

Rapid Processing of Invisible Fearful Faces in the Human Amygdala

Yingying Wang,^{1*}  Lu Luo,^{2*} Guanpeng Chen,^{3,4,5} Guoming Luan,^{6,7,8} Xiongfei Wang,⁶  Qian Wang,^{3,4,5} and  Fang Fang^{3,4,5}

¹Department of Psychology and Behavioral Sciences, Zhejiang University, Hangzhou 310028, Zhejiang, China, ²School of Psychology, Beijing Sport University, Beijing 100084, China, ³School of Psychological and Cognitive Sciences and Beijing Key Laboratory of Behavior and Mental Health, Peking University, Beijing 100871, China, ⁴IDG/McGovern Institute for Brain Research, Peking University, Beijing 100871, China, ⁵Peking-Tsinghua Center for Life Sciences, Peking University, Beijing 100871, China, ⁶Department of Functional Neurosurgery, Sanbo Brain Hospital, Capital Medical University, Beijing 1000932, China, ⁷Beijing Key Laboratory of Epilepsy, Epilepsy Center, Sanbo Brain Hospital, Capital Medical University, Beijing 100093, China, ⁸Beijing Institute for Brain Disorders, Beijing 100069, China, and ⁹Department of Clinical Neuropsychology, Sanbo Brain Hospital, Capital Medical University, Beijing 100093 China

Rapid detection of a threat or its symbol (e.g., fearful face), whether visible or invisible, is critical for human survival. This function is suggested to be enabled by a subcortical pathway to the amygdala independent of the cortex. However, conclusive electrophysiological evidence in humans is scarce. Here, we explored whether the amygdala can rapidly encode invisible fearful faces. We recorded intracranial electroencephalogram (iEEG) responses in the human (both sexes) amygdala to faces with fearful, happy, and neutral emotions rendered invisible by backward masking. We found that a short-latency intracranial event-related potential (iERP) in the amygdala, beginning 88 ms poststimulus onset, was preferentially evoked by invisible fearful faces relative to invisible happy or neutral faces. The rapid iERP exhibited selectivity to the low spatial frequency (LSF) component of the fearful faces. Time-frequency iEEG analyses further identified a rapid amygdala response preferentially for LSF fearful faces at the low gamma frequency band, beginning 45 ms poststimulus onset. In contrast, these rapid responses to invisible fearful faces were absent in cortical regions, including early visual areas, the fusiform gyrus, and the parahippocampal gyrus. These findings provide direct evidence for the existence of a subcortical pathway specific for rapid fear detection in the amygdala and demonstrate that the subcortical pathway can function without conscious awareness and under minimal influence from cortical areas.

Key words: amygdala intracranial electroencephalogram; low spatial frequency; subcortical pathway; unconscious

Significance Statement

Automatic detection of biologically relevant stimuli, such as threats or dangers, has remarkable survival value. Here, we provide direct intracranial electrophysiological evidence that the human amygdala preferentially responds to fearful faces at a rapid speed, despite the faces being invisible. This rapid, fear-selective response is restricted to faces containing low spatial frequency information transmitted by magnocellular neurons and does not appear in cortical regions. These results support the existence of a rapid subcortical pathway independent of cortical pathways to the human amygdala.

Introduction

The ability to rapidly process emotional signals, whether visible or invisible, may offer an evolutionary advantage in enabling threat detection. The amygdala is suggested to play a key role in this process. Human brain imaging studies have shown elevated amygdala activities to threat-related stimuli, such as fearful faces (Phan et al., 2002), even when the stimuli are invisible (Whalen et al., 1998; Morris et al., 1998b; Williams et al., 2004) or presented to cortically blind patients (Morris et al., 2001; Tamietto et al., 2009). However, being unable to measure very fast neural responses in deep brain structures, traditional brain imaging techniques only provide indirect evidence for

intracranial electroencephalogram (iEEG), which enables the direct electrophysiological recording with a high temporal resolution in the amygdala, a previous study has revealed fear-selective amygdala responses occurring at a rapid speed (Méndez-Bértolo et al., 2016). However, 1-3.31.5(v)-tvtd

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contact was amplified using a Nicolet clinical amplifier. iEEG data at each electrode contact site were sampled at 256 Hz for one patient and 512 Hz for the remaining patients. All signals were online high-pass filtered at 0.16 Hz using a two-way least-squares finite impulse response filter and referenced to a forehead scalp electrode. Implantation sites of the EEG electrodes were determined exclusively by clinical criteria.

Stimuli

We compiled the faces of 96 different actors (48 females) posing with fearful, happy, and neutral expressions from two databases, Radboud Faces Database (<https://rafd.socsci.ru.nl/RaFD2/RaFD?p=main>) and NimStim Set of Facial Expressions (<https://danlab.psychology.columbia.edu/content/nimstim-set-facial-expressim17.668>). Images were processed following the procedure by

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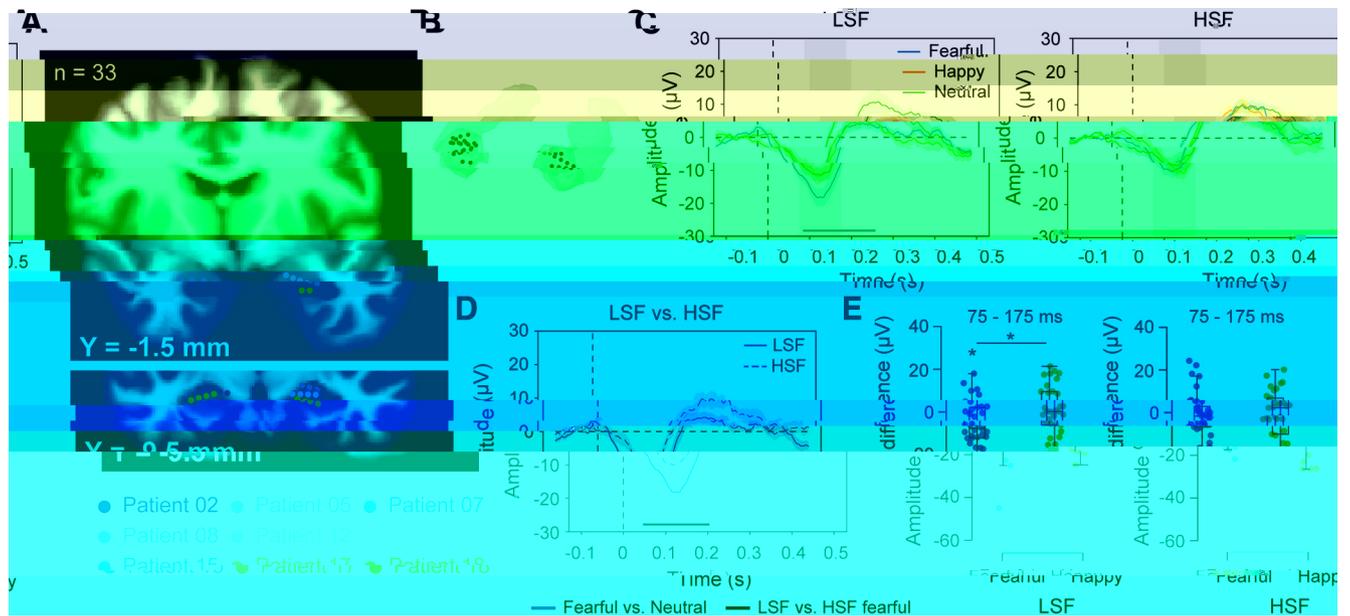


Figure 2. iERPs in the amygdala. **A**, Electrode contact locations in the amygdala for all included patients in coronal sections of the MNI canonical T1 image. Anterior-posterior positions are indicated by Y coordinates. Contacts belonging to the same patient are depicted in the same color. **B**, Electrode contacts (black) in semitransparent segmented amygdalae (beige). **C**, iERPs from 11 amygdalae of nine patients to invisible fearful, happy, and neutral faces with only LSF (left) or HSF (right) components. Bottom, The blue horizontal bar indicates a time cluster that shows significant response differences between the fearful and neutral faces. **D**, iERP comparison between the LSF and HSF fearful faces. Bottom, The black horizontal bar indicates time clusters that show significant response differences between the LSF and HSF fearful faces. The shaded areas around the iERP curves represent the SEM across contacts. **E**, Peak amplitude differences between the LSF/HSF fearful/happy and LSF/HSF neutral faces within the time window of 75–175 ms (gray shaded areas in **C**). The vertical shading in **C** represents the 100-ms time window surrounding the iERP peak. The boxes in box plots show the interquartile range and the median. Whiskers in box plots represent the minimum and maximum in the dataset. * $p < 0.05$ (two-tailed paired t tests, Bonferroni corrected).

same effect, this test deals with the multiple-comparison problem while taking into account the interdependency of the data. For each sample, a paired sample t value was computed. All samples whose t value exceeded the a priori threshold of uncorrected $p < 0.025$ (to correct for the neutral condition being compared twice with fearful/happy conditions) were retained. These t values were subsequently clustered on the basis of temporal adjacency, and the sum of the t values within a cluster was used as the cluster-level statistic. The cluster with the maximum sum was subsequently used as a test statistic. After a permutation step, which randomized the data across the two conditions and recalculated the test statistic 1000 times, we obtained a reference distribution of the maximum cluster-level summed t values to evaluate the statistic of the actual data. Clusters with a t value greater than the 99th percentile ($p < 0.01$) in the permutation distribution were considered significant. The first time point of a significant cluster was then defined as the response latency of the cluster.

To examine the iERP peak amplitude difference across the emotion conditions, we implemented linear mixed-effects models with the lme4 package in R 3.6.3 software. Models were fitted using restricted maximum likelihood. To determine the effect of the predictors of interest, including emotion, spatial frequency, and their interaction, we used the likelihood ratio test to compare models with and without each predictor of interest. The electrodes, amygdala sides, and patients were included as random factors.

Time-frequency analysis. Time-frequency analyses were performed on the epoched iEEG data using continuous Morlet wavelet transformation (function *cwt*) in MATLAB. For each contact, time-frequency maps with a frequency range from 2 to 50 Hz were calculated for each trial; then the amplitudes of the time-frequency maps were averaged across trials. Paired sample t tests comparing the time-frequency maps for the fearful/happy versus neutral faces were performed point-by-point for the amygdala (see Fig. 3A,C), EVA (see Fig. 5A), FG (see Fig. 5B), and PHG (see Fig. 5C) contacts. To reduce false positives, samples with t values exceeding a threshold of $p < 0.005$ were retained. A cluster-based permutation test was then applied with a cluster threshold of $p < 0.05$ (two tailed). For each comparison that showed at least one significant cluster, the earliest time-frequency point of the earliest cluster was defined as the response latency of the comparison effect.

Data availability

Data and codes are available on request from corresponding author Fang Fang at ffang@pku.edu.cn.

Results

Rendering face images invisible

To validate that our backward masking procedure rendered the face images invisible, patients performed an emotion discrimination task. Those who showed an accuracy rate higher than the one-tailed 5% cutoff (39%) of the chance distribution of correct choices (chance level = 33.33%) were excluded (Degonda et al., 2005; see above, Materials and Methods). As shown in Table 2, although the backward masking procedure was effective in blocking the awareness of the LSF (accuracy: mean = 28.78%, SD = 12.32%; d' , mean = 0.12, SD = 0.16) and HSF (accuracy, mean = 27.78%, SD = 11.64%; d' , mean = 0.12; SD = 0.19) faces, it failed to work for the BSF faces (accuracy, mean = 45.06%, SD = 21.08%; d' , mean = 0.92, SD = 1.02), which is in line with previous findings (Pessoa et al., 2005). Therefore, we only included the LSF and HSF faces in the iEEG experiment.

Rapid amygdala responses to invisible fearful faces

We tested 13 patients with amygdala electrodes, nine of whom (10 electrodes with 33 contacts; 6 right, 2 left, and 1 bilateral amygdalae) met our inclusion criteria (Fig. 2A,B, Table 1). To explore amygdala responses to invisible emotions, we compared the fearful/happy versus neutral face processing for the LSF and HSF conditions separately. Cluster-based permutation tests were performed at all time points between -100 and 500 ms around face onset. For the fearful versus neutral face comparison, a significant time cluster was identified at 88 – 256 ms after face onset in the LSF condition; fearful faces induced a more significant iERP response than neutral faces at a cluster threshold of $p <$

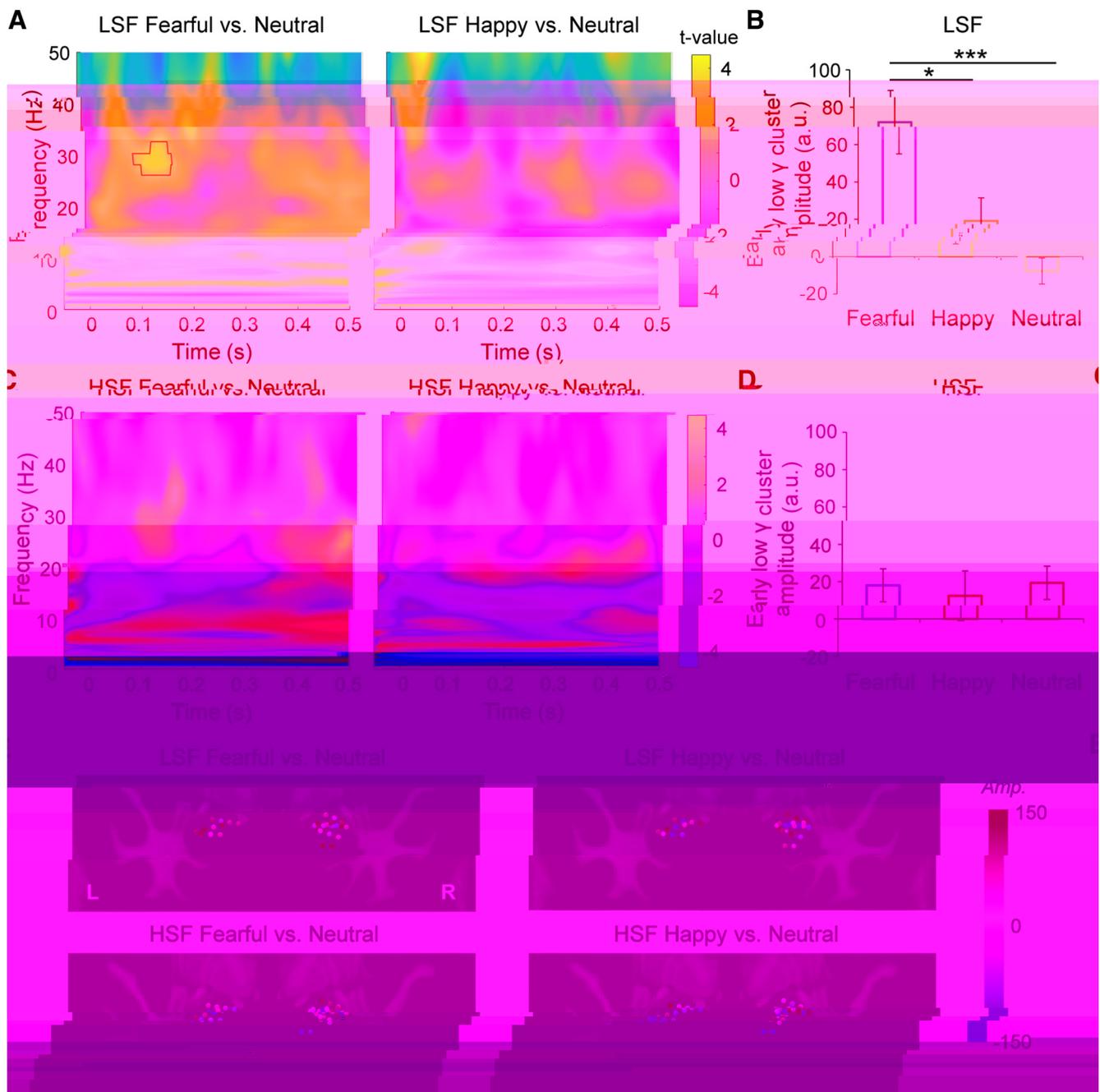


Figure 3. Time-frequency analyses of iEEGs in the amygdala. **A**, Statistical parametric maps of the time-frequency representation for the fearful (left) and happy (right) versus neutral face comparisons in the LSF condition. Red contour indicates the significant time-frequency cluster. **B**, Comparison of early low gamma amplitudes (a.u., arbitrary unit; frequency, 27–33 Hz; time, 45–118 ms) between the fearful/happy and neutral faces in the LSF condition. **C**, Statistical parametric maps of the time-frequency representation for the fearful (left) and happy (right) versus neutral face comparisons in the HSF condition. **D**, Comparison of early low gamma amplitudes between the fearful/happy and neutral faces in the HSF condition. **E**, The amplitude (Amp.) differences of the early low gamma cluster for single amygdala contacts. Error bars indicate SEM across contacts. *** $p < 0.001$, * $p < 0.05$ (two-tailed paired t tests, Bonferroni corrected).

0.01 (Fig. 2C, left). Meanwhile, no significant cluster was identified in the HSF condition (Fig. 2C, right). No response difference was observed between the happy and neutral face processing in either the LSF or HSF condition (Fig. 2C). We then compared the iERP responses between the LSF and HSF fearful faces. A significant cluster was identified showing a larger iERP response to the LSF than to the HSF fearful faces at an early latency (Fig. 2D, 50–202 ms).

To confirm the above findings, we extracted the iERP peak amplitude within the time window of 75–175 ms (Fig. 2C, gray shaded areas) for each emotion and SF condition. A linear

mixed-effects model that included the electrodes, amygdala sides, and patients as random factors was used to examine the iERP peak amplitude difference across the emotion conditions. We found a marginally significant emotion by SF interaction effect [$\chi^2(2) = 5.51, p = 0.064$]. Consistent with the finding in the cluster-based permutation test on iERP waveforms, the main effect of emotion was significant in the LSF condition [$\chi^2(2) = 9.16, p = 0.010$] but not in the HSF condition [$\chi^2(2) = 0.63, p = 0.731$]. Specifically, the peak amplitude was larger for the LSF fearful faces than for the LSF neutral faces (Fig. 2E, left; $t_{(32)} = 2.84, p = 0.024$ Bonferroni

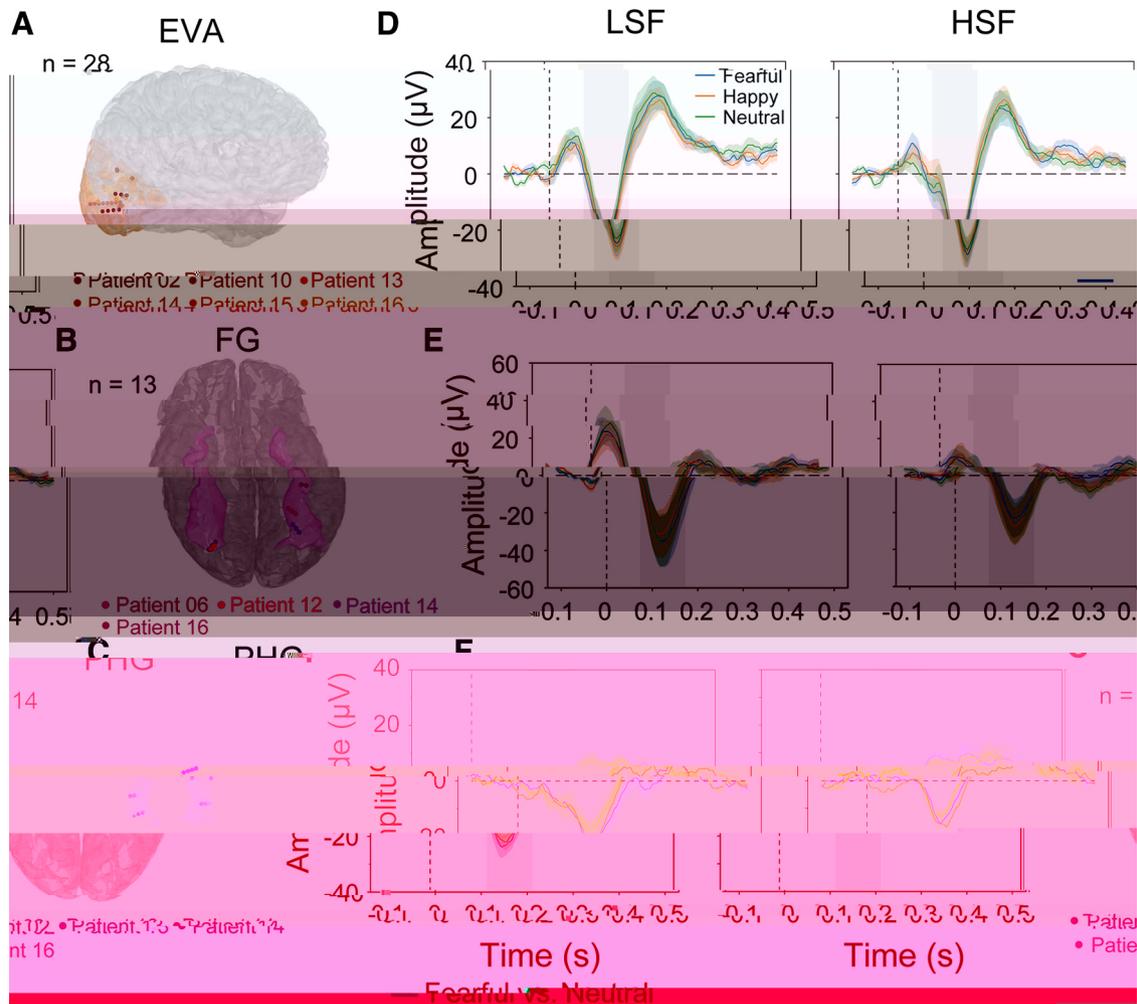


Figure 4. iERPs in visual cortex. *A–C*, Electrode contact locations in the EVAs (*A*), the FG (*B*), and the PHG (*C*). Contacts belonging to the same patient are depicted in the same color. *D–F*, iERPs to invisible fearful, happy, and neutral faces with only the LSF (left) or HSF (right) component in EVA, FG, and PHG. The horizontal bar indicates time clusters that show significant response differences between the fearful and neutral faces. The shaded areas around the iERP waveforms represent the SEM across contacts. The horizontal bar refers to the blue horizontal bar in Fig. 4*D* (right). The vertical shadings in *D–F* represent the 100-ms time window surrounding the iERP peak.

corrected, Cohen’s $d = 0.49$). The peak amplitude difference between the LSF fearful and neutral faces was also significantly larger than that between the LSF happy and neutral faces (Fig. 2*E*, left; $t_{(32)} = 2.55$, $p = 0.048$ Bonferroni corrected, Cohen’s $d = 0.44$). No peak amplitude difference between the fearful/happy faces and the neutral faces was observed with the HSF component (p values > 0.05 ; Fig. 2*E*, right). Altogether, these findings demonstrate a rapid, LSF-specific amygdala response to invisible fearful faces, supporting the subcortical emotion pathway model (Vuilleumier et al., 2003).

Rapid low gamma oscillations to invisible fearful faces

To further depict the frequency profiles of the iEEGs in the human amygdala, we performed a time-frequency analysis on the iEEGs in each emotion and SF condition. We found that the amygdala showed an early power increase (45–118 ms) at low gamma band (27–33 Hz) in response to the LSF fearful faces relative to the LSF neutral faces (Fig. 3*A*, left). Such a difference was not found in the LSF happy versus LSF neutral face comparison (Fig. 3*A*, right) or in the HSF condition (Fig. 3*C*). The mean amplitude of the early low gamma cluster was significantly higher for the LSF fearful faces than those for the LSF happy ($t_{(32)} = 2.68$, $p = 0.024$ Bonferroni corrected, Cohen’s $d = 0.47$) and

neutral ($t_{(32)} = 4.50$, $p < 0.001$ Bonferroni corrected, Cohen’s $d = 0.78$) faces (Fig. 3*B*). There was no difference in the HSF condition (Fig. 3*D*; p values > 0.05). We further visualized the amplitude differences of the early low gamma cluster for amygdala contacts on a brain template. As shown in Figure 3*E*, the effect was not localized to specific dominant contacts but was distributed across multiple contacts. Therefore, the rapid, LSF-specific amygdala response to the invisible fearful faces may be driven by the low gamma band oscillations.

No selective rapid response to invisible fearful faces in the visual cortex

Although the rapid LSF-specific amygdala response to the invisible fearful faces suggests a subcortical pathway for fear processing, it does not exclude the possibility that the fearful face information can be transmitted via cortical pathways. To examine this possibility, we analyzed cortical responses in patients who had electrode contacts in cortical regions along the ventral visual pathway, including the EVAs, the FG, and the PHG.

For the EVA contacts (Fig. 4*A*; 6 patients, 8 electrodes with 28 contacts in total), in contrast with the effects observed in the amygdala, we did not find any early effect in the LSF or HSF condition with the fearful/happy faces, relative to the neutral faces. A

late-latency cluster (344–375 ms) was identified for the fearful versus neutral face comparison in the HSF condition, suggesting that the selectivity to HSF fearful faces emerged at a late stage (Fig. 4D, right). Next, we extracted the iERP peak amplitude within a 100 ms window surrounding the peak (i.e., 75–175 ms) for each emotion and SF condition (Fig. 4D, gray shaded areas). The linear mixed-effects model, same as that applied to the amygdala contacts, showed no emotion by SF interaction effect in the EVA [$\chi^2(2) = 0.05, p = 0.974$]. For the FG contacts (Fig. 4B; 4 patients, 5 electrodes with 13 contacts), no cluster showed significantly different iERPs to the fearful/happy versus neutral faces in either the LSF (.

2007) and human (Oya et al., 2002; Krolak-Salmon et al., 2004; Mormann et al., 2008; Pourtois et al., 2010) amygdala mostly reported responses at a latency later than 100 ms. Potentially benefiting from the use of a larger sample size and more recording trials, an earlier human iEEG study found a faster amygdala response to fearful than to happy and neutral faces at 74 ms after stimulus onset (Méndez-Bértolo et al., 2016). The 88 ms effect latency to LSF fearful faces in our study is consistent with this result and extends this effect to invisible stimuli. We further identified that the rapid amygdala response emerged at the low gamma frequency band at an earlier latency of 45 ms. Previous studies have also associated the gamma band power increase occurring at a latency as early as ~50 ms in the subcortical structures, including the superior colliculus, pulvinar, and the amygdala, with face and emotion processing (Oya et al., 2002; Sato et al., 2011; Le et al., 2019). Here, the low gamma band effect was earlier than that found in iERPs. Considering that the iERPs are broadband signals, the rapid low gamma effect might be swamped by noise in other frequency bands, resulting in the delayed effect onset in the iERPs (Sato et al., 2011). This can also explain previous inconsistent findings in iERP studies (Allison et al., 1999; Krolak-Salmon et al., 2004). Together, the human amygdala is likely to discriminate fearful from neutral faces within 100 ms, regardless of the stimulus visibility.

The evidence for rapid amygdala response alone is not sufficient to support the subcortical pathway model. The multiroad model has suggested that subcortical visual processing is not necessarily faster than cortical processing (Pessoa and Adolphs, 2010). This model suggests that there exist shortcut connections in the corticocortical and subcortico-cortical pathways so that transmission of emotional information could be implemented rapidly. Although this assumption is tempting, direct evidence for the multiroad model is lacking. The multiroad hypothesis is difficult to be falsified by the iEEG technique. Because of the limited number of recording sites, it is hard to exhaust all potential shortcuts for the cortical pathway to the amygdala. Probing unconscious processing is an ideal way to examine the low-road and the multiroad models. First, subcortical regions have been found to be preferentially recruited for unconscious rather than conscious visual processing. In fear conditioning, invisible conditioned faces activated the amygdala more than visible faces. Likewise, an invisible conditioned stimulus could induce coactivation among the amygdala, the superior colliculus, and the pulvinar, but the coactivation was not apparent if the conditioned stimulus was visible (Morris et al., 1998a, 1999). In contrast, invisible faces are either insufficient to evoke cortical responses or evoke very weak cortical responses, especially in the ventral visual pathway (Jiang and He, 2006; Tamietto and de Gelder, 2010; Axelrod et al., 2015), suggesting that the cortical visual pathway is not a major source of the amygdala response to invisible stimuli. These findings are consistent with our finding of LSF specificity, a feature of subcortical information transmission, in the amygdala but not in cortical areas along the ventral visual pathway to invisible fear. It should be noted that because the dorsal visual pathway can process invisible visual information (Fang and He, 2005; Jiang and He, 2006; Mo et al., 2022), future studies should investigate the potential contribution of cortical regions in the dorsal pathway to the rapid amygdala response, even though the dorsal pathway is not sensitive to face information (Fang and He, 2005).

The present finding on invisible fear complements the literature on rapid emotion processing in the amygdala. The rapid

amygdala response to invisible fearful faces and the absence of early effects in the visual cortices demonstrate the existence of a subcortical pathway independent of cortical inputs. Such a subcortical pathway for unconscious fear detection has ecological advantages, allowing detection of coarse emotional information even when the cortical pathway is unavailable. So far, rapid, selective amygdala response has been demonstrated in both visible and invisible fear processing, with direct and indirect measures (Sato et al., 2011; Garrido et al., 2012; Méndez-Bértolo et al., 2016; McFadyen et al., 2017). Although both visible and invisible fear information recruits the subcortical pathway, they could still be segregated and transmitted to different subparts of the amygdala (Liddell et al., 2004; Williams et al., 2004, 2006). For instance, it has been shown that the dorsal amygdala exhibited dominant activation to visible fearful faces. In contrast, the ventral amygdala was more active to faces rendered invisible by binocular suppression (Lerner et al., 2012). There is also evidence that implicit and explicit fear processing activate different sides of the amygdala (Morris et al., 1998b; Williams et al., 2006). More studies are needed to explore the interaction between cortical and subcortical pathways during visible and invisible threat information processing.

We found that the rapid amygdala response is specific to the LSF face component. This is in line with the low-road model that the amygdala receives coarse visual information through a subcortical magnocellular route sensitive to LSF information (Pessoa and Adolphs, 2010). In contrast to the LSF specificity in the amygdala response, the EVA showed specificity to HSF fear in the iERP result. This dissociation between subcortical and cortical structures in SF has previously been reported in fMRI studies that showed larger signals to LSF than HSF fearful faces in the superior colliculus, pulvinar, and amygdala, and larger signals to HSF faces in the extrastriate visual cortex (Vuilleumier et al., 2003). The fMRI evidence, however, could not provide sufficient temporal information. Although MEG could overcome this problem, it cannot directly measure the activities of deep brain structures. So researchers have used indirect methods such as dynamic causal modeling on MEG data to examine information transmission to the amygdala (Garrido et al., 2012). Recent studies demonstrated a pulvinar-amygdala connection supporting rapid emotion processing, but the connection was not affected by SF (McFadyen et al., 2017, 2019). Because of the low spatial resolution of MEG, this could be because of that, the human pulvinar receives both magnocellular and parvocellular retinal inputs (Cowey et al., 1994) and transmits information to the amygdala through multiple pathways (Pessoa and Adolphs, 2010; Diano et al., 2017). The iEEG recording overcomes these problems of the traditional neuroimaging techniques. With direct evidence from iEEG recording, Méndez-Bértolo et al., (2016) and we all argue that the amygdala preferentially processes LSF information.

Our results provide conclusive evidence for the rapid processing of invisible fearful faces in the human amygdala. This rapid processing is specific to the low spatial frequency component and is independent of cortical regions in the ventral pathway, supporting the existence of a functionally independent subcortical pathway for automatic fear processing.

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