Rapid Processing of Invisible Fearful Faces in the Human Amygdala

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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 rapid fear processing in the amygdala. Taking advantage of...
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, whether such a rapid amygdala response occurs with invisible fears is still unknown.

Based on rodent research (LeDoux, 1996), a low-road model suggests that rapid fear detection in the amygdala is enabled through a subcortical pathway, which transmits coarse information through the superior colliculus and pulvinar to the amygdala, bypassing the typically time-consuming cortical pathways (Tamietto and de Gelder, 2010). Alternatively, a multiroad model proposes that cortical pathways, which contain a multitude of shortcut anatomic routes relaying visual information to the amygdala from the extrastriate visual cortex, can be equally fast at transmitting fear as the subcortical pathway through the superior colliculus and pulvinar to the amygdala, as observed in the amygdala for low spatial frequency information (BSF) (LeDoux, 2000). Therefore, if a low road exists, rapid threat detection should be observable in the amygdala for low spatial frequency information independent of stimulus visibility and cortical involvement. If multiple cortical routes are recruited as proposed by the multiroad model, rapid threat detection in the amygdala would not be observed for invisible stimuli.

To explore the characteristics and temporal dynamics of the amygdala response to invisible fear while minimizing cortical contributions, here, we recorded iEEG signals in patients with medication-resistant epilepsy while they were presented with fearful, happy, or neutral faces rendered invisible by backward masking. The faces were presented in their intact format—low spatial frequency (BSF)—or were spatially filtered to contain only their low spatial frequency (LSF) or high spatial frequency (HSF) components. Electrode contacts were localized in the amygdala and cortical areas along the ventral visual pathway. We identified an early iERP and an early gamma band response in the amygdala specific to invisible LSF fearful faces, supporting the existence of a fast subcortical pathway that deals with unconscious threats.

### Materials and Methods

**Subjects**

Subjects were 18 patients (13 males, all right handed, 19–46 years old) with pharmacologically intractable epilepsy (Table 1). Among them, 13 were implanted with amygdala electrodes, 7 with fusiform gyrus (FG) electrodes, 8 with parahippocampal gyrus (PHG) electrodes, and 9 with visual area (EVA; i.e., V1, V2, and V3) electrodes. They were admitted to the Sanbo Brain Hospital, Capital Medical University, to localize seizure foci for potential surgical resection. The study was performed 3 or 4 d after the stereotactic electrode implantation. All patients had self-reported normal vision and provided written informed consent for their participation. The experimental procedure was approved by the Ethics Committee of the Sanbo Brain Hospital of Capital Medical University and the Human Subject Review Committee of Peking University. No statistical method was used to predetermine the sample size, but our sample size is similar to those reported in previous studies (Oya et al., 2002; Krolak-Salmon et al., 2004; Sato et al., 2011; Méndez-Bértolo et al., 2016).

**Recording**

Each electrode had 10–18 independent recording contacts (0.8 mm in diameter, 2 mm in length, spacing 3.5 mm apart; Huake Hengsheng Medical Technology; Lu et al., 2021). The signal from each recording

<table>
<thead>
<tr>
<th>Patient No.</th>
<th>Sex</th>
<th>Age at onset of epilepsy</th>
<th>Amygdala contacts*</th>
<th>EVA contacts*</th>
<th>FG contacts*</th>
<th>PHG contacts*</th>
<th>Etiology</th>
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<td>19</td>
<td>4 (R)</td>
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<td>20</td>
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*Number of contacts in an electrode: M, Male; F, Female; L, left; R, right.
were filtered using a low-pass cutoff of low or high spatial frequency information, the original face images (BSF) cropped to exclude most hair and background. To create faces containing with Psychtoolbox-3 extensions (Brainard, 1997). Specifically, 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. To create faces containing low or high spatial frequency information, the original face images (BSF) were filtered using a low-pass cutoff of <6 cycles per image (LSF) and a high-pass cutoff of >24 cycles per image (HSF), respectively. Each identity appeared in all nine conditions (3 emotions × 3 spatial frequencies). For each patient, 432 images were randomly selected from the image set, resulting in 48 images per condition. Faces with the same emotion and spatial frequency should not appear more than three times in a row. Visual stimuli were presented using MATLAB (MathWorks) software with Psychtoolbox-3 extensions (Brainard, 1997).

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-expressions). Images were processed following the procedure by McFadyen et al. (2017). Specifically, 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. To create faces containing low or high spatial frequency information, the original face images (BSF) were filtered using a low-pass cutoff of <6 cycles per image (LSF) and a high-pass cutoff of >24 cycles per image (HSF), respectively. Each identity appeared in all nine conditions (3 emotions × 3 spatial frequencies). For each patient, 432 images were randomly selected from the image set, resulting in 48 images per condition. Faces with the same emotion and spatial frequency should not appear more than three times in a row. Visual stimuli were presented using MATLAB (MathWorks) software with Psychtoolbox-3 extensions (Brainard, 1997).

Experimental design
Faces were centrally displayed on an LCD screen (refresh rate, 60 Hz) for 33 ms, followed by a 467 ms white noise mask, whose mean luminance matched that of the face images (Fig. 1). A fixation cross was then presented on the screen for 2000 ms, during which patients judged whether the facial expression was fearful, happy, or neutral via key pressing. This forced-choice emotion-discrimination task was used as an objective criterion to assess emotion awareness. A chin set was used to keep the viewing distance and to keep the patient’s head as still as possible. Patients were asked to avoid verbalization and minimize eye blinks. The iEEG experiment. Furthermore, contacts that were in the seizure onset zone or severely contaminated by epileptic activity were removed. Overall, nine patients with amygdala electrodes (10 electrodes with 33 contacts) were retained. Using the same inclusion criteria as above, six patients with EVA electrodes (8 electrodes with 28 contacts; V1, 16 contacts; V2, 8 contacts; V3, 4 contacts), four patients with FG electrodes (5 electrodes with 13 contacts), and four patients with PHG electrodes (6 electrodes with 14 contacts) were retained (Table 1).

Electrode localization. To localize the electrodes, we integrated the anatomic information of the brain provided by preoperative magnetic resonance imaging (MRI) and the position information of the electrodes provided by postoperative computer tomography (CT). For each patient, we first coregistered the postimplant CT with the preimplant anatomic T1-weighted MRI for each patient using SPM12 software (https://www.fil.ion.ucl.ac.uk/spm/software/spm12/). We then identified electrode traces in the aligned CT images and calculated the coordinates of contacts in Brainstorm (http://neuroimage.usc.edu/brainstorm; Tadel et al., 2011). To assign the anatomic label to each contact, we performed subcortical and cortical segmentations based on individual preoperative T1 MRI using FreeSurfer version 6.0 (Dale et al., 1999). We identified amygdala contacts as those localized in the amygdala and further verified them in each patient’s native T1 space. An anatomic atlas for retinotopic visual areas V1–V3 (Benson et al., 2014) was used to locate EVA contacts. A high-resolution single-subject atlas (USCBRAIN; Joshi et al., 2022) was used to locate FG and PHG contacts. To identify cortical contacts, we projected each contact to the nearest vertex on the individual cortical surface using MATLAB function dsearch and assigned the contact to a cortical area based on the projected vertex. For illustration purposes, the coordinates of contacts were normalized to the MNI space and visualized on the template brain cvs_avg35_inMN1152.

Preprocessing. Preprocessing was performed using the FieldTrip toolbox (Oostenveld et al., 2011) in MATLAB R2020b. Raw iEEG data from each contact were imported into MATLAB. For each contact of each electrode, epochs from −100–500 ms prestimulus onset were extracted from continuous iEEG data. Data epochs containing interictal epileptic spikes or recording artifacts were identified by visual inspection and removed from the analysis. Detrending and baseline correction (100 ms prestimulus baseline) were then performed. No filtering was applied to avoid latency artifacts because of waveform distortion. Finally, epochs were averaged across trials for each experimental condition to obtain iERPs for each contact.

iERP analysis. To determine the time points of significant iERP difference between the fearful/happy faces and the neutral faces in the LSF and HSF conditions, a cluster-based nonparametric permutation test was applied to the iERP amplitude across all contacts (Maris and Oostenveld, 2007). By clustering neighboring samples (i.e., time points) that show the
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 \( t \) value. Values within a cluster were subsequently clustered on the basis of \( t \) values exceeding a threshold of \( p < 0.01 \) 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 paired \( t \) tests, Bonferroni corrected).

**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 amygdala) 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 <
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 corrected).

**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).
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 ($t_{(32)} = 2.55, p = 0.048$ 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. 2E, 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. 3A, left). Such a difference was not found in the LSF happy versus LSF neutral face comparison (Fig. 3A, right) or in the HSF condition (Fig. 3C). 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. 3B). There was no difference in the HSF condition (Fig. 3D; $p$ 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 3E, 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. 4A; 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 [\(\chi^2(2) = 0.05, p = 0.974\)]. 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 (Fig. 4E, left) or the HSF (Fig. 4E, right) condition. No emotion by SF interaction was found with the peak amplitudes [\(\chi^2(2) = 3.69, p = 0.158\)] either. For the PHG contacts (Fig. 4C; 4 patients, 6 electrodes with 14 contacts), no early effect was found for the fearful/happy faces relative to the neutral faces, and no emotion by SF interaction was found with the peak amplitudes [\(\chi^2(2) = 1.17, p = 0.556\)] either. Because the effects in the early visual cortex occurred much later than those in the amygdala, they could not explain the rapid response in the amygdala.

We further performed time-frequency analyses on cortical iEEGs. As shown in Figure 5, no early effects were found for the fearful/happy versus neutral face comparisons in EVA (Fig. 5A, D), FG (Fig. 5B,E), or PHG (Fig. 5C,F) in either the LSF or the HSF condition. Only late effects at the beta band were found in FG (Fig. 5B). Collectively, the absence of rapid responses to invisible LSF fearful faces in the ventral cortical stream argues against the possibility that the rapid discrimination of invisible fearful faces in the amygdala arises from neural activities in EVA, FG, or PHG.

**Discussion**

Subcortical sensory pathways have been suggested to be sufficient for rapid and unconscious processing of ecologically important stimuli, but direct electrophysiological support is lacking. Here, we reported intracranial ERP evidence that the human amygdala could selectively process invisible fearful faces containing only low spatial frequency information at an early latency of \(~88\) ms. Time-frequency analyses further identified that the rapid fear detection in the amygdala was associated with increased power at the low gamma frequency band. Critically, such early fear-selective responses were absent in cortical areas along the ventral visual pathway, excluding their contribution to the amygdala response. These findings strongly support the low-road model suggesting that threat information can be transmitted through a subcortical magnocellular route to the amygdala independent of the cortical pathways in humans.

Controversies remain over the response latency of the amygdala to fear. Although rapid amygdala responses to visible fearful or threatening stimuli have been reported within 100 ms after stimulus onset in magnetoencephalogram (MEG) studies (Luo et al., 2007, 2009, 2010; Bayle et al., 2009; Maratos et al., 2009; Hung et al., 2010; McFadyen et al., 2017), single-neuron and iEEG recordings in the monkey (Gothard et al.,...
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 neu-
tral 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 amygd-
ala response emerged at the low gamma frequency band at
an earlier latency of 45 ms. Previous studies have also associ-
ated 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 broad-
band 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 pre-
vious 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 suffi-
cient to support the subcortical pathway model. The multiroad
model has suggested that subcortical visual processing is not nec-
essarily 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 collicu-
lus, 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 transmis-
sion, 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 informa-
tion (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 litera-
ture 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 sub-
cortical 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 visi-
ble and invisible fear processing, with direct and indirect meas-
ures (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 dif-
ferent 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 tempo-
ral information. Although MEG could overcome this problem,

References
studies of human face perception. I: potentials generated in occipitotem-