

Intact rapid detection of fearful faces in the absence of the amygdala

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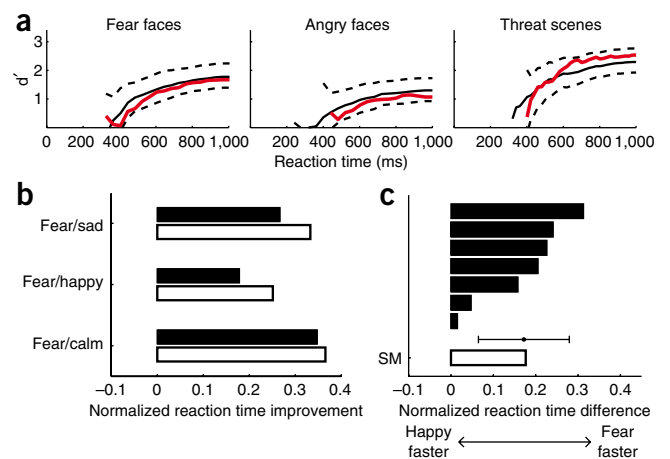
The amygdala is thought to process fear-related stimuli rapidly and nonconsciously. We found that an individual with complete bilateral amygdala lesions, who cannot recognize fear from faces, nonetheless showed normal rapid detection and nonconscious processing of those same fearful faces. We conclude that the amygdala is not essential for early stages of fear processing but, instead, modulates recognition and social judgment.

Subject SM has complete bilateral lesions of the amygdala and is impaired in her recognition of fear¹, an impairment that is consistent with previous studies showing activation of the amygdala to overt and masked fear faces². These studies have suggested that the amygdala is involved in pre-attentive, rapid processing, whereby the amygdala receives subcortical visual information via the superior colliculus and pulvinar thalamus³. Such a picture is similar to the known subcortical route for the amygdala in auditory fear conditioning, as demonstrated in rats, and is consistent with blood oxygen level-dependent

activation of the amygdala by nonconscious fearful faces in humans⁴. However, there are discrepancies with this view of amygdala function. Some neuroimaging studies have found that the amygdala's response to fearful faces is strongly modulated by conscious detectability, at least when backward masking is used⁵. Electrophysiological latencies recorded in the amygdala are, by and large, inconsistent with rapid visual processing⁶ and there is no direct anatomical evidence to support the rapid visual subcortical route that has been hypothesized⁷. These discrepancies suggest that the amygdala modulates social judgments of fear, rather than initial pre-attentive detection.

To help resolve this debate regarding the amygdala's contribution to fear processing, we tested subject SM on rapid detection of fear- and threat-related stimuli. In our first experiment, subjects saw a target stimulus (fearful face, angry face or scene showing threat) next to neutral stimuli for 40 ms (unmasked) and had to push a button as rapidly as possible to indicate which face showed more fear/anger or which scene was more threatening (Supplementary Fig. 1). SM's performance on this task was completely normal for all three threat-related categories (Fig. 1a). As reported previously¹, SM rated the intensity of fear shown in the same face stimuli substantially lower than did the controls (2.8 and 3.7 s.d. below the normal mean on the two testing sessions). Control experiments ruled out several possible interpretations (Supplementary Methods and Supplementary Table 1). First, we used backward masking in the control experiments, as it might be required to prevent afterimages to demonstrate the amygdala's rapid fear detection. Second, the control experiments compared fearful faces with sad and happy faces, rather than just

Figure 1 Intact rapid, automatic and nonconscious detection of fearful faces in the absence of the amygdala. **(a)** Rapid detection of fear- and threat-related images. Viewers were shown two images side by side for 40 ms (unmasked), one neutral and the other showing fear, anger or threat. We carried out three experiments, one with fearful versus neutral faces, the second with angry versus neutral faces and the third with threat-related images versus neutral images. Subjects were asked to push a button as quickly as possible to indicate if the target image that showed more fear/anger or was more threatening was on the left or the right. Speed and accuracy tradeoffs in discriminating fear were normal in two sessions for SM (red) compared with 12 controls (solid black line indicates the mean and the dotted lines indicate the 95% confidence interval). Accuracy was quantified by d' , the difference between the z-transformed hit and the false alarm rate. **(b)** Visual search for fear. Subjects detected an oddball target among distractors; both were perceived as belonging either to the same category (for example, mild and extreme fear) or to different categories (for example, neutral and mild fear), even though they differed geometrically by the same degree. SM showed normal category boundary effects in reaction time. The black bars indicate the average across three age-matched controls and the white bars indicate SM's performance. **(c)** Breaking into consciousness probed by continuous flash suppression. Fearful faces broke interocular suppression faster than happy faces in SM (white) to the same degree as in controls (black). Subjects clicked a mouse as soon as any part of the face became visible. The dot and error bar indicate the mean and the s.d. for seven control subjects. All subjects gave written informed consent as approved by the institutional review board of the California Institute of Technology.



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neutral faces, as SM might simply have been discriminating 'emotional' from 'neutral' using specific low-level features of neutral faces, rather than detecting fear in particular. Third, the control experiments used NimStim faces, which SM had never seen before, as SM may have been overtrained with the Ekman faces, which she saw many times in various experiments. Across all of these tasks, SM showed entirely normal rapid detection of fearful faces.

In a second experiment, we found an analogous pattern; despite impaired categorization of fearful faces when given unlimited time, SM showed normal effects of category boundaries on speeded visual search. In this experiment, we dissociated physical from psychological similarity by showing subjects faces that had been morphed between neutral and fearful expressions (**Supplementary Fig. 2**). We first asked subjects to categorize these morphs as being neutral or afraid; as expected, subjects showed sharp category boundaries for the morphs, a categorical perception effect that has been well documented⁸. SM's category boundary was significantly shifted ($P < 0.0005$), and she required a greater intensity of fear to categorize a morph as being afraid (**Supplementary Fig. 3**). We then gave subjects a visual search task in which they were asked to detect, as rapidly as possible, which face in an array was different from the rest (no specific information was given about the basis of that difference). Two versions of this search task showed subjects targets (more fearful morphs) and distractors (less fearful morphs) that always differed by the same physical morph distance, but which either spanned the mean normal category boundary or did not (**Supplementary Methods**). All subjects showed faster search times for targets and distractors that spanned the neutral/fear category boundary, than for those that did not span the category boundary, as did SM (the controls were, on average, 15% faster and SM was 26% faster; their 95% confidence intervals overlapped). Thus, SM showed normal effects of the neutral-fear category boundary (as derived from the controls) on implicit rapid visual search for fearful faces, despite impaired overt categorization of the same faces. To show that these findings were not limited to fear-neutral discriminations, we carried out an identical experiment with morphs for happy/fear and sad/fear using the Karolinska directed faces rather than the Ekman faces; the controls were, on average, 18% and 27% faster, respectively, and SM was 25% and 33% faster, respectively (**Fig. 1b**). Moreover, SM's accuracy was >99% in all conditions. Thus, in a search task, SM implicitly discriminated between fearful and other expressions with the same fear category effects as normal subjects.

In a third experiment, we focused more specifically on the amygdala's role in nonconscious processing of fear. We used continuous flash suppression^{9,10} to measure the potency of a fearful face in overcoming strong interocular suppression. Subjects were presented with a stream of flashes of Mondrian patterns at 10 Hz to the right eye while an emotional face was gradually introduced into one quadrant to the left eye; we used both Ekman face set stimuli and NimStim stimuli to ensure that there was no idiosyncratic effect of the Ekman faces as a result of SM's greater familiarity with them (**Supplementary Methods and Supplementary Fig. 4**). In our normal subjects, we found that fearful facial expressions break through into consciousness more rapidly than happy expressions (**Fig. 1c**), as has been seen previously¹⁰. To our surprise, SM showed exactly the same fear advantage in breaking interocular suppression. Thus, fearful faces gain access to consciousness in SM just as rapidly as in control subjects.

There was one qualitative exception to SM's otherwise entirely intact processing of fearful faces. SM performed somewhat worse on fear-sad discriminations (z score = -1.18) than on other discriminations (fear-neutral z score = -0.77 and fear-happy z score = -0.62 ;

Supplementary Methods and Supplementary Table 1), although this difference was small. It may be that SM can distinguish fear on the basis of valence (for example, from happiness), but has relatively greater difficulty for more subordinate-level discriminations between fear and other negatively valenced emotions (for example, from sad), a possibility that could be probed in greater detail in future experiments with larger numbers of trials.

Taken together, our findings suggest that the amygdala is not essential for nonconscious, rapid fear detection. It is still possible that the amygdala participates in such processing, provided that it results from indirect modulation. Our interpretation is also consistent with earlier findings that SM's impaired explicit fear recognition can be rescued if she is instructed to look at the eyes in faces, something she fails to do spontaneously¹¹. In the absence of the amygdala, explicit fear recognition may be impaired as a result of an absence of the amygdala's normal modulation of information processing (for example, directing visual attention to the eyes in faces). More puzzling is that individuals with blindsight resulting from primary visual cortex lesions show amygdala activation by fearful faces¹², a finding that could be taken as evidence for a subcortical visual route to the amygdala involved in nonconscious fear processing. However, although cortical damage is sufficient to prevent conscious vision in such individuals, it may be incomplete and could permit sparse cortical input to the amygdala that is sufficient to account for the observed activation. Alternatively, a retino-collicular-pulvinar-cortical pathway might indirectly route visual information to the amygdala via spared extrastriate cortical areas. Our conclusions are also not inconsistent with an early role for emotion in driving attention³, even in the absence of conscious awareness¹³, but argue that the amygdala is not a necessary substrate for this role. Instead, we favor the idea that the amygdala modulates other cognitive processes on the basis of an appraisal-like evaluation of the biological relevance of stimuli¹⁴ and contributes to explicit judgments about the fear shown in fearful faces once substantial cortical processing has already taken place.

Note: Supplementary information is available on the Nature Neuroscience website.

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AUTHOR CONTRIBUTIONS

N.T., F.M. and R.A. designed the study and wrote the paper. N.T. and F.M. executed most of the study and analyzed all of the data. C.F. and M.Y. helped with aspects of the data collection.

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