Processing of Fearful Faces Exhibits Characteristics of Subcortical Functions

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A subcortical pathway is thought to have evolved to facilitate fear information transmission, but direct evidence for its existence in humans is lacking. In recent years, rapid, preattentive, and preconscious fear

achieve rapid and automatic processing of threat information (LeDoux, 1996; Öhman & Mineka, 2001; Pessoa & Adolphs, 2010). However, due to the deep location and rapid response of the subcortical structures, which pose methodological challenges for functional magnetic resonance imaging, magnetoencephalography, and electroencephalogram (EEG) techniques, evidence for such a subcortical pathway to the amygdala in humans has mainly been inferred indirectly from neuroimaging and behavioral findings. For instance, compared to neutral information, threat information, such as fearful faces, snakes, and electric shock signals, can be detected rapidly (Bannerman et al., 2010; Méndez-Bértolo et al., 2016; Wang et al., 2023), preattentively (Luo et al., 2010; Morris et al., 1999; Vuilleumier et al., 2001), and preconsciously (Gomes et al., 2018; Morris et al., 1998, 1999; Whalen et al., 1998), suggesting its independence from the cortical pathways. However, an alternative to the subcortical pathway model suggests that some shortcut cortical pathways could achieve such threat processing equally well (Pessoa & Adolphs, 2010), casting further doubt on the existence of the subcortical pathway.

To validate the subcortical pathway hypothesis, indirect evidence has been gathered from an array of different studies using different approaches. To date, support for the subcortical pathway has come from three main sources. First, neuroimaging studies have shown enhanced responses to fear information in the amygdala in the absence of conscious awareness, either due to unconscious manipulations of backward masking (Morris et al., 1998; Wang et al., 2023; Whalen et al., 1998; L. M. Williams et al., 2006) or interocular suppression (Pasley et al., 2004; M. A. Williams et al., 2004) or due to visual cortex lesions in blindsight patients (Morris et al., 1999; Vuilleumier et al., 2002). Unconscious processing reduces the involvement of cortical brain regions, indirectly hinting at information transmission through subcortical pathways. Second, the fear-selective response in the amygdala, as evidenced by intracranial EEG recording (Inagaki et al., 2023; Méndez-Bértolo et al., 2016; Sato et al., 2011; Wang et al., 2023) and magnetoencephalography modeling (McFadyen et al., 2017), was elicited with a very short latency, not long enough for the information to reach the amygdala via the canonical cortical pathway. Third, anatomical and functional connectivity between the critical nodes in the suggested subcortical pathway (Pessoa & Adolphs, 2010), the SC, pulvinar, and amygdala, has been elucidated in the human brain (Garvert et al., 2014; McFadyen et al., 2017, 2019; Morris et al., 1999; L. M. Williams et al., 2006), providing a structural basis for subcortical information transmission. Therefore, the first two lines of evidence undermine the possibility of information transmission via the canonical cortical pathway, while the third line of evidence supports the possibility of the existence of the subcortical pathway. However, prone to its own methodological and interpretive limitations, each piece of the above evidence is susceptible to alternative explanations on its own (Pessoa & Adolphs, 2010). Furthermore, none of the above evidence demonstrates the involvement of the SC or pulvinar in threat processing, leaving a missing link in the evidence supporting the subcortical pathway hypothesis.

If threat information is transmitted via a subcortical pathway, then its perception should reflect the characteristics of the subcortical structures in the pathway, regardless of whether these characteristics are related to emotion processing or not. Following this logic, researchers have investigated the low spatial frequency (LSF) selectivity of threat processing. Since the subcortical pathway consists primarily of magnocellular neurons tuned to LSF information, the threat information transmitted through this pathway should be limited to its LSF component (Vuilleumier et al., 2003). This is indeed what has been observed in fear processing in the human amygdala (Méndez-Bértolo et al., 2016; Vuilleumier et al., 2003; Wang et al., 2023), although incompatible and opposing evidence has also been reported (e.g., McFadyen et al., 2017; Stein et al., 2014). In addition to LSF selectivity, subcortical regions differ largely from cortical visual regions in other characteristics. A key feature of the subcortex is its reliance on monocular neurons. Visual input is monocularly segregated through the subcortex up to Layer IV of the primary visual cortex (V1; Horton et al., 1990; Menon et al., 1997); beyond Layer IV of V1, signals from each eye are no longer segregated. Therefore, visual information presented sequentially to the same as opposed to separate, eyes can be processed by the same set of subcortical neurons (Gabay, Burlingham, & Behrmann, 2014; Gabay, Nestor, et al., 2014; Zhao et al., 2023).

In addition, the SC has distinct characteristics from other subcortical regions, including the lateral geniculate nucleus (LGN), a subcortical node in the cortical pathway. First, the SC lacks retinal input from the short-wavelength-sensitive (S-) cones, which instead project to the LGN and the pulvinar via the koniocellular pathway (Marrocco & Li, 1977; Schiller & Malpeli, 1977). Thus, the SC has lower sensitivity to short-wavelength stimuli such as purple/blue gratings than the LGN and the pulvinar (Bertini et al., 2008; Marzi et al., 2009; Savazzi & Marzi, 2004; Sumner et al., 2002; Tamietto et al., 2009). Second, building on the findings of a nasal–temporal asymmetry in fiber projections from the hemiretinae to the SC (Perry & Cowey, 1985; Pollack & Hickey, 1979), higher visual sensitivity is expected for the temporal than for the nasal hemifield (Bertini et al.2008 ;

convergently hinting that subcortical regions are involved in threat processing. These results, together with the existing evidence for rapid, preconscious fear processing in the amygdala and the structural basis for the subcortical pathway, suggest the existence of a subcortical pathway to the human amygdala for threat processing.

Experiment 1: Same-Eye Advantage for LSF Fear Perception

Experiment 1 aimed to explore whether the processing of fearful faces relies on subcortical structures. Using a monocular/dichoptic paradigm (Gabay, Burlingham, & Behrmann, 2014; Gabay, Nestor, et al., 2014), we presented two consecutive faces, a priming face and a probe face, monocularly to the same eye or dichoptically to different eyes. Because the subcortex contains only monocular neurons, it should be invisible to priming faces presented to the different eye. Therefore, if fear processing takes place in the subcortex, the priming effect in the subcortex should be observed in the same-eye condition rather than in the different-eye condition. That is, a same-eye facilitation effect is expected for fear processing. Furthermore, because the subcortical pathway is thought to carry only crude visual input to the amygdala through magnocellular neurons (Vuilleumier et al., 2003), the same-eye facilitation should be selective to the LSF component.

Method

Transparency and Openness

All data of all experiments are publicly available via Open Science Framework and are accessible at https://osf.io/dnx5m/. The experiments reported here were not preregistered and the data were collected in 2022–2023.

Participants

Participants were 30 adults (21 participants reported their gender as female and nine as male, 19–27 years, $M_{\text{age}} = 22.1$ years, $SD = 5.6$) recruited from Zhejiang University. The sample size was similar to conventional sample sizes in prior experiments using the same paradigm (Collins et al., 2017; Gabay, Burlingham, & Behrmann, 2014; Zhao et al., 2023). All participants had normal or corrected-to-normal vision and were naive to the purpose of the experiments. They provided written informed consent and received monetary compensation for participation. The experimental procedure was approved by the Human Subject Review Committee of Zhejiang University.

Apparatus and Software

The stimuli were presented on a 21-in. cathode-ray tube screen with a refresh rate of 75 Hz and a resolution of 1,024 × 768 pixels. Participants viewed the screen with both eyes through a stereoscope so that the left and right halves of the screen were projected to the left and right eyes, respectively. A cardboard divider was attached to the chin rest to block the participants' direct view of the screen. A white rectangular frame (5° × 6.3°) was presented at the center of each half of the screen to minimize eye movements. Participants adjusted the stereoscope to fuse the perception of two eyes before starting the experiment. The MATLAB (The MathWorks) and Psychtoolbox-3 toolbox were used to display the visual stimuli.

Materials

Stimuli were faces of 48 actors (24 females) posing fearful and neutral expressions. The faces were obtained from two databases: Radboud Faces Database (https://www.socsci.ru.nl:8180/RaFD2/RaFD) and NimStim Set of Facial Expressions (https://danlab.psychology.columbia.edu/content/nimstim-set-facial-expressions). Images were processed following the procedure by McFadyen et al. (2017). All images were gray-scaled, equalized in mean luminance, reshaped into the same size (5° × 6.3°), and cropped to exclude most hair and background. In addition to the original (broad spatial frequency [BSF]) face images, faces containing low- or high-spatial-frequency information were created by filtering the BSF faces using a low-pass cutoff of <6 cycles per image (LSF) and a high-pass cutoff of >24 cycles per image (high spatial frequency [HSF]; Wang et al., 2023), respectively. Images were drawn randomly from the stimuli set for each condition for each participant.

Procedure

Each trial started with the appearance of a white fixation cross at the center of the rectangular frame in each visual field for 500 ms. Two faces, one priming and one probe face, were then presented sequentially on the screen, each for 200 ms and interleaved by a 500-ms fixation interval (Figure 1). The two consecutive faces were presented to the same eye in the same-eye condition and to different eyes in the different-eye condition. In both conditions, the priming face was presented to the left and right eyes with equal possibility. Participants judged whether the probe face showed the same facial expression as the priming face or not. The response was required to be made within 3,000 ms, as in related studies (Méndez-Bértolo et al., 2016; Wang et al., 2023; Xu et al., 2023).

Participants completed a total of 720 trials in nine blocks (80 trials/block). The priming and probe faces showed the same emotion in half of the trials. The order of trials from different emotion conditions and eye source conditions was randomized within each block. Faces containing different spatial frequency information were presented in separate blocks. Perceptual fusion from the two eyes was checked at the beginning of each block.

Results

We explored whether the monocular versus dichoptic presentation of consecutive faces induced different priming effects. We extracted trials in which the priming and probe faces expressed the same emotion and calculated the percentage of correct responses. Considering that evidence for the subcortical processing of neutral faces has also been observed (Garvert et al., 2014; Santos et al., 2011), we do not have a strong hypothesis about the same-eye advantage effect in the neutral face condition. Therefore, analyses on the fearful and neutral faces were performed separately. First, we performed a 3 (spatial frequency [SF]: BSF, LSF, and HSF) × 2 (eye source: same and different) repeated measures analysis of variance (ANOVA) on the discrimination accuracy of the fearful faces. A significant interaction effect between the two factors was observed (Figure 2), $F(2, 58) = 3.21$, $p = .048$, $\eta_p^2 = .10$. Simple effect analyses focusing on the priming effect showed that the emotion discrimination in the same-eye condition was superior to that in the different-eye condition for the LSF fearful face condition, $M_{\text{difference}} = 4.33$, 95% confidence interval (CI) [2.10, 6.58],

$t(29) = 3.95$, $p < .001$, Cohen's $d = 0.72$. No significant same-eye advantage was observed for the BSF, $M_{\text{difference}} = 0$, 95% CI [−2.72, 2.72], $t(29) = 0$, $p = 1.000$, Cohen's $d = 0$, or HSF, $M_{\text{difference}} = 0.44$, 95% CI [−2.34, 3.23], $t(29) = 0.33$, $p = .747$, Cohen's $d = 0.06$, fearful face condition. Next, we performed the same analysis on the neutral face condition. No significant interaction effect between SF (BSF, LSF, and HSF) and eye source (same and different) was observed, $F(2, 58) = 1.55$, $p = .222$, $\eta_p^2 = .05$. Besides, the priming effect was not significant for the BSF, $M_{\text{difference}} = 0.67$, 95% CI [−0.95, 2.28], $t(29) = 0.84$, $p = .405$, Cohen's $d = 0.15$; LSF, $M_{\text{difference}} = 0.67$, 95% CI [−2.80, 4.13], $t(29) = 0.39$, $p = .697$, Cohen's $d = 0.07$; or HSF, $M_{\text{difference}} = -2.11$, 95% CI [−4.61, 3.89], $t(29) = -1.73$, $p = .095$, Cohen's $d = 0.32$, neutral face condition. Therefore, fearful faces containing only LSF information produced a facilitation effect on fear detection of faces presented to the same eye. Because this same-eye advantage was not observed for fearful faces containing HSF information or for neutral faces, the contribution of factors unrelated to LSF fear processing, such as interruptions on perception in the dichoptic presentation condition due to binocular fusion, was excluded.

To rule out speed-accuracy trade-off, we also performed a 3 (SF: BSF, LSF, and HSF) × 2 (eye source: same and different) repeated measures ANOVA on the response time (RT) in the fearful and neutral face conditions, respectively. No significant SF by eye source interaction effect was observed for RT in the fearful, $F(2, 58) = 1.88$, $p = .162$, $\eta_p^2 = .06$, or neutral face condition, $F(2, 58) = 0.38$, $p = .685$, $\eta_p^2 = .01$. The main effect of eye source was not significant, fearful; $F(1, 29) = 0.31$, $p = .583$, $\eta_p^2 = .01$; neutral; $F(1, 29) = 2.27$, $p = .143$, $\eta_p^2 = .07$, either. Furthermore, no significant same- versus different-eye RT difference was observed for the LSF fearful, $M_{\text{difference}} = -0.01$, 95% CI [−0.04, 0.23], $t(29) = -0.63$, $p = .536$, Cohen's $d = 0.11$; or neutral, $M_{\text{difference}} = -0.05$, 95% CI [−0.14, 0.04], $t(29) = -1.05$, $p = .304$, Cohen's $d = 0.19$, face conditions.

Experiment 2: Insensitivity of Fearful Faces to LSF Priming Mediated by S-Cones

Experiment 2 further investigated the subcortical stage at which the same-eye advantage occurs. We took advantage of the different sensitivities to short-wavelength stimuli of the SC, a critical node in the subcortical pathway, and the LGN, a subcortical node in the cortical pathway. Specifically, the SC has no S-cones and is therefore invisible to short-wavelength stimuli (e.g., purple/blue gratings), whereas the LGN has S-cones and is able to detect short-wavelength stimuli (Marrocco & Li, 1977; Schiller & Malpeli, 1977). We speculate that if the same-eye advantage is due to fear processing by the SC, then the effect will be abolished when the fearful face is primed with short-wavelength stimuli that are invisible to the SC. Conversely, if the same-eye advantage is due to fear processing by the LGN, then the effect will still be observed when the fearful face is primed with short-wavelength stimuli. To test this hypothesis, we conducted two experiments. Experiment 2a used face stimuli from the Western culture. To confirm the effects and to control for the potential influence of cultural factors, Experiment 2b replicated Experiment 2a using face stimuli from a Chinese face image data set.

Method

Power Analysis

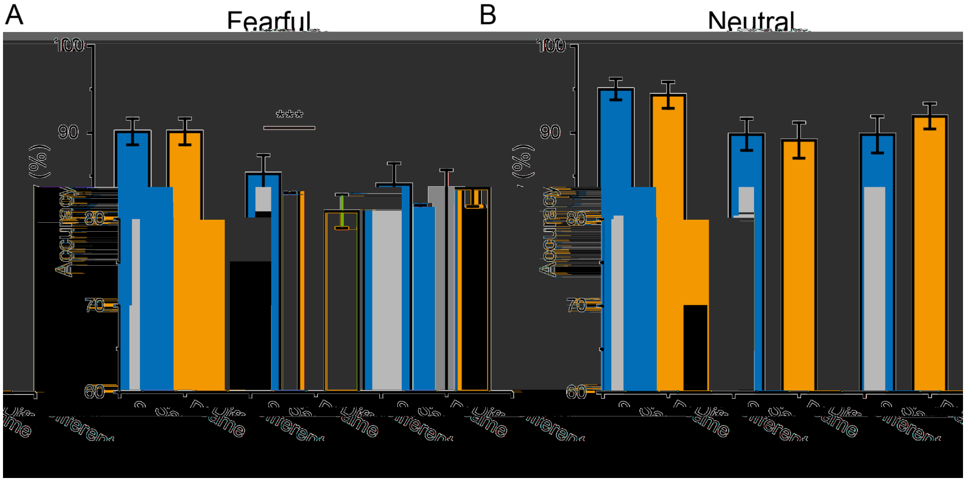
A power analysis was performed based on the effect size of the shared component of Experiment 1 and Experiment 2, that is, the same-eye facilitation effect for LSF fearful faces in Experiment 1. The power analysis revealed that 28 participants were required to achieve a significant same-eye facilitation effect ($\alpha = .05$) with a power of 95%.

Participants

Experiment 2a and Experiment 2b each recruited 30 (Experiment 2a: 17 participants reported their gender as female and 13 as male, 18

Figure 2

Percentage of Correct Emotion Discrimination for Fearful and Neutral Faces



Note. (A) Same-eye presentation induced a facilitation effect on LSF but not HSF or BSF fear discrimination than different-eye presentation. (B) No same-eye versus different-eye presentation difference was observed for the neutral face independent of the SF information it contained. Error bars represent SEMs across participants. LSF = low spatial frequency; HSF = high spatial frequency; BSF = broad spatial frequency; SF = spatial frequency; SEM = standard error of the mean. See the online article for the color version of this figure.
*** $p < .001$ (significant differences between the monocular and dichoptic presentation conditions).

participants reported their gender as female and nine as male, 18–28 years, $M_{\text{age}} = 21.4$ years, $SD = 6.0$) adults from Zhejiang University. All participants had normal or corrected-to-normal vision, were not color blind, and were naive to the purpose of the experiments. They provided written informed consent and received monetary compensation for participation. The experimental procedure was approved by the Human Subject Review Committee of Zhejiang University.

Materials

The same apparatus was used as in Experiment 1. In both experiments, LSF face images were used as probes while LSF gratings were used as priming stimuli. The face images in Experiment 2a were the LSF face images from Experiment 1. Sixty LSF face images were drawn randomly from the stimuli set for each condition for each participant, resulting in a total of 480 images being used. To prevent cultural influences on emotion recognition caused by unfamiliarity with and misrecognition of facial expressions from other cultures (Wang et al., 2019), Experiment 2b used face images from the Chinese Facial Affective Picture System (Gong et al., 2011). The LSF face images were created using the same criteria as Experiment 1. In each trial, a face image from a certain condition was randomly selected from the 25 LSF face images for each participant. As the total number of face images was roughly half that used in Experiments 1 and 2a, we reduced the number of trials to 240 in Experiment 2b.

Experiments 2a and 2b used the same priming grating stimuli. The priming grating stimuli had a cutoff of 5 cycles per image. There were two types of grating stimuli: gray (colorimetric values: $x = 0.30$, $y = 0.30$) and chromatic purple/blue ($x = 0.183/0.270$, $y = 0.087/0.087$; Tamietto et al., 2009). To ensure that the SF information was determined solely by the color differences in the gratings, the gratings were carefully matched for their physical attributes; that is, all stimuli had the same mean luminance (10.8 cd/m^2) and were of the same size (8°). The gratings were oriented 45° clockwise or counterclockwise relative to the vertical orientationAQ11.

Procedure

The procedure, which was identical in Experiments 2a and 2b, was similar to that in Experiment 1 except that gray or purple/blue gratings were used as the priming stimuli (Figure 3). Specifically, a gray or purple/blue LSF grating was presented for 200 ms to a random eye. After a 500-ms interval, an LSF fearful or neutral face was presented to the same (monocular presentation) or different (dichoptic presentation) eye than the LSF grating for 200 ms. Participants were asked to judge whether the probe face showed a fearful or neutral expression and did not need to respond to the gratings. The response was required to be made within 3,000 ms. Participants completed 480 trials in six blocks (80 trials/block). The order of trials from different conditions was randomized within each block. Perceptual fusion from the two eyes was checked at the beginning of each block.

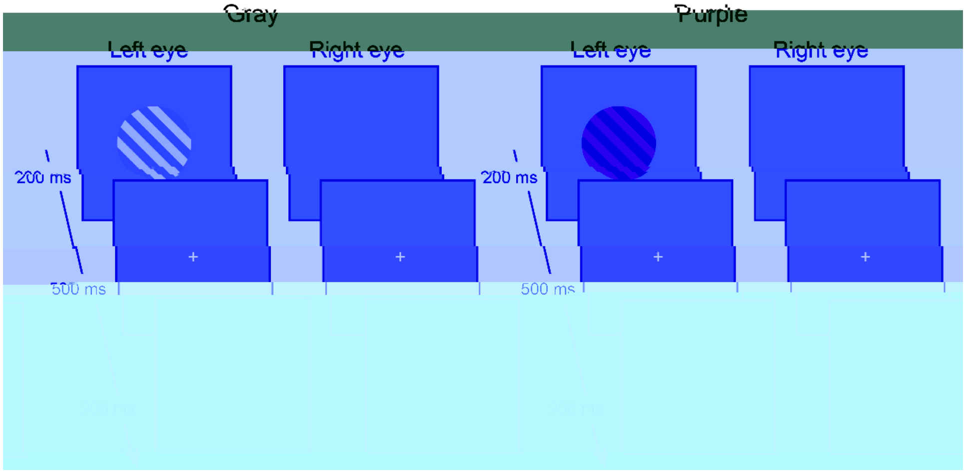
Results

Experiment 2a

Given that the monocular advantage was only observed for the LSF fearful faces in Experiment 1, we predicted that the subcortical characteristics would be present in the fearful but not in the neutral condition. Therefore, for Experiment 2a, we performed a 2 (priming condition: gray and purple) × 2 (eye source: same and different) × 2 (emotion: fearful vs. neutral) repeated measures ANOVA

Figure 3

The Experimental Procedure in Experiments 2a and 2b



Note. A gray (left) or purple/blue (right) grating with LSF information was presented to one eye through a stereoscope, followed by an LSF face image presented to the same (left) or different (right) eye. Participants judged the emotion the probe face expressed. From the *NimStim Set of Facial Expressions* (https://danlab.psychology.columbia.edu/content/nimstim-set-facial-expressions). LSF = low spatial frequency; ms = milliseconds. See the online article for the color version of this figure.

on the emotion recognition accuracy of the probe faces. The three-way interaction effect was significant (Figure 4A), $F(1, 29) = 12.18$, $p = .002$, $\eta_p^2 = .30$, suggesting different results patterns in the fearful and neutral face condition. Further analysis showed that the priming condition by eye source interaction effect was significant in the fearful face condition, $F(1, 29) = 16.13$, $p < .001$, $\eta_p^2 = .36$. Simple effect analyses showed a same-eye advantage for LSF fearful faces primed by a gray LSF grating. Specifically, when the gray LSF grating was presented to the same eye, the recognition of LSF fearful faces was increased significantly when compared to the grating being presented to the different eye, $M_{\text{difference}} = 4.02$, 95% CI [2.06, 5.98], $t(29) = 4.20$, $p < .001$, Cohen's $d = 0.77$. No significant same-eye versus different-eye difference was observed in the purple/blue grating priming condition, $M_{\text{difference}} = -2.24$, 95% CI [−4.81, 0.33], $t(29) = -1.78$, $p = .086$, Cohen's $d = 0.33$. In contrast to the fearful face condition, the priming condition by eye source interaction effect was not significant for the neutral face condition, $F(1, 29) = 0.14$, $p = .712$, $\eta_p^2 = .01$. No significant same-eye advantage was observed under either gray, $M_{\text{difference}} = -2.05$, 95% CI [−4.23, 0.00], $t(29) = -1.93$, $p = .063$, Cohen's $d = 0.35$, or purple/blue, $M_{\text{difference}} = -1.53$, 95% CI [−3.59, 0.54], $t(29) = -1.51$, $p = .141$, Cohen's $d = 0.28$, LSF grating priming. Therefore, the same-eye facilitation effect was abolished when S-cones, which exist in the LGN but not in the SC, were stimulated. This result suggests that the SC underlies the same-eye advantage of LSF fear processing.

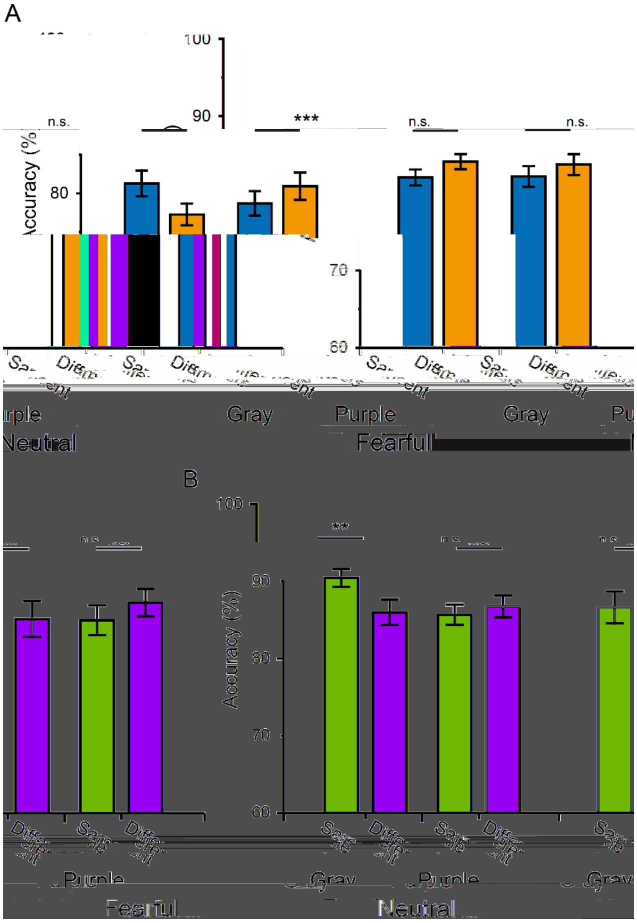
To rule out the speed-accuracy trade-off, we performed a 2 (priming condition: gray and purple) × 2 (eye source: same and different) × 2 (emotion: fearful vs. neutral) repeated measures ANOVA on the RT. No significant three-way interaction effect was observed, $F(1, 29) = 1.20$, $p = .282$, $\eta_p^2 = .04$, and no significant priming condition by eye source interaction effect was observed for RT in either emotion condition, fearful, $F(1, 29) = 1.01$, $p = .324$, $\eta_p^2 = .03$; neutral, $F(1, 29) = 0.11$, $p = .740$, $\eta_p^2 = .004$. The main effect of eye source was not significant, fearful, $F(1, 29) = 0.11$, $p = .738$, $\eta_p^2 = .003$; neutral, $F(1, 29) = 2.01$, $p = .167$, $\eta_p^2 = .06$, either. Simple effects analyses further showed no significant same- versus different-eye RT difference under the gray, fearful, $M_{\text{difference}} = -0.01$, 95% CI [−0.03, 0.01], $t(29) = -0.85$, $p = .403$, Cohen's $d = 0.15$; neutral, $M_{\text{difference}} = -0.01$, 95% CI [−0.03, 0.01], $t(29) = -0.93$, $p = .358$, Cohen's $d = 0.17$, or purple/blue, fearful, $M_{\text{difference}} = 0.003$, 95% CI [−0.02, 0.02], $t(29) = 0.29$, $p = .774$, Cohen's $d = 0.05$; neutral, $M_{\text{difference}} = -0.01$, 95% CI [−0.03, 0.01], $t(29) = -1.34$, $p = .191$, Cohen's $d = 0.24$, LSF grating priming.

Experiment 2b

The same analyses were performed as in Experiment 2a. First, we performed a 2 (priming condition: gray and purple) × 2 (eye source: same and different) × 2 (emotion: fearful vs. neutral) repeated measures ANOVA on the emotion recognition accuracy of the probe faces. The three-way interaction effect was not significant (Figure 4B), $F(1, 29) = 0.32$, $p = .576$, $\eta_p^2 = .01$. Nevertheless, we went on to investigate whether the priming effects differed for different eye sources in the fearful and neutral emotion conditions, respectively. We performed a 2 (priming condition: gray and purple) × 2 (eye source: same and different) on the fearful face condition and found a significant priming condition by eye source interaction effect, $F(1, 29) = 5.95$, $p = .021$, $\eta_p^2 = .17$, suggesting that the same-eye advantage was different in the two priming conditions. Simple effect analyses further showed that, when the gray LSF grating was presented to the same eye, the recognition of LSF fearful faces was increased significantly when compared to the grating being presented to the different eye, $M_{\text{difference}} = 4.47$, 95% CI [1.38, 7.54], $t(29) = 2.96$, $p = .006$, Cohen's $d = 0.54$. No significant same-eye versus different-eye difference was observed in the purple/blue grating priming condition, $M_{\text{difference}} = -1.10$, 95% CI

Figure 4

Emotion Recognition Accuracy Under Different Priming Conditions



Note. Emotion recognition results of Experiments 2a (A) and 2b (B). In both experiments, gray rather than purple LSF grating induced a facilitation effect on LSF fear recognition when the grating and the face was presented to the same eye than to different eyes. No same-eye versus different-eye facilitation effect was observed for neutral faces independent of whether the priming grating was gray or purple. Error bars represent SEMs across participants. LSF = low spatial frequency; n.s. = nonsignificant; SEM = standard error of the mean. See the online article for the color version of this figure.
** $p < .01$. *** $p < .001$ (significant differences between the monocular and dichoptic priming conditions).

[−4.54, 2.33], $t(29) = -0.66$, $p = .518$, Cohen's $d = 0.12$. In contrast to the fearful face condition, the priming condition by eye source interaction effect was not significant for the neutral face condition, $F(1, 29) = 2.70$, $p = .111$, $\eta_p^2 = .09$. No significant same-eye advantage was observed under either gray, $M_{\text{difference}} = 1.48$, 95% CI [−1.85, 4.81], $t(29) = 0.91$, $p = .371$, Cohen's $d = 0.17$, or purple/blue, $M_{\text{difference}} = -2.30$, 95% CI [−4.83, 0.24], $t(29) = -1.85$, $p = .075$, Cohen's $d = 0.34$, LSF grating priming. Therefore, our results consistently show that the same-eye facilitation effect was abolished when S-cones, which exist in the LGN but not in the SC, were stimulated.

Finally, we performed a 2 (priming condition: gray and purple) × 2 (eye source: same and different) × 2 (emotion: fearful vs. neutral) repeated measures ANOVA on the RT. No significant three-way interaction effect was observed, $F(1, 29) = 1.72$, $p = .200$, $\eta_p^2 = .06$. No significant priming condition by eye source interaction effect was observed for RT in either emotion condition, fearful, $F(1, 29) = 0.003$, $p = .960$, $\eta_p^2 = .00$; neutral, $F(1, 29) = 2.25$, $p = .145$, $\eta_p^2 = .07$. However, we still explored the same-eye effects in each priming and emotion condition. Simple effects analyses showed significant same- versus different-eye RT differences under the gray LSF grating priming for both emotions, fearful, $M_{\text{difference}} = -0.02$, 95% CI [−0.04, −0.003], $t(29) = -2.44$, $p = .021$, Cohen's $d = 0.44$; neutral, $M_{\text{difference}} = -0.02$, 95% CI [−0.05, −0.001], $t(29) = -2.14$, $p = .041$, Cohen's $d = 0.39$, and under the purple/blue LSF grating priming for fearful, $M_{\text{difference}} = -0.02$, 95% CI [−0.04, −0.003], $t(29) = -2.38$, $p = .024$, Cohen's $d = 0.43$, but not neutral, $M_{\text{difference}} = -0.002$, 95% CI [−0.03, 0.02], $t(29) = -0.21$, $p = .837$, Cohen's $d = 0.04$, emotion. Therefore, the same-eye facilitation effect in the gray grating priming condition was unlikely due to speed-accuracy trade-off.

Experiment 3: Nasal–Temporal Asymmetry for Saccades to LSF Fear

To strengthen the evidence for the involvement of the SC in fear processing, Experiment 3 further explored another characteristic of the SC, namely the nasal–temporal asymmetry of fear processing. Since more fibers are projected to the SC from the nasal hemiretina than from the temporal hemiretina (Perry & Cowey, 1985; Pollack & Hickey, 1979), the SC is expected to be more sensitive to fear information presented to the temporal than to the nasal hemifield. Furthermore, given that the SC is involved in oculomotor behavior (Bannerman et al., 2010; Cynader & Berman, 1972; Koller & Rafal, 2019), this function is likely to be reflected directly in the saccadic response. Therefore, in Experiment 3, we used eye-tracking to investigate the saccadic response to fearful faces that were presented in either the temporal or the nasal hemifield. Two independent experiments were performed to ensure the reliability of the results.

Participants

The same sample size determination and participant recruitment criteria were used as in Experiment 2. Thirty adults from Zhejiang University took part in Experiments 3a (20 participants reported their gender as female and 10 as male, 19–31 years, $M_{\text{age}} = 23.1$ years, $SD = 7.3$) and 3b (23 participants reported their gender as female and seven as male, 19–29 years, $M_{\text{age}} = 22.2$ years, $SD = 7.1$), respectively.

Materials

Stimuli in Experiment 3a were LSF and HSF face images (10° × 12.6°) from Experiment 1. The stimuli in Experiment 3b were LSF and HSF fearful and neutral face images from the Chinese Facial Affective Picture System (Gong et al., 2011). Images of 25 identities were obtained for each condition. The same criteria as in Experiment 1 were used to generate the LSF and HSF face images. Images were drawn randomly from the stimuli set for each condition for each participant.

Eye-Tracking Apparatus

An Eyelink1000 eye-tracking device continuously recorded eye position at a sampling rate of 500 Hz. Eyelink1000 analysis software was used to measure saccade latency and velocity. The same processing criteria were utilized in both experiments. Saccades were detected with a velocity of 30 degrees/second and acceleration of 8,000 degrees/second^2. Trials with saccades faster than 50 ms were excluded from the analysis.

Procedure

The experiment comprised two eye-tracking sessions carried out under monocular eye viewing using an eye patch. One session was completed with left eye viewing and the other with right eye viewing. Sessions were counterbalanced to control for order effects. Participants were instructed to place their head and chin on a chin rest and to look straight at the center of the computer screen (Figure 5).

The procedure was identical in Experiments 3a and 3b. A white fixation was constantly presented at the center of the screen. A trial started when the eye position was maintained within 2° from the central fixation for 1,000 ms. After a 200-ms gap, two faces, one neutral and one fearful, were presented on the left and right sides of the central fixation, with an eccentricity of 12°. Depending on which eye was used, the left and right image could correspond to either the temporal or nasal hemifield. The pairs of neutral and fearful faces stayed for 100 ms on the screen in three possible random stimulus onset asynchronies: (a) fearful preceding neutreeSes3(po253(oking)by49.7(on)n)-630(50)-2sonb2.2((a))-25.3(n)0(-)]TJT(t)0(r)19.1ceserprec414.1(-248.1(fe426.23b

saccade latency. The three-way interaction effect was not significant (Figure 6D), $F(1, 29) = 0.07$, $p = .786$, $\eta_p^2 = .003$. Next, we per-

as valence, arousal, and dominance. A thorough investigation involving diverse stimuli and measurement approaches is essential to decipher the driving factors behind the observed effects. Without answering the above questions, it is still immature to conclude the function and mechanism of the subcortical pathway. Furthermore, from an ecological perspective, the subcortical processing hypothesis emphasizes speed over accuracy. However, in the present study, subcortical characteristics were primarily reflected in recognition accuracy (Experiments 1 and 2). Although it is anticipated that the subcortical characteristics should manifest in recognition speed, future studies are required to investigate this hypothesis. Finally, it remains elusive regarding the influence of cultural factors on subcortical fear processing. Despite the subcortical pathway hypothesis emphasizing the processing of coarse, LSF information (LeDoux, 1996; Vuilleumier et al., 2003), it does not dismiss cultural influences, as the influence of cultural factors on face and emotion recognition has been demonstrated across different information scales (Chen et al., 2018; Jack et al., 2009, 2012). By comparing recognition outcomes using faces from the Chinese (e.g., Experiment 2b) and Western (e.g., Experiment 2a) cultures, we observed heightened recognition accuracies for fearful faces ($ps < .02$) and a more pronounced facilitation in LSF fear recognition (see Figure 4B). Notably, the same-eye advantage in the luminance-defined priming condition persisted in both experiments, suggesting that subcortical processing may be, at least in part, independent of cultural influences. However, a nuanced investigation into the specific impact of cultural factors on subcortical processing of threat information is essential, necessitating future research endeavors.

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