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Looking more masculine among females: Spatial context modulates gender perception of face and biological motion

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Abstract

Perception of visual information highly depends on spatial context. For instance, perception of a low-level visual feature, such as orientation, can be shifted away from its surrounding context, exhibiting a simultaneous contrast effect. Although previous studies have demonstrated the adaptation aftereffect of gender, a high-level visual feature, it remains largely unknown whether gender perception can also be shaped by a simultaneously presented context. In the present study, we found that the gender perception of a central face or a point-light walker was repelled away from the gender of its surrounding faces or walkers. A norm-based opponent model of lateral inhibition, which accounts for the adaptation aftereffect of high-level features, can also excellently fit the simultaneous contrast effect. But different from the reported contextual effect of low-level features, the simultaneous contrast effect of gender cannot be observed when the centre and the surrounding stimuli are from different categories, or when the surrounding stimuli are suppressed from awareness. These findings on one hand reveal a resemblance between the simultaneous contrast effect and the adaptation aftereffect of high-level features, on the other hand highlight different biological mechanisms underlying the contextual effects of low- and high-level visual features.

KEYWORDS

consciousness, contextual effect, gender perception, simultaneous contrast effect

INTRODUCTION

In nature, nothing exists alone in space or in time. Most often our perception of an object is reshaped by its spatial or temporal context. A grey skirt looks close to white when hanging near black ones, but not

that bright when hanging near white ones. Since an object being contrasted by its context may perceptually pop out, our visual system is accustomed to this contextual effect at the sacrifice of full precision (e.g., the actual colour of the skirt) after long-term evolution. As such, it has attracted numerous psychologists to explore the characteristics and mechanisms of contextual effects (Schwartz et al., 2007).

The simultaneous contrast effect is a classical contextual effect in the spatial dimension, that perception of a visual stimulus is affected by the contextual stimuli presented simultaneously (Gibson, 1933). For instance, the aforementioned skirt example essentially reflects a simultaneous lightness contrast effect. The simultaneous contrast effect in a centre-surround arrangement has been extensively demonstrated for many low-level visual features, including colour (Brown & MacLeod, 1997; Ekroll & Faul, 2012), motion (Anstis & Casco, 2006), spatial frequency (Klein et al., 1974), orientation (Gibson & Radner, 1937) and so on. The occurrence of the simultaneous contrast effect is largely due to feature-selective inhibition of neurons responding to the central stimuli (McDonald et al., 2009). Take the tilt illusion as an example, the lateral inhibition mechanism repels the perceived orientation of a vertical centre grating away from the tilted surrounding orientation (Gilbert & Wiesel, 1990; Yuan et al., 2017).

In contrast, another well-explored contextual effect is the adaptation aftereffect, which takes place in the temporal dimension (Schwartz et al., 2007). Different from the simultaneous contrast effect, it has been demonstrated that the adaptation aftereffect not only occurs for low-level visual features, but also for high-level stimuli including body size (e.g., Brooks et al., 2018), perceived number (e.g., Burr & Ross, 2008) and face properties (Webster et al., 2004; see also Webster & Macleod, 2011 for a review). Among these findings, Webster et al. (2004) found that prolonged exposure to a female face caused the perceived gender of a subsequent ambiguous face to be more masculine, whereas adaptation to a male face triggered an opposite change. Such gender aftereffect has also been demonstrated for biological motion (BM) (Jordan et al., 2006; Troje et al., 2006), which can convey sufficient gender information even only portrayed by a handful of point lights attached to the main joints of a person (Johansson, 1973; Kozlowski & Cutting, 1977). Importantly, both the aftereffects of low-level (e.g., tilt aftereffect) and high-level features (e.g., gender aftereffect) are accounted for by similar inhibition mechanisms (Seriès et al., 2009; Zhao et al., 2011).

Given the numerous psychophysical and electrophysiological resemblance between the spatial and temporal contextual effects (see more details in Schwartz et al., 2007), it is possible that the simultaneous contrast effect can also be extended to the processing of high-level visual features. To this end, the current study aimed to empirically investigate whether the simultaneous contrast effect occurs for high-level visual features and whether it fits well with the model prediction of a lateral inhibition mechanism. Specifically, in Experiment 1a, we measured the influence of surrounding facial gender on the perceived gender of a central face, while in Experiment 1b, we employed BM displays (the point-light walkers) as stimuli to test the ubiquity of the simultaneous contrast effect of gender irrespective of gender carriers (Troje, 2002).

According to the lateral inhibition mechanism, the tilt illusion decreases as the surrounding and central stimulus onset asynchrony increases and vanishes when the temporal gap exceeds about 400 ms (Corbett et al., 2009; Durant & Clifford, 2006; Yuan et al., 2017). If the simultaneous contrast effect of gender is regulated by a similar lateral inhibition mechanism, it would disappear when a relatively long temporal gap was introduced between the surrounding and central stimuli. To test this hypothesis, we added a 500-ms temporal gap between the surrounding and central stimuli in Experiment 2.

The contextual effects of high-level features (e.g., gender), albeit can be explained by a lateral inhibition mechanism similar to that of low-level features (e.g., orientation) (Pond et al., 2013; Zhao et al., 2011), may have some unique characteristics based on the processing hierarchy. As visual features are processed through a cortical hierarchy from the primary visual cortex to the inferior temporal cortex (Bao et al., 2020; Hubel & Wiesel, 1959; Serre et al., 2007), high-level features, such as gender, can be extracted from many different stimulus categories (e.g., face and BM) with remarkable differences from low-level features (Kozlowski & Cutting, 1977; Webster et al., 2004). It then raises an intriguing possibility that gender can be represented and perceived not only in a category-specific manner but also in a category-general manner. This issue could be probed by investigating the cross-category contextual effect. If the gender representation is category-general, the contextual effect would be able to transfer

across different categories, otherwise, there would be no cross-category contextual effect. Some studies have found cross-category adaptation aftereffects of gender when the adapting and test stimuli are, respectively, from object and face categories (Javadi & Wee, 2012), or from body and face categories (Ghuman et al., 2010; Kessler et al., 2013; Palumbo et al., 2015), but others have not (Hiris et al., 2016; Kovács et al., 2006). Here to shed light on this issue from the perspective of the spatial contextual effect, we examined in Experiment 3 whether the simultaneous contrast effect of gender can be observed in a category-general manner by adopting face and BM as the central and surrounding stimuli, respectively. Specifically, we assessed whether the simultaneous contrast effect could occur on BM surrounded by faces in Experiment 3a and on face surrounded by BMs in Experiment 3b.

Another unique characteristic of high-level contextual effects closely related to the processing hierarchy is their dependence on awareness, as the higher the processing hierarchy, the more strongly the feature representation relies on awareness (Nguyen et al., 2003). For instance, in the early visual cortex, there is only a small proportion of neurons whose firing rates are mediated by awareness (Leopold & Logothetis, 1996), whereas in the inferior temporal cortex, the firing rates of almost all neurons are affected (Sheinberg & Logothetis, 1997). Many studies have found that the contextual effect of low-level features can occur independent of awareness, for example, the tilt illusion and tilt aftereffect are both evident even when the inducers are presented in absence of awareness (Clifford & Harris, 2005; Mareschal & Clifford, 2012; Zou et al., 2016). However, the contextual effect of high-level features (e.g., gender) is presumably awareness-dependent. First, some evidence has shown that conscious awareness is necessary for the processing of high-level features (e.g., gender and race in Amihai et al., 2011 and identity in Moradi et al., 2005, but see Cao et al., 2021). Second, studies employing a continuous flash suppression (CFS) paradigm do not support an awareness-independent aftereffect of face and BM gender (Amihai et al., 2011; Faivre & Koch, 2014). To comprehensively characterize whether the spatial contextual effect of gender depends on awareness, Experiment 4a and 4b separately evaluated the simultaneous contrast effect of gender for face and BM in an invisible within-category context.

Taken together, we implemented four experiments to systematically investigate the simultaneous contrast effect of gender. Experiments 1 and 2 were conducted to confirm the existence of this effect and demonstrate its lateral inhibition mechanism. Experiment 3 probed the cross-category property of the simultaneous contrast effect of gender, and Experiment 4 probed its dependence on awareness.

GENERAL METHODS

Participants

A total of 136 Chinese participants aged from 18 to 31 ($M \pm SD = 22.5 \pm 2.0$) years took part in the study. Experiments 1a, 1b, 2a and 2b each recruited 10 participants (six females in Experiments 1a and 2a, and seven females in Experiments 1b and 2b), and Experiments 3a, 3b, 4a and 4b each recruited 24 participants (12 females in Experiment 3a, and 13 females in Experiments 3b, 4a and 4b). The sample size was determined based on gender adaptation studies, as there were no previous studies that had measured the simultaneous contrast effect of high-level visual features. A two-tailed power analysis using G*Power (Version 3.1.9.4) (Faul et al., 2007) confirmed that a sample size of 10 participants would afford 80% power to detect a gender aftereffect for stimuli from the same category (Cohen's $d = 1$ in Troje et al., 2006), and a sample size of 19 participants would afford 80% power to detect a gender aftereffect for cross-category stimuli or invisible stimuli (Cohen's $d = 0.7$ in Kessler et al. (2013) for cross-category stimuli and in Adams et al. (2010) and Amihai et al. (2011) for invisible stimuli). Considering the simultaneous contrast effects for cross-category or invisible stimuli, if exist, may be smaller in magnitude, the sample size in Experiments 3 and 4 was increased to 24. All participants had normal or corrected-to-normal vision and provided written informed consent before the experiments. The protocols of the research were approved by the institutional review board of the Institute of Psychology, Chinese Academy of Sciences.

Stimuli

Face

The photographs of 10 females and 10 males in frontal view and neutral expression were taken from Chinese volunteers. Two average faces (one female and one male), created from the 10 female and 10 male faces separately, were used in Experiments 1a, 2a, 3a and 4a as the surrounding faces. A morphing spectrum was generated between the average male and the average female prototypes, serving as the central test stimuli (with the male face proportion of 29%, 36%, 43%, 50%, 57%, 64%, 71%) in Experiments 1a, 2a, 3b and 4a. The luminance of all the face photographs was matched using Photoshop (Adobe Photoshop, Inc.) and the sizes were standardized to $3.48^\circ \times 4.02^\circ$. All the surrounding photos were 4.29° eccentricity around the central stimuli in Experiments 1a, 2a, 3a and 4a.

Biological motion

Point-light biological motion sequences were adopted from Troje (2002), which were created by videotaping a walking actor. The degree of masculinity or femininity was defined by the walker's position on a gender axis. For instance, a position +1 means a masculine walker 1 standard deviation (*SD*) away from the mean, whereas a position -1 indicates a feminine walker 1 *SD* away from the mean. Considering the biases (somewhat more female than the mathematical average) in gender perception (Troje et al., 2006), we set the female surroundings at -2.45 *SD* and the male surroundings at 1.55 *SD* in Experiments 1b, 2b, 3b and 4b. The test stimuli in Experiments 1b, 2b, 3a and 4b were defined as seven equidistant steps from -0.9 *SD* (female) to 0 *SD* (male). All the test and surrounding point-light walkers, subtending approximately $3.22^\circ \times 3.68^\circ$ in visual angle, were shown in frontal view and refreshed at a rate of 30 Hz. One gait cycle of the point-light walker lasted 1 s, and the initial frame of the point-light walker was randomized in each trial to avoid participants' prediction. The surrounding point-light walkers in horizontal were 3.22° and those in vertical were 5.09° eccentricity around the central stimuli in Experiments 1b, 2b, 3b and 4b.

Stimuli were displayed using MATLAB (Mathworks, Inc.) together with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). All the stimuli were presented on a grey background and the viewing distance in Experiments 1–3 was 57 cm. In Experiment 4, the stimuli presented to the two eyes were displayed on a GOOVIS Pro Head-mounted 3D monitor with a side-by-side mode. The CFS display consisted of high-contrast, coloured noise patterns that changed at a rate of 10 Hz. Fusion frames ($15.71^\circ \times 15.71^\circ$) were used to facilitate stable binocular alignment.

Procedure

In Experiment 1a, each trial began with fixation on a central cross ($0.43^\circ \times 0.43^\circ$) for 500 ms. Thereafter a central target face, simultaneously surrounded by four identical faces (female/male), was presented for 300 ms. Then the fixation reappeared on the screen until a response was made. The centre of all surrounding stimuli floated randomly within an area of $0.26^\circ \times 0.26^\circ$. Participants were required to press one of two keys on a standard keyboard to indicate the gender of the central stimulus while ignoring the surrounding stimuli. Participants accomplished 280 trials with half trials for each surrounding condition (i.e., male and female surrounding stimuli). Each of the seven test faces was repeated 20 times for each condition. There were short breaks after every 70 trials.

The procedure of the other experiments was almost the same as Experiment 1a except for the following. In Experiment 1b, the stimuli were changed to point-light walkers. In Experiment 2a and 2b, a 500-ms temporal gap was introduced between the central and surrounding stimuli. That is, the surrounding stimuli were presented for 300 ms firstly, followed by a blank of 500 ms and then the central stimuli with a duration of 300 ms. In Experiment 3a, four faces surrounded one central point-light walker, while in

Experiment 3b, four point-light walkers surrounded one central face (Figure 1). In Experiment 4a, after a 500 ms binocular presentation of a fixation cross, dynamic CFS masks were presented to the dominant eye for 300 ms, with nothing in the non-dominant eye (Figure 2). Then, the surrounding faces (with gradually increased contrast from 0 to 0.2) and a central face (with full contrast) were presented to the non-dominant eye for 300 ms, during which the dynamic CFS masks and the central face were simultaneously presented to the dominant eye. Finally, the dynamic CFS masks remained for additional 200 ms to eliminate any possible aftereffect. Participants were required to press the up arrow key to abort the trial whenever any part of the surrounding stimuli became visible. Experiment 4b adopted the same procedure as experiment 4a except that the faces were replaced by point-light walkers (Figure 2).

Following the main part of Experiment 4, all participants completed an awareness measurement with a total of 58 trials to assess suppression effectiveness objectively. In these awareness measurement, visual stimuli and procedure were identical to those in the main experiment, except that the surrounding stimulus was only presented in one out of the four positions and participants were instructed to indicate the position by pressing one of the four corresponding keys. Thus, this forced-choice experiment assessed participants' ability to localize the surrounding stimulus, yielding an objective measure of surrounding stimuli's visibility.

Data analysis

For each participant under each condition, we calculated the proportions that a face or point-light walker was judged as a male and fitted them with a Boltzmann sigmoid function: $f(x) = 1 / (1 + \exp [(x - x_0) / \omega])$,

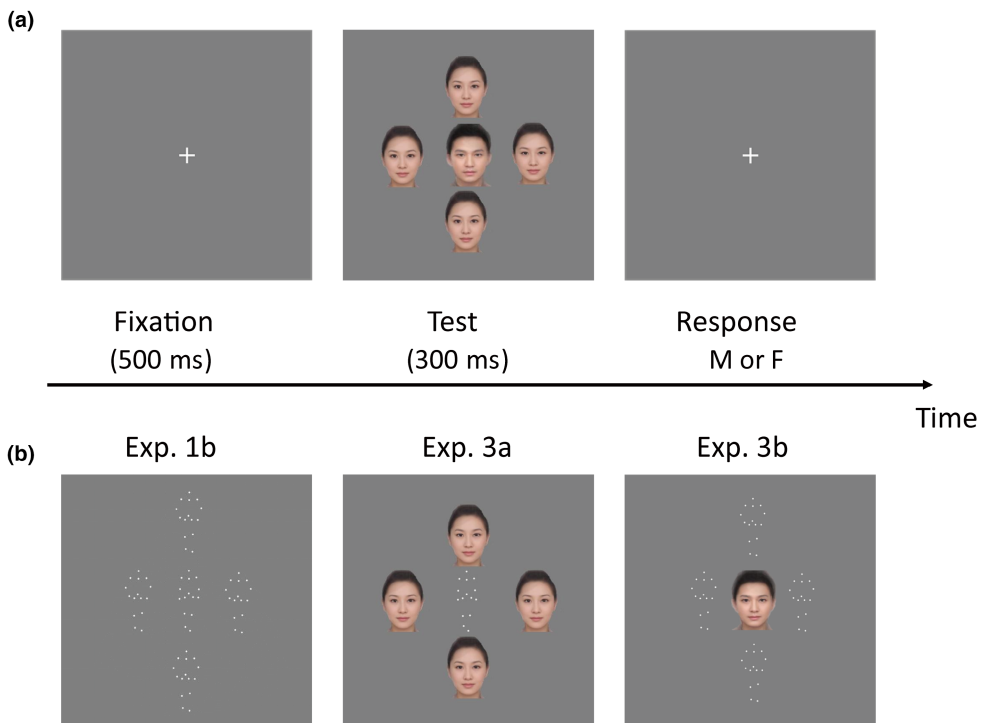


FIGURE 1 Schematic diagram of the experimental paradigm. (a) the trial procedure of experiment 1a. A fixation was shown 500 ms firstly in each trial, followed by a central morphed face surrounded by gender-specific faces (300 ms). Participants were required to press one of two buttons to indicate the gender of the central stimuli while ignoring the surrounding stimuli. (b) the stimuli presented in the test period. The pictures showed on left, middle, right represent diagram of experiment 1b, 3a, 3b in the test period, respectively.

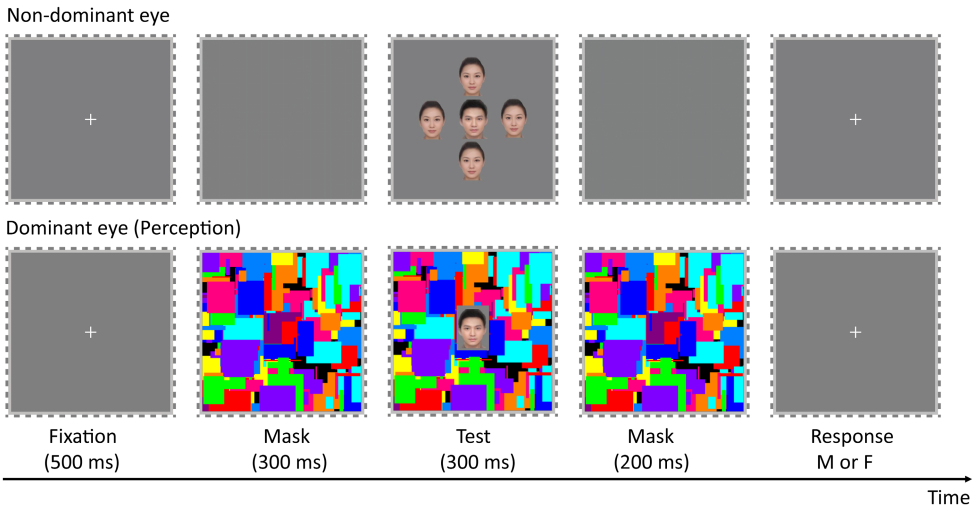


FIGURE 2 Schematic illustration of the stimuli presented to the dominant and non-dominant eye in experiment 4a. Each trial began with a binocular presentation of a fixation cross for 500 ms, then, dynamic CFS masks were presented to the dominant eye for 300 ms, with nothing shown in the non-dominant eye. Next, the central and surrounding faces were presented for 300 ms to the non-dominant eye, with the central face and the dynamic CFS masks simultaneously presented to the dominant eye. After that, the dynamic CFS masks remained for 200 ms, participants were required to press one of two buttons to indicate the gender of the central face.

where x corresponds to the masculinity of test stimuli, x_0 corresponds to the point of subjective equality (PSE, the masculinity of the test stimuli yielding male and female reports with equal probability, see Troje et al., 2006). The discriminability of the stimuli's gender was indexed by the difference limen (DL), which is estimated by half the interquartile range of the fitted function. The data of PSE and DL were entered into a paired-sample T -test with two different surrounding conditions (female/male) in all experiments. If PSE_{male} (the PSE in the male surrounding condition) is larger than PSE_{female} (the PSE in the female surrounding condition), it indicates a contrast effect; if PSE_{male} is smaller than PSE_{female} , it indicates an assimilation effect. In addition, we calculated the Bayesian factor (BF_{10}), which can provide evidence for alternative hypothesis (H_1) or null hypothesis (H_0). Specifically, $BF_{10} < 1/3$ indicated moderate evidence for H_0 ; and $BF_{10} > 3$ indicated moderate evidence for H_1 (Lee & Wagenmakers, 2014).

Modelling

Based on the lateral inhibition mechanism, there are two competitive gender coding models, the norm-based opponent model (broadly tuned 2-pool) and the exemplar-based multichannel model (narrowly tuned) (Pond et al., 2013; Zhao et al., 2011). Some studies have demonstrated that the aftereffects of high-level aspects (e.g., gender, identity) of faces are better explained by the former (Jeffery et al., 2018; Pond et al., 2013). If the spatial contextual effect shares the similar mechanism of the temporal contextual effect, the norm-based opponent coding model could also account for the simultaneous contrast effect of gender. In the norm-based opponent coding, gender (as an attribute of stimuli) is represented in two pools of neurons, one of which tuned to male stimuli and the other tuned to female stimuli. These two pools of neuron's response curves are expressed as two logistic functions with different male strength relative to the neutral gender, (d), with equal responses on neutral gender (g).

$$F^+(d) = \frac{1}{1 + e^{-\left(\frac{d-g}{s}\right)}} \tag{1}$$

$$F^-(d) = \frac{1}{1 + e^{-\left(\frac{d+g}{s}\right)}} \quad (2)$$

where F^+ and F^- determines the male and female channel sensitivity, respectively; s determines the steepness of the function. Simultaneous contrast induced by any given male strength (d_A) is modelled as reducing each channel's response to different male strength (d), which is proportional to each channel's response to the given surrounding stimuli:

$$F_A^+(d) = (1 - \alpha F_0^+(d_A)) \times F_0^+(d) \quad (3)$$

$$F_A^-(d) = (1 - \alpha F_0^-(d_A)) \times F_0^-(d) \quad (4)$$

where a determines the degree of contrast and the subscripts A and 0 denote responses with and without surrounding contrast, respectively. The response integrated from the two pools of neurons with surrounding contrast

$$M_A(d) = \frac{F_A^+(d) - F_A^-(d)}{F_A^+(d) + F_A^-(d)} \quad (5)$$

is taken to be corrupted by sensory noise drawn from a normal distribution with mean zero and standard deviation, σ_N , such that the probability that the two-channel response exceeds zero:

$$p(M_A(d) > 0) = \Phi\left(\frac{M_A(d) - 0}{\sigma_N}\right) \quad (6)$$

where Φ denotes the cumulative distribution function of the normal distribution. The only parameters available to vary are s , a and σ_N . The formulas were adapted from the model in the Appendix of Jeffery et al. (2018), the two-channel model. We adjusted the parameter values to search for the best-fitting set for the data obtained in Experiment 1 (using MATLAB function *fminsearch*).

RESULTS

In Experiment 1, where the same category stimuli were presented simultaneously, the paired-sample t -test revealed significant simultaneous contrast effect of gender. Specifically, when the central and surrounding faces were presented at the same time in Experiment 1a, the central morphed faces were more likely to be judged as opposite to the surrounding facial gender (see Figure 3a, $PSE_{\text{male}} = 53.50\% \pm 6.08\%$, $PSE_{\text{female}} = 48.40\% \pm 5.92\%$; $t(9) = 3.26$, $p = .01$, Cohen's $d = 1.03$, 95% CI = [1.57, 8.64], $BF_{10} = 6.31$). Similarly, Experiment 1b confirmed a simultaneous contrast effect of BM gender: the central point-light walker was more likely to be perceived as a male when surrounded by female point-light walkers and vice versa (see Figure 3b, $PSE_{\text{male}} = -0.41 \pm 0.09$ SD, $PSE_{\text{female}} = -0.49 \pm 0.09$ SD; $t(9) = 3.89$, $p = .004$, 95% CI = [0.04, 0.13], Cohen's $d = 1.23$, $BF_{10} = 13.93$). The discrimination sensitivity of the central stimuli measured by DL was not affected by the gender of surrounding stimuli (face: $t(9) = 0.20$, $p = .85$, 95% CI = [-3.83, 4.57], Cohen's $d = 0.06$, $BF_{10} = 0.31$; BM: $t(9) = 0.07$, $p = .95$, 95% CI = [-0.06, 0.06], Cohen's $d = 0.02$, $BF_{10} = 0.31$). To rule out the possibility that the simultaneous contrast effect of face gender is confounded by identity, we conducted another two experiments, in which different surrounding faces (thus multiple identities) were adopted across trials and observed the same simultaneous contrast effect (More details in the Appendix S1). All these results demonstrated a simultaneous contrast effect for high-level visual properties, consistent with previous findings on high-level adaptation aftereffect (Brooks et al., 2018; Webster et al., 2004).

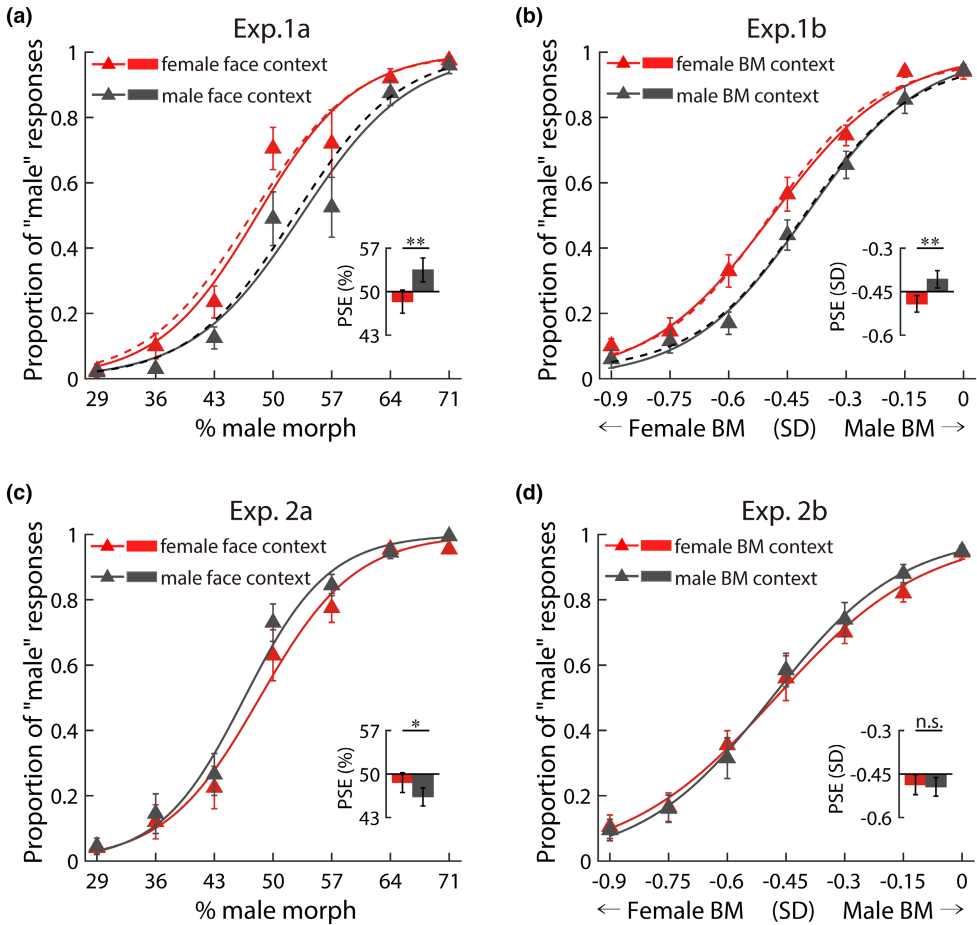


FIGURE 3 Results for experiments 1 and 2. The triangular indicates the proportion of the central face or BM perceived as male with simultaneously presented context (a, b), or with asynchronously presented context (c, d). The data fitted by the psychometric function were plotted using solid lines. Inset shows the PSEs. Error bars show standard errors. * $p < .05$; ** $p < .01$. n.s., not significant. The data predicted by the norm-based opponent model were plotted using dashed lines in (a) and (b).

Moreover, we confirmed that the norm-based opponent model provided a good fit for the data obtained in Experiment 1 (see dashed lines in Figure 3a,b), with $s = 16.18$, $a = .16$, $\sigma_N = 0.31$ for the simultaneous contrast effect of face gender,¹ and $s = 0.25$, $a = .16$, $\sigma_N = 0.46$ for the simultaneous contrast effect of BM gender,² which suggests the simultaneous contrast effects of face and BM gender can be explained by a similar inhibition model as the adaptation aftereffect.

If the simultaneous contrast effect of gender reflects the perceptual process predicted by the lateral inhibition mechanism, it ought to disappear when a relatively long temporal gap is inserted between the surrounding and central stimuli based on previous findings on the tilt illusion. As expected, Experiment 2 revealed no evident contrast effect when the surrounding and central stimuli were presented asynchronously (see Figure 3c,d, there was a significant assimilation effect of face gender, showing that the gender judgement of the central face was biased to the gender of surrounding faces: $PSE_{male} = 46.33\% \pm 4.61\%$,

¹The norm-based opponent model also provided good fit for the two additional experiments, with $s = 6.01$, $\alpha = .22$, $\sigma_N = 0.45$ and $s = 6.68$, $a = .12$, $\sigma_N = 0.36$, respectively.

²Notably, the s for face and BM gender has apparently different scales (29–71 for face and –0.9–0 for BM). The value 0.25 in the scale of BM gender was equal to 11.75 in the scale of face gender.

$PSE_{\text{female}} = 48.63\% \pm 5.04\%$; $t(9) = 3.25, p = .01, 95\% \text{ CI} = [0.70, 3.90]$, Cohen's $d = 1.03, BF_{10} = 6.17$; no significant contrast effect of BM gender: $PSE_{\text{male}} = -0.49 \pm 0.10 \text{ SD}$, $PSE_{\text{female}} = -0.49 \pm 0.11 \text{ SD}$; $t(9) = -0.29, p = .78, 95\% \text{ CI} = [-0.07, 0.05]$, Cohen's $d = 0.09, BF_{10} = 0.32$). And there were no significant changes of the discrimination sensitivity for the central test stimuli under different contexts (face: $t(9) = -1.17, p = .27, 95\% \text{ CI} = [-2.65, 0.85]$, Cohen's $d = 0.37, BF_{10} = 0.53$; BM: $t(9) = -1.56, p = .15, 95\% \text{ CI} = [-0.14, 0.03]$, Cohen's $d = 0.49, BF_{10} = 0.78$). Even there was an unexpected assimilation effect for face gender³ when target and surroundings were asynchronously presented (which also demonstrated the absence of the contrast effect), the results of Experiment 2 confirmed that the simultaneous contrast effect obtained in Experiment 1 essentially reflects the perceptual process based on lateral inhibition mechanism.

In Experiment 3, we investigated whether the simultaneous contrast effect of gender can occur in a cross-category manner. The results showed that the simultaneous contrast effect of BM gender cannot transfer to a face context, and vice versa (Figure 4a,b; BM test stimuli: $PSE_{\text{male}} = -0.44 \pm 0.09 \text{ SD}$, $PSE_{\text{female}} = -0.44 \pm 0.10 \text{ SD}$; $t(23) = -0.22, p = .83, 95\% \text{ CI} = [-0.03, 0.03]$, Cohen's $d = 0.05, BF_{10} = 0.22$; face test stimuli: $PSE_{\text{male}} = 48.66\% \pm 3.83\%$, $PSE_{\text{female}} = 49.18\% \pm 3.61\%$; $t(23) = -1.92, p = .07, 95\% \text{ CI} = [-1.08, 0.04]$, Cohen's $d = 0.39, BF_{10} = 1.03$). In addition, the discrimination sensitivity was not affected by the surrounding gender information (BM test stimuli: $t(23) = 0.08, p = .93, 95\% \text{ CI} = [-0.04, 0.04]$, Cohen's $d = 0.02, BF_{10} = 0.22$; face test stimuli: $t(23) = -0.09, p = .93, 95\% \text{ CI} = [-2.01, 1.85]$, Cohen's $d = 0.02, BF_{10} = 0.22$). Thus, there was no evidence that the simultaneous contrast effect of gender could transfer to a context composed of stimuli from different categories. These results suggest that the simultaneous contrast effect of gender (at least for face and BM) likely takes place in a category-specific manner.

In Experiment 4, using the CFS paradigm, we investigated whether the simultaneous contrast effect of gender can be induced by invisible surrounding stimuli (Figure 4c,d). The simultaneous contrast effect was not evident (face: $PSE_{\text{male}} = 47.82 \pm 4.49\%$, $PSE_{\text{female}} = 48.57 \pm 4.25\%$; $t(23) = -1.52, p = .14, 95\% \text{ CI} = [-1.76, 0.27]$, Cohen's $d = 0.31, BF_{10} = 0.59$; BM: $PSE_{\text{male}} = -0.47 \pm 0.09 \text{ SD}$, $PSE_{\text{female}} = -0.47 \pm 0.10 \text{ SD}$; $t(23) = -0.55, p = .59, 95\% \text{ CI} = [-0.03, 0.02]$, Cohen's $d = 0.11, BF_{10} = 0.25$). The discrimination sensitivity was unaffected by the surrounding gender information too (face: $t(23) = -1.33, p = .20, 95\% \text{ CI} = [-2.47, 0.54]$, Cohen's $d = 0.27, BF_{10} = 0.47$; BM: $t(23) = 0.54, p = .60, 95\% \text{ CI} = [-0.03, 0.05]$, Cohen's $d = 0.11, BF_{10} = 0.24$). In the awareness measurement, the participants' accuracy in localizing the invisible face or BM were not significantly different from chance [face: $24.56\% \pm 4.83\%$, $t(23) = -0.45, p = .66, 95\% \text{ CI} = [-0.02, 0.02]$, Cohen's $d = 0.09, BF_{10} = 0.24$; BM: $24.63\% \pm 4.24\%$, $t(23) = -0.43, p = .67, 95\% \text{ CI} = [-0.02, 0.01]$, Cohen's $d = 0.09, BF_{10} = 0.23$], ensuring that the suppressed surrounding stimuli were truly invisible to participants. Taken together, these results suggest that the simultaneous contrast effect of gender may not occur unconsciously, in contrast to the contextual effect of low-level visual features (Clifford & Harris, 2005; Mareschal & Clifford, 2012; Zou et al., 2016).

DISCUSSION

In the current study, we adopted a simultaneous contrast paradigm to investigate whether and how gender perception of face and BM is modulated by the gender information simultaneously conveyed by a spatial context. The findings that gender perception of face or BM was repelled away from the gender of surrounding faces or BMs confirmed the hypothesis that a contrast effect in spatial domain (i.e., a spatial contextual effect) could also occur for high-level visual features, similar to the adaptation aftereffect (i.e., a temporal contextual effect) observed with high-level properties (Brooks et al., 2018; Burr & Ross, 2008; Webster et al., 2004). This simultaneous contrast effect is in agreement with our daily experience: a man of medium height looks like a dwarf when he stands next to tall basketball players but looks like a giant when he stands beside some little kids.

It should be noted that previous studies investigating the spatial contextual effect of high-level visual features did not reveal such a contrast effect (Bindemann et al., 2005; Cheng et al., 2022; Lecker

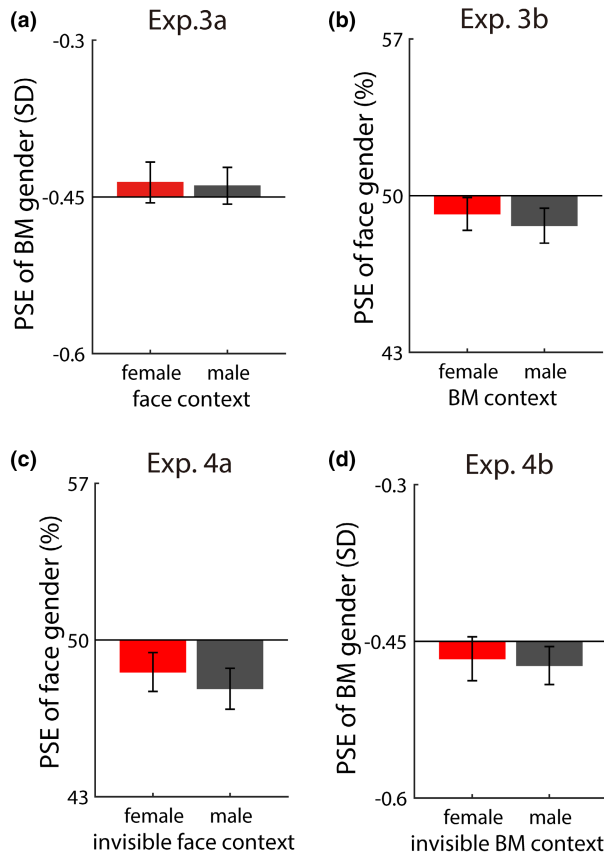


FIGURE 4 Results from experiments 3–4. PSE values of the central BM or face surrounded by gender stimuli from different categories (a, b) or by invisible gender stimuli from the same category (c, d). No significant simultaneous contrast effect was found in these two experiments.

et al., 2017, 2020). In a flanker task, Bindemann et al. (2005) did not observe a reaction facilitation in judging the gender of a central face when it was congruent than incongruent with the gender of the simultaneously presented surrounding faces, possibly because that face gender judgement was less susceptible to its context if the test faces were with explicit gender information. But notably, the flanker task largely probes response conflicts and may not directly reflect perceptual changes, while the psychophysical test adopted in the current study examines how perception of faces with ambiguous gender is affected by its context and reveals more of the perceptual changes.

Different from the simultaneous contrast effect of gender observed here, there are some other studies showing an assimilation contextual effect in space (e.g., on emotion in Lecker et al., 2020; Lecker et al., 2017; on walking direction in Cheng et al., 2022). Generally, these effects can be well accounted for by a perceptual bias induced by prior experience rather than lateral inhibition. According to the daily experience, people would be more likely to perceive that the facial and body expressions are consistent, or that one's walking direction is aligned with his/her group members. Therefore, the simultaneous contrast effect and the assimilation effect essentially reflect the different aspects of the spatial contextual effect of high-level visual features. Generally speaking, the perception of socially relevant features, such as emotion, is more prone to an assimilation effect, while the perception of biologically relevant features, such as gender, is more likely to show a simultaneous contrast effect.

Given the resemblance between the spatial and the temporal contextual effects of low-level visual features,⁴ such as the tilt illusion and tilt aftereffect (Schwartz et al., 2007), it is probable that there exists a common or shared computational mechanism between the temporal and the spatial contextual effects of high-level visual features as well. Computational studies have revealed that the adaptation aftereffect of high-level features can be characterized by a similar lateral inhibition model that has well explained the contextual effect of low-level features (e.g., orientation) (Jeffery et al., 2018; Pond et al., 2013; Zhao et al., 2011). By assuming that gender is encoded by only two clusters of neurons separately tuned to male and female, the norm-based opponent coding model perfectly accounts for the unique characteristic that gender aftereffects flatten out or continue to grow larger when the adaptors change from normal to extreme masculinity/femininity (i.e., beyond the range of face masculinity/femininity existing in the real world) (Pond et al., 2013). Here, we showed that the norm-based opponent coding model also provided an excellent fit for the observed simultaneous contrast effect of gender conveyed by either face or BM, confirming that spatial contextual effect of high-level visual features can be accounted for by a certain type of the lateral inhibition model.

Another supportive evidence for this lateral inhibition mechanism was provided by our finding that the simultaneous contrast effect of gender was mediated by the temporal synchrony between the central and surrounding stimuli, as the introduction of a 500-ms temporal separation between them completely erased the simultaneous contrast effect. This echoes with previous studies on low-level features, which demonstrated a disappearance of the tilt illusion with a relatively long temporal gap (Corbett et al., 2009; Durant & Clifford, 2006; Yuan et al., 2017). It is probably because the surround suppression of neural activities lasts ~200 ms after the context disappears (Ishikawa et al., 2010; Shimegi et al., 2014).

Despite similar inhibition models for the contextual effects of low- and high-level features, we expected the contextual effect of high-level features to be category-general since high-level features (e.g., gender) can be discriminated irrespective of stimulus category and may be represented more abstractly. This assumption can be validated by a cross-category contextual effect of gender. However, in the current study, there was little evidence that the simultaneous contrast effect of gender could transfer across stimuli from different categories. From the temporal view, some previous studies have observed a cross-category adaptation of gender across face and body (Ghuman et al., 2010; Kessler et al., 2013; Palumbo et al., 2015), for instance, face gender perception is biased to the opposite gender of the adapting body (Ghuman et al., 2010), even in an orientation-independent manner (Kessler et al., 2013). But on the contrary, there was no cross-category adaptation of gender across other stimulus categories (Hiris et al., 2016; Kovács et al., 2006). In particular, similar to our findings, adapting to faces (or bodies) did not induce BM gender aftereffects (Hiris et al., 2016). Above all, neither the adaptation aftereffect (a temporal contextual effect) nor the simultaneous contrast effect (a spatial contextual effect) of gender can transfer across face and BM, which does not support a category-general representation of gender (at least for face and BM).

Gender can be represented in a category-general manner if there exist downstream brain areas that encode gender information across stimulus categories. Accordingly, a cross-category contextual effect is accomplished by selectively inhibiting the neurons tuned to abstract gender information in the downstream areas. But counterintuitively, no brain area has yet been found to be responsible for the shared neural representations of gender information conveyed by face and body (Foster et al., 2019), although the cross-category adaptation across body and face is robust (Ghuman et al., 2010; Kessler et al., 2013; Palumbo et al., 2015). The cross-category adaptation may instead be induced by an inter-inhibition of the gender neurons in one category-specific area by their counterparts in the other category-specific area, especially considering the close neighbourhood between the fusiform face area (FFA, Kanwisher, 1997; Puce et al., 1996) and the fusiform body area (FBA, Peelen & Downing, 2005; Schwarzlose et al., 2005). On the other hand, BM prominently activates superior temporal sulcus (STS) (Thurman et al., 2016; Yovel & O'Toole, 2016), which is a bit further away from FFA than FBA. It is unclear the failure to observe a cross-category contextual effect between BM and face is due to a lack of shared gender representation in one convergent area or a lack of inter-inhibition between category-specific areas.

⁴Here we mainly refer to the contrast effect.

Intriguingly, the contextual effects of high- and low-level features differentially depend upon conscious awareness of the context. In sharp contrast with the contextual effect of invisible orientations (Clifford & Harris, 2005; Mareschal & Clifford, 2012; Zou et al., 2016), both the adaptation aftereffect and the simultaneous contrast effect vanish with invisible face or BM (facial gender and race in Amihai et al., 2011; BM gender in Faivre & Koch, 2014; facial identity in Moradi et al., 2005; facial and BM gender in our Experiment 4). Unlike orientation, the high-level features, such as faces, strongly rely on holistic processing (Richler et al., 2011; Wang et al., 2012). This vital ability is destroyed in the absence of visual awareness (Harris et al., 2011), which impairs the processing of invisible faces and in turn demolishes the contextual effect. But there is an exception that the aftereffect of facial emotion can occur in an awareness-independent manner (Adams et al., 2010). This might be explained by the dissociable neural processing between facial emotion and facial gender/race/identity. The subcortical circuit in charge of emotion processing can be robustly activated unconsciously (Williams et al., 2004), while the activation of cortical regions responsible for facial gender/race/identity processing (e.g., the fusiform gyrus) is much reduced or essentially abolished under invisible condition (Fang & He, 2005; Jiang & He, 2006).

However, it has been shown recently that invisible BM can induce faster responses to probes presented at the same location in a short time (Sun et al., 2017), and after prolonged exposure to invisible BM, the gender perception would be biased towards the same gender of the adaptors, exhibiting an assimilation effect (Faivre & Koch, 2014). Inconsistent with Faivre and Koch (2014), our study found neither a contrast nor an assimilation effect when the surrounding BM stimuli were rendered invisible. There was a crucial difference between these two studies that may partially account for this discrepancy. The simultaneously presented BM context in our study lasted only 300 ms, which is significantly shorter than theirs (3 s for the invisible BM adaptor). Given that the assimilation effect increases when an invisible stimulus is repeatedly presented (equal to an extension of the total presentation time) (Atas et al., 2013), the presentation duration in our study may not be long enough to induce an invisible assimilation effect, despite that it does not affect the contextual effect in the visible condition. But notably, regardless of whether BM gender can be unconsciously extracted or not, we and Faivre and Koch (2014) both found no contrast effect of perceived gender with invisible BM context, consistently demonstrating that the lateral inhibition of gender perception cannot occur unconsciously.

CONCLUSION

The current study demonstrates the simultaneous contrast effect in the perception of high-level visual features, similar to the adaptation aftereffect. The simultaneous contrast effect of high-level visual features can be well fitted by the norm-based opponent coding model and vanishes when the central and surrounding stimuli are temporally separated. Moreover, the contextual effect of high-level features may be category-specific and awareness-dependent. These findings offer indispensable evidence for the resemblance between the simultaneous contrast effect (i.e., a spatial contextual effect) and the adaptation aftereffect (i.e., a temporal contextual effect) of high-level features. In combination with previous studies that explore the similarities between different contextual effects (Pond et al., 2013; Schwartz et al., 2007; Zhao et al., 2011), the current study on one hand suggests a similar computational implementation of the contextual effects, and the other hand implies different biological mechanisms underlying low- and high-level contextual effects.

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AUTHOR CONTRIBUTIONS

All the authors contributed to the study design. W. Liu collected and analysed the data under the supervision of X. Yuan and Y. Jiang. W. Liu drafted the manuscript, and Y. Cheng, X. Yuan and Y. Jiang provided critical revisions. All the authors approved the final manuscript for submission.

CONFLICT OF INTEREST

The authors declare no competing interest.

DATA AVAILABILITY STATEMENT

All data have been made publicly available via the Institutional Knowledge Repository, Institute of Psychology, Chinese Academy of Sciences and can be accessed at <http://ir.psych.ac.cn/handle/311026/41815>.

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