might be prey and should be reacted to with little delay (Preuss, Trivedi, vom Berg-Maurer, Ryu, & Bollmann, 2014). However, rather than in isolation, objects appear in a spatiotemporal context. Converging evidence suggests that human visual size perception is highly context-dependent. For instance, an object appears larger when surrounded by small items than when the same object is surrounded by large items (the Ebbinghaus illusion).

Many studies have found that human visual size perception is modulated by threatening information (Shiban et al., 2016; Stefanucci & Proffitt, 2009; van Ulzen, Semin, Oudejans, & Beek, 2008; Vasey et al., 2012; Whitaker, McGraw, & Pearson, 1999), even when the threatening information is below the level of conscious awareness. In particular, when observers cannot consciously perceive the threatening information, i.e., they cannot explicitly discriminate any difference between the collision and the near-miss stimuli, visual stimuli on the collision path appear larger than those on the near-miss path (Chen, Yuan, Xu, Wang, & Jiang, 2016). A specialized subcortical visual pathway (through the superior colliculus and the pulvinar to the amygdala) has been suggested to detect threat-related signals outside conscious awareness (Hedger, Adams, & Garner, 2015; Jiang & He, 2006). Notably, it has been found that subcortical processing of threatening stimuli operates primarily on low-spatial-frequency (LSF) information (but see also McFadyen, Mermillod, Mattingley, Halász, & Garrido, 2017; Stein, Seymour, Hebart, & Sterzer, 2014). Specifically, Vuilleumier, Armony, Driver, and Dolan (2003) demonstrate that LSF information is crucial to

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produce activations to fearful relative to neutral faces in the amygdala. Conversely, high-spatial-frequency (HSF) information is not found to induce differential activations to fearful compared to neutral faces in the amygdala.

Therefore, we hypothesized that context-dependent visual size perception might be largely mediated by LSF information which is received via magnocellular channels and provides rapid coarse visual signals (McFadyen et al., 2017; Méndez-Bértolo et al., 2016; Öhman, 2005; Vuilleumier et al., 2003). To probe this issue, we adopted a sensitization procedure combined with the Ebbinghaus illusion. Specifically, during the sensitization phase, participants were repeatedly exposed to low- or high-pass filtered faces or gratings, and were asked to discriminate the gender or the orientation of them, respectively. This was immediately followed by a test phase, during which the magnitude of the Ebbinghaus illusion was measured.

There is convincing evidence that the LSF and HSF channels are related to the processing of global and local stimuli, respectively. For instance, Shulman, Sullivan, Gish, and Sakoda (1986) adapt participants to either LSF or HSF content of the stimuli. The LSF adaptation has a greater effect on the response time (RT) to the global stimulus than to the local stimulus. Moreover, several studies have demonstrated that removal of LSFs (i.e., by means of filtering or contrast balancing) removes or greatly reduces the global precedence effect (Badcock, Whitworth, Badcock, & Lovegrove, 1990; Hughes, Fendrich, & Reuter-Lorenz, 1990; Jiang & Han, 2005; Lagasse, 1993). Furthermore, reduced Ebbinghaus illusion effect evoked by culture (de Fockert, Davidoff, Fagot, Parron, & Goldstein, 2007), age (Káldy & Kovács, 2003), gender (Phillips, Chapman, & Berry, 2004) and psychiatric disorders like autism (Happé, 1996) has been associated with bias toward local processing. Therefore, we expected that prior sensitization to LSF stimuli would increase the Ebbinghaus illusion effect compared to prior sensitization to HSF stimuli.

Methods

Participants

A total of 32 participants (14 male; 18 female; mean age = 21.7 years) took part in the study. Ten took part in Experiment 1a, 12 participated in Experiment 1b, and the remaining 10 participated in Experiment 2. All participants had normal or corrected-to-normal eyesight and provided informed consent. The study was approved by the institutional review board of Liaoning Normal University, and it adhered to the tenets of the Declaration of Helsinki. All participants were naïve to the purpose of the experiments.

Stimuli

Stimuli were displayed using MATLAB (MathWorks, Natick, MA) together with the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). The Ebbinghaus configuration was composed of a central circle (1.1° × 1.1°) surrounded by four small (0.6° × 0.6°) or large (1.7° × 1.7°) circles. The initial size of a comparative circle varied from trial to trial ranging from 0.86° to 1.37° in steps of 0.06°. There was neither spatial nor temporal overlap between the comparative circle and the illusory configuration. Face images (3.4° × 5.1°) had neutral expressions with an equal number of male and female (two males and two females) in frontal views and direct gaze selected from the NimStim face-stimulus set (Tottenham et al., 2009). They were assigned identical root mean square (RMS) contrast and average luminance values. All hair and nonfacial features were removed, and only the central face area was left. We manipulated SF content by passing the face images through a second-order Butterworth filter, using a high-pass cutoff of more than 6 cycles/° for HSF faces and a low-pass cutoff of less than 2 cycles/° for LSF faces, following previous studies (Schyns & Oliva, 1999; Stein et al., 2014; Vlamings, Goffaux, & Kemner, 2009). Gratings were sinusoidal (contrast, 0.1; spatial frequency (SF), 1 or 6 cycles/°) in a square aperture (4.9° × 4.9°) presented on a gray background with one of four possible orientations (30°, 60°, 120°, or 150°). The monitor was calibrated for proper gamma correction prior to experiment commencement with a SpectraScan PR-655 Spectroradiometer. The mean luminance of images of faces and gratings was 104.0 and 127.5 cd/m^2, respectively. Participants were positioned 57 cm from a gray computer screen (1,440 × 900 at 60 Hz) with their head positioned in a chin rest.

Procedure

Experiment 1a

The experiment was composed of two sessions (see Figure 1), i.e., a LSF (2 cycles/°) session and a HSF (6 cycles/°) session, with an interval of at least 12 hours. The session sequence was counterbalanced between participants. Each session included two phases. During the sensitization phase, a low- or high-pass filtered face was presented at the screen center for 0.3 s after the disappearance of a fixation point. Participants were required to press buttons to indicate the gender of the faces as accurately and fast as possible. There was a

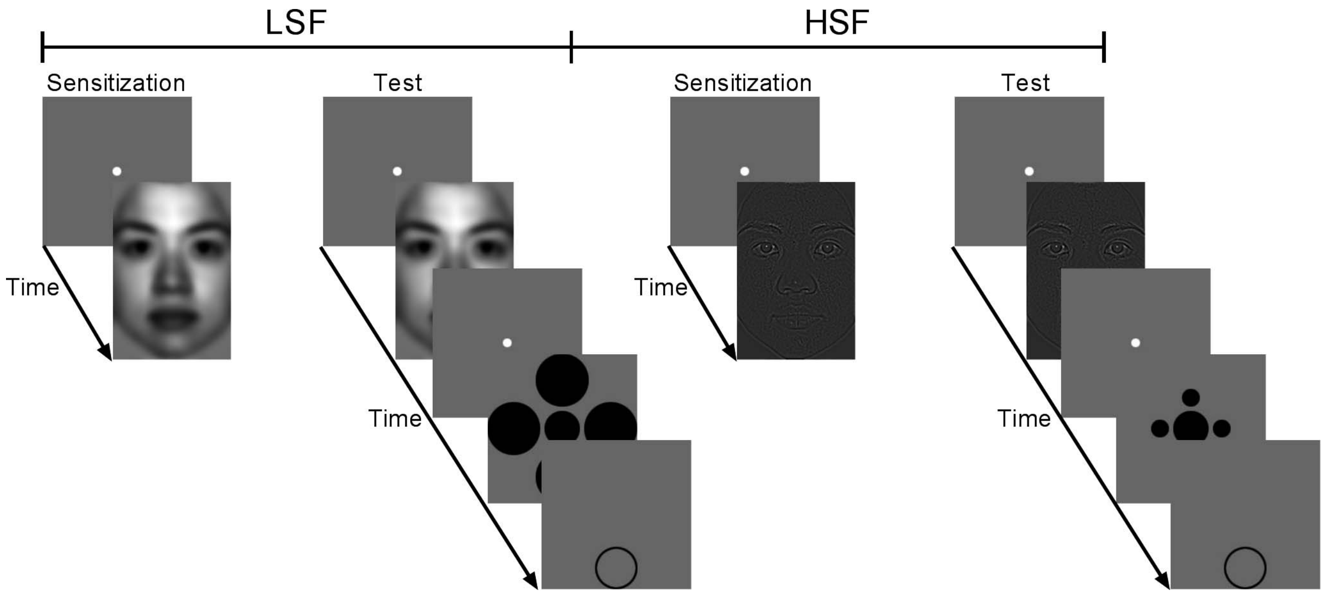

Figure 1. Schematic representation of the experimental procedure in Experiment 1a. The experiment was composed of two sessions (low- and high-spatial frequencies), each of which included two phases. During the sensitization phase, a filtered face image was presented at the screen center for 0.3 s. Participants were asked to discriminate the gender of the face as accurately and rapidly as possible. During the test phase, participants sequentially performed the gender discrimination task and the size adjustment task in each trial. The face stimulus depicted is from the NimStim Face Stimulus Set (Model #18; reprinted with permission, http://www.macbrain.org/resources.htm).

total of 160 trials with 80 trials in each condition. During the test phase which followed immediately, the filtered face stimuli were displayed for 0.3 s at the beginning of each trial to strengthen the SF bias produced by sensitization. Participants were required to perform the gender discrimination task. After the key press, they were presented with the Ebbinghaus configuration at the screen center for 0.5 s, followed by a comparative circle that was presented in the lower visual field. The participants were asked to adjust the size of the comparative circle to match the central target without time limit.

Experiment 1b

The stimuli and procedures were similar to those of Experiment 1a. To exclude the potential influence of low-level perceptual confounds, average luminance and RMS contrast values of eight filtered face images were equalized using the SHINE toolbox for MATLAB (Willenbockel et al., 2010).

Experiment 2

The procedures were similar to those of Experiment 1a. LSF and HSF gratings were adopted instead of filtered faces. The gratings were presented for 0.1 s (see Figure 2). During the sensitization phase, participants were required to press buttons to indicate the orientation of the gratings as quickly and accurately as possible. During the test phase, which followed immediately, the participants were required to sequentially perform the orientation discrimination task and the size adjustment task in each trial.

Results

We calculated the perceived size of the central target based on the difference between the measured size and physical size as follows: $\frac{measured\ size - physical\ size}{physical\ size} \times 100\%$. The measured size was the size of the comparative circle that was perceived as the same size of the central target, and the physical size was the physical size of the central target. The illusion magnitude was measured as the difference of the perceived sizes of the central targets surrounded by small and large inducers. For all the experiments, we collected the RTs and perceived sizes of the targets from trials with correct responses. The perceived size of the target was entered into a 2×2 repeated measures analysis of variance (ANOVA) with size of inducers (large vs. small) and SF of stimuli (low vs. high).

In Experiment 1a, the proportions of correct responses on gender discrimination task were 0.98 and 0.99 in the two phases, respectively. There was no significant difference between the LSF and HSF conditions with accuracy and RTs during the sensitization: accuracy, $t(9) = 1.72$, $p = 0.119$, $d = 0.55$; RTs,

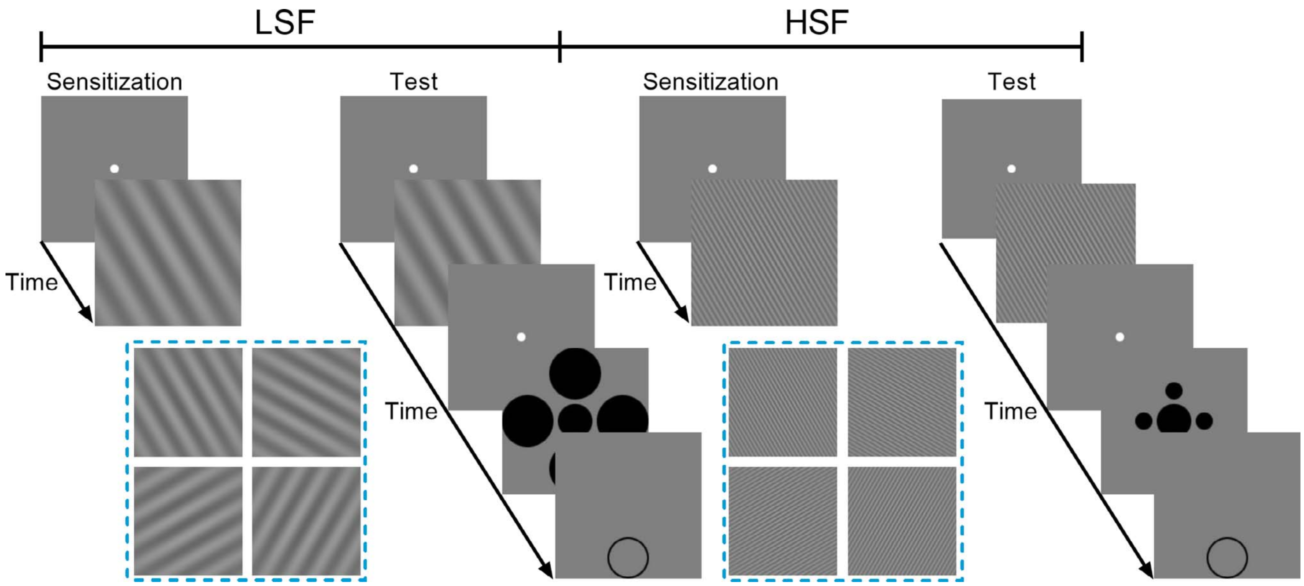

Figure 2. Schematic representation of the experimental procedure and examples of gratings as used in Experiment 2. The experiment was composed of two sessions (low- and high-spatial frequencies), each of which included two phases. During the sensitization phase, a grating with one of four possible orientations was presented at the screen center for 0.1 s. Participants were asked to discriminate the orientation as accurately and rapidly as possible. During the test phase, participants sequentially performed the orientation discrimination task and the size adjustment task in each trial.

$t(9) = -1.85$, $p = 0.097$, $d = 0.59$; and the test: accuracy, $t(9) = 1.04$, $p > 0.250$, $d = 0.33$; RTs: $t(9) = -2.17$, $p = 0.058$, $d = 0.69$, phases. For the size adjustment task, results of repeated measures ANOVA revealed a significant main effect of size of inducers, $F(1, 9) = 10.99$, $p = 0.009$, $\eta_p^2 = 0.55$; and a significant main effect of SF of faces, $F(1, 9) = 5.29$, $p = 0.047$, $\eta_p^2 = 0.37$. Notably, there was a significant interaction between these two variables, $F(1, 9) = 5.65$, $p = 0.041$, $\eta_p^2 = 0.39$. Further analysis demonstrated that the illusion magnitude, which was significant under each of the SF conditions: LSF, $M = 13.61\%$, 95% CI = [4.25%, 22.98%], $t(9) = 3.29$, $p = 0.009$, $d = 1.04$; HSF, $M = 10.29\%$, 95% CI = [3.20%, 17.39%], $t(9) = 3.28$, $p = 0.010$, $d = 1.04$; was significantly larger for the LSF condition than the HSF condition, mean difference = 3.32%, 95% CI = [0.16%, 6.48%], $t(9) = 2.38$, $p = 0.041$, $d = 0.75$; see Figure 3A.

In Experiment 1b, the proportions of correct responses on gender discrimination task were 0.96 and 0.99 in the two phases, respectively. There was no significant difference between the LSF and HSF conditions with respect to accuracy during the two phases: sensitization, $t(11) = -0.74$, $p > 0.250$, $d = 0.21$; test, $t(11) = 0.36$, $p > 0.250$, $d = 0.11$; and RTs during the test phase, $t(11) = -2.09$, $p = 0.061$, $d = 0.60$. The RTs of the LSF condition, however, was significantly faster than that of the HSF condition during the sensitization phase, $t(11) = -3.18$, $p = 0.009$, $d = 0.92$. For the size adjustment task, results of repeated measures ANOVA revealed a significant main effect of size of inducers, $F(1, 11) = 28.79$, $p < 0.001$, $\eta_p^2 = 0.72$; and a significant main effect of SF of faces, $F(1, 11) = 7.17$, $p = 0.022$, $\eta_p^2 = 0.40$. Notably, there was a significant interaction between these two variables, $F(1, 11) = 6.27$, $p = 0.029$, $\eta_p^2 = 0.36$. Further analysis demonstrated that the illusion magnitude was significant under each of the SF conditions: LSF, $M = 9.55\%$, 95% CI = [5.33%, 13.77%], $t(11) = 4.98$, $p < 0.001$, $d = 1.44$; HSF, $M = 6.98\%$, 95% CI = [4.20%, 9.77%], $t(11) = 5.53$, $p < 0.001$, $d = 1.60$. Notably, the illusion magnitude was significantly larger for the LSF than the HSF conditions: mean difference = 2.57%, 95% CI = [0.31%, 4.82%], $t(11) = 2.50$, $p = 0.029$, $d = 0.72$; see Figure 3B. Results of independent-samples t test revealed that the disparity of illusion magnitudes between the LSF and the HSF conditions was comparable in Experiments 1a and 1b: mean difference = 0.75%, 95% CI = [–2.79%, 4.30%], $t(20) = 0.45$, $p > 0.250$, $d = 0.19$, $BF_{01} = 3.09$; see Figure 3C.

In Experiment 2, the proportions of correct responses on orientation discrimination task were 0.98 and 0.99 in the two phases, respectively. There were no evident differences in accuracy and RTs between the LSF and HSF conditions during the sensitization: accuracy, $t(9) = -0.13$, $p > 0.250$, $d = 0.04$; RTs, $t(9) = -1.73$, $p = 0.118$, $d = 0.55$; and the test: accuracy, $t(9) = 0$, $p = 1$, $d = 0$; RTs, $t(9) = -1.43$, $p = 0.186$, $d = 0.45$, phases. For the size adjustment task, results of repeated measures ANOVA revealed a significant main effect of size of inducers, $F(1, 9) = 65.39$, $p < 0.001$, $\eta_p^2 = 0.88$. Importantly, there was a significant interaction between

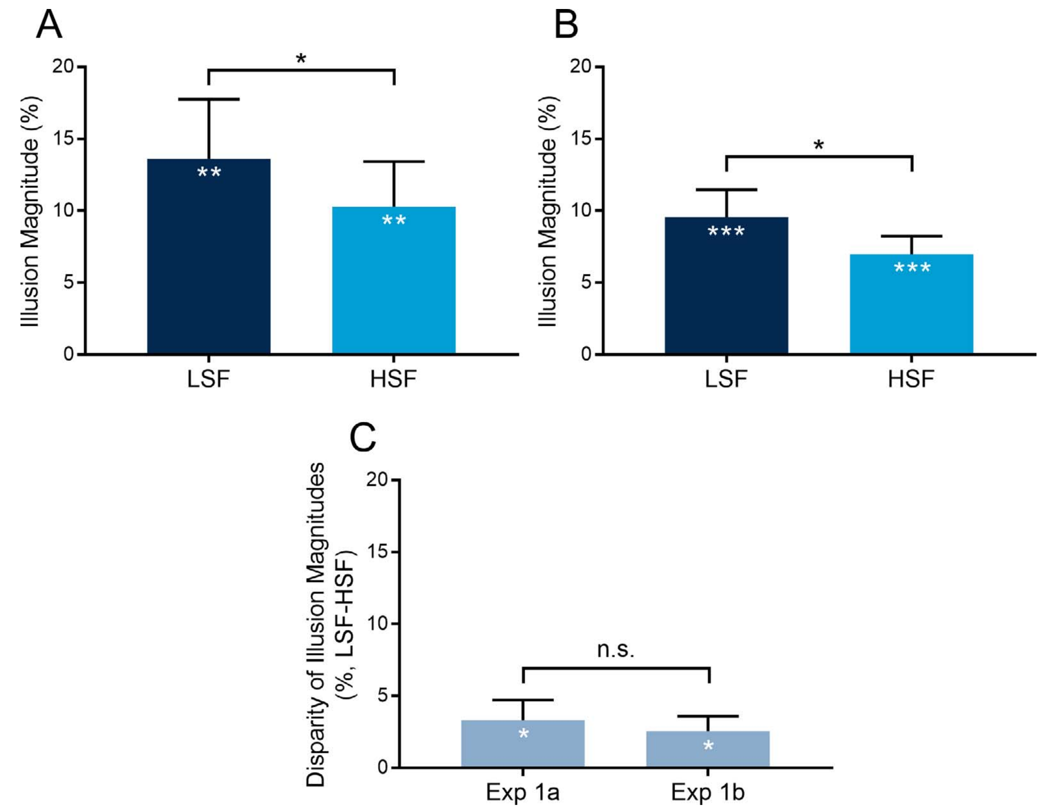

Figure 3. Results of Experiment 1. The illusion magnitude as a function of low- and high-spatial frequencies (LSF and HSF) conditions in Experiment 1a (A) and Experiment 1b (B), and the disparity of illusion magnitudes between the LSF and HSF conditions in Experiments 1a and 1b (C). Error bars represent one standard error of the mean. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$; n.s. (not significant).

size of inducers and SF of gratings, $F(1, 9) = 8.00$, $p = 0.020$, $\eta_p{}^2 = 0.47$. Further analysis demonstrated that the illusion magnitude was significant under each of the SF conditions: LSF, $M = 12.53\%$, 95% CI = [9.08%, 15.97%], $t(9) = 8.22$, $p < 0.001$, $d = 2.60$; HSF, $M = 10.27\%$, 95% CI = [7.09%, 13.44%], $t(9) = 7.32$, $p < 0.001$, $d = 2.31$. The illusion magnitude was significantly larger for the LSF than HSF conditions: mean difference = 2.26%, 95% CI = [0.45%, 4.07%], $t(9) = 2.83$, $p = 0.020$, $d = 0.89$; see Figure 4A. Results of independent-samples t test revealed that the disparity of illusion magnitudes between the LSF and HSF conditions was comparable to that in Experiment 1b: mean difference = –0.31%, 95% CI = [–3.11%, 2.49%], $t(20) = -0.23$, $p > 0.250$, $d = 0.10$, $BF_{01} = 3.28$; see Figure 4B.

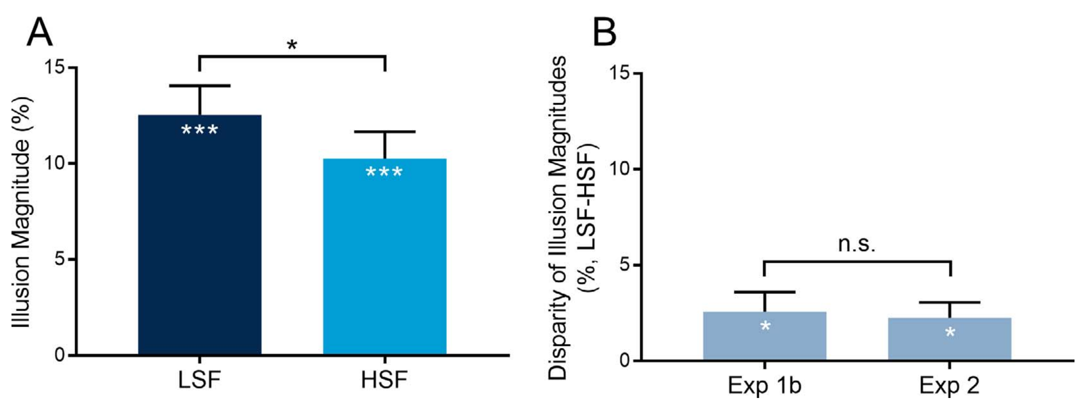

Figure 4. Results of Experiment 2. The illusion magnitude as a function of low- and high-spatial frequencies (LSF and HSF) gratings in Experiment 2 (A), and the disparity of illusion magnitudes between the LSF and HSF conditions in Experiments 1b and 2 (B). Error bars represent one standard error of the mean. *$p < 0.05$, ***$p < 0.001$; n.s (not significant).

Discussion

In the current study, we investigated the effect of SF bias on context-dependent visual size perception by sensitizing participants to a stream of either low- or high-pass filtered faces or gratings and measuring the Ebbinghaus illusion magnitude in succession. The results demonstrated that the illusion magnitude was significantly larger with prior sensitization to LSF faces than to HSF faces (Experiment 1a). This SF bias was independent of average luminance and RMS contrast differences of filtered face images (Experiment 1b), consistent with previous study (Vlamings et al., 2009). Comparative strength of SF bias was also obtained when LSF and HSF gratings were used (Experiment 2). Therefore, our results suggested that context-dependent visual size perception was biased by SF, with LSF information enlarging the contextual modulation effect relative to HSF information. This SF bias was independent of low-level features (average luminance and RMS contrast) and specific stimuli (faces and gratings) being used.

Sensitization to different SFs can influence the usage of SF bands for visual recognition in a variety of visual domains (Morrison & Schyns, 2001; Oliva & Schyns, 1997; Ozgen, Payne, Sowden, & Schyns, 2006; Schyns & Oliva, 1999). For instance, Oliva and Schyns (1997) repeatedly presented participants with either LSF or HSF scenes combined with noise on the opposite scale, and asked them to categorize scenes. Subsequently, a hybrid scene composed of a LSF scene and a HSF scene was displayed to participants. Those who were sensitized with LSF scenes reported seeing the LSF content, while those sensitized with HSF scenes reported seeing the HSF content of hybrids. Similarly, the SF bias induced by an initial face task (HSF bias from expressive vs. nonexpressive discrimination task, or LSF bias from expression categorization task) can be transferred to a subsequent task (gender discrimination of faces) which shows no SF bias alone (Schyns & Oliva, 1999). Moreover, increased LSF sensitivity acquired by learning to discriminate SF variations in gratings can transfer to face processing, but this improved LSF sensitivity modifies the processing of LSF faces instead of HSF faces (Peters, van den Boomen, & Kemner, 2017). By using similar sensitization procedure, our study resonates well with previous findings and shows that SF bias also has a role in context-dependent visual size perception with LSF enlarging contextual modulation effect relative to HSF, extending the effects of SF bias in visual perception.

It is important to note that, in the current study, participants were naïve to experimental design and didn't notice the implicit connection between the filtered stimuli and the following illusory configuration. Therefore, the effect of SF bias on context-dependent size perception is likely to occur quite automatically. The purported subcortical visual pathway (superior colliculus-pulvinar-amygdala) has been suggested to facilitate early processing of LSF information (Corradi-Dell'Acqua et al., 2014; Vuilleumier et al., 2003) which enhances activities in visual areas via feedback projections (Morris et al., 1998; Rotshtein, Malach, Hadar, Graif, & Hendler, 2001; Vlamings et al., 2009). Therefore, based on this converging evidence and our current findings, we propose that the processing of context-dependent visual size information might involve magnocellular projections from subcortical areas via LSF channel.

Recent studies have revealed that context-dependent visual size perception correlates directly or indirectly with the anatomical and functional properties of V1 (Fang, Boyaci, Kersten, & Murray, 2008; Murray, Boyaci, & Kersten, 2006; Pooresmaeili, Arrighi, Biagi, & Morrone, 2013; Schwarzkopf, Song, & Rees, 2011). Notably, the spatial distribution of V1 activities induced by perceived size information is arranged in a retinotopic manner. That is, activations in response to perceptually larger object occur in a more eccentric position in V1 compared to perceptually smaller object (Fang et al., 2008; Murray et al., 2006; Sperandio, Chouinard, & Goodale, 2012). Ozgen et al. (2006) have found that the SF sensitization effect is retinal location specific, suggesting the involvement of relatively early visual processing stage in effects of SF sensitization. Furthermore, the representation of SF in occipital cortex is organized retinotopically (Kenemans, Baas, Mangun, Lijffijt, & Verbaten, 2000; Sasaki et al., 2001). For instance, Henriksson, Nurminen, Hyvärinen, and Vanni (2008) reveal that in the retinotopic area of the occipital cortex, LSF selectivity is observed as the eccentricity of the grating is increased. Similarly, Musel et al. (2013) demonstrate that, compared with HSF, LSF scene categorization elicits activation in the anterior half of the calcarine fissures linked to the peripheral visual field. In contrast, compared with LSF, HSF scene categorization elicits activation in the posterior part of the occipital lobes, which are linked to the fovea visual field. Therefore, in the current study, when the faces or the gratings were low-pass filtered, they might activate visual areas corresponding to more peripheral visual field, and then facilitate the subsequent processing of surrounding inducers in the Ebbinghaus configuration and result in larger illusion effect, as compared with when the faces or the gratings were high-pass filtered.

Sensitization, different from adaptation, is a form of nonassociative learning in which repeated administration of a stimulus results in the progressive amplification of a response. While sensitization to a stimulus can be readily generalized to a related stimulus/task, the aftereffect of adaptation is commonly specific to the adapted stimulus/task. Moreover, the time courses and the outcomes produced by sensitization and adaptation are different. In the studies using adaptation procedure (Bonnar, Gosselin, & Schyns, 2002; Shulman et al., 1986), prior exposure to LSF stimuli (noise or grating, 3 min 20 s or 12 s in each trial) resulted in perception of HSF component of an ambiguous image or increased RTs of global processing, and prior exposure to HSF stimuli resulted in perception of LSF component of the ambiguous image or increased RTs of local processing. However, in the studies using sensitization procedure (Ozgen et al., 2006; Peters et al., 2017), prior exposure to LSF stimuli (scene or grating, 125 ms or 67 ms in each trial) resulted in more frequently report of LSF component of hybrids and faster RTs of LSF neutral faces, and prior exposure to HSF stimuli resulted in more frequently report of HSF component of hybrids. In our study, relative to HSF stimuli, prior exposure to LSF stimuli (face or grating, 300 ms or 100 ms in each trial) resulted in increased Ebbinghaus illusion effect, which is associated with increased global processing. Therefore, our results are consistent with the sensitization rather than the adaptation consequence.

In summary, the current study shows that SF bias produced by sensitization takes effect on context-dependent visual size perception, with LSF information enlarging the contextual modulation effect relative to HSF information. Our findings extend the understanding of SF bias induced by sensitization, and suggest that the processing of context-dependent visual size information might involve magnocellular projections from subcortical areas via LSF channel.

Keywords: spatial frequency, *Ebbinghaus illusion*, *faces*, *gratings*

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Corresponding author: Lihong Chen; Yi Jiang.
Email: lihongchen@lnnu.edu.cn; yijiang@psych.ac.cn.
Address: Research Center of Brain and Cognitive Neuroscience, Liaoning Normal University, Dalian, People's Republic of China; Institute of Psychology, Chinese Academy of Sciences, Beijing, People's Republic of China.

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