Report

Cortical Responses to Invisible Faces: Dissociating Subsystems for Facial-Information Processing

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Summary

Perceiving faces is critical for social interaction. Evidence suggests that different neural pathways may be responsible for processing face identity and expression information. By using functional magnetic resonance imaging (fMRI), we measured brain responses when observers viewed neutral, fearful, and scrambled faces, either visible or rendered invisible through interocular suppression. The right fusiform face area (FFA), the right superior temporal sulcus (STS), and the amygdala responded strongly to visible faces. However, when face images became invisible, activity in FFA to both neutral and fearful faces was much reduced, although still measurable; activity in the STS was robust only to invisible fearful faces but not to neutral faces. Activity in the amygdala was equally strong in both the visible and invisible conditions to fearful faces but much weaker in the invisible condition for the neutral faces. In the invisible condition, amygdala activity was highly correlated with that of the STS but not with FFA. The results in the invisible condition support the existence of dissociable neural systems specialized for processing facial identity and expression information. When images are invisible, cortical responses may reflect primarily feedforward visual-information processing and thus allow us to reveal the distinct functions of FFA and STS.

Results and Discussion

Humans are social creatures. One of the most important sources of information in human interaction is the face. As such, face perception is one of the most highly developed visual skills in humans. Bruce and Young (1986) proposed an influential model of face perception with separate functional routes for the recognition of facial identity and facial expression [1]. More recently, Haxby and colleagues (2000) further suggested two functionally and neurologically distinct pathways for the visual analysis of faces: One codes changeable facial properties (such as expression, lipspeech, and eye gaze) and involves the superior temporal sulcus (STS), whereas the other codes invariant facial properties (such as identity) and involves the lateral fusiform gyrus [2]. These models share the idea of distinct pathways for the visual analysis of facial identity and expression. It should be noted that although evidence from behavioral and neuropsychological studies of patients with impaired face perception after brain damage and studies of non-human primates support the existence of two systems of facial processing [3–8], recent neuroimaging studies in normal human observers yield a less consistent picture because considerable overlap has been found in activation patterns in response to different face-processing tasks [9–12].

Here, we examined this issue by presenting participants with faces containing neutral and fearful expressions. These images were either presented binocularly (visible) or dichoptically with strong suppression noise and thus rendered invisible due to interocular suppression. The inclusion of faces with neutral and fearful expressions and the manipulation of stimulus-visibility states provide us with a unique opportunity to examine the distinct loci and pathways for processing invariant and changeable facial properties with and without feedback influence from a conscious representation of facial information. We hypothesize that facial identity and expression information is initially registered and processed in relatively independent subsystems following feed-forward pathways. Neural subsystems in the brain are highly interconnected. Initially distinct facial processes interact with one another through both lateral interactions as well as feedback modulations; thus, the overall neural response in different brain areas may not reflect the relatively independent analysis for different types of facial information.

Rendering Face Images Invisible

In conventional binocular rivalry, two different images are dichoptically shown to the two eyes, and the observer's percept alternates between one image and the other. By making one of the two competing stimuli much stronger (high contrast, dynamic, and full of contours, etc.) than the other, one can make the strong stimulus dominant for much longer durations. In an extreme case, a static image in one eye can be completely suppressed for quite a long time by continuous flashing of random Mondrian images (around 10 Hz) to the corresponding location in the other eye; such is the so-called continuous flash suppression (CFS) [13]. We adopted this CFS procedure and further reduced the contrast of the suppressed images to achieve a very long-lasting suppression effect [14].

In the invisible condition, observers viewed a composite of dynamic red Mondrain patterns and static green faces through red-green anaglyph glasses, rendering the face images invisible. In the visible condition, the face images were presented to both eyes without the Mondrian patterns (Figure 1). The contrast of the face images was adjusted for each individual observer to ensure that the intact and scrambled faces were fully suppressed during the entire session. All observers underwent behavioral experiments in two separate sessions (before and after they were scanned) in which they were asked to make a Two-Alternative Forced Choice

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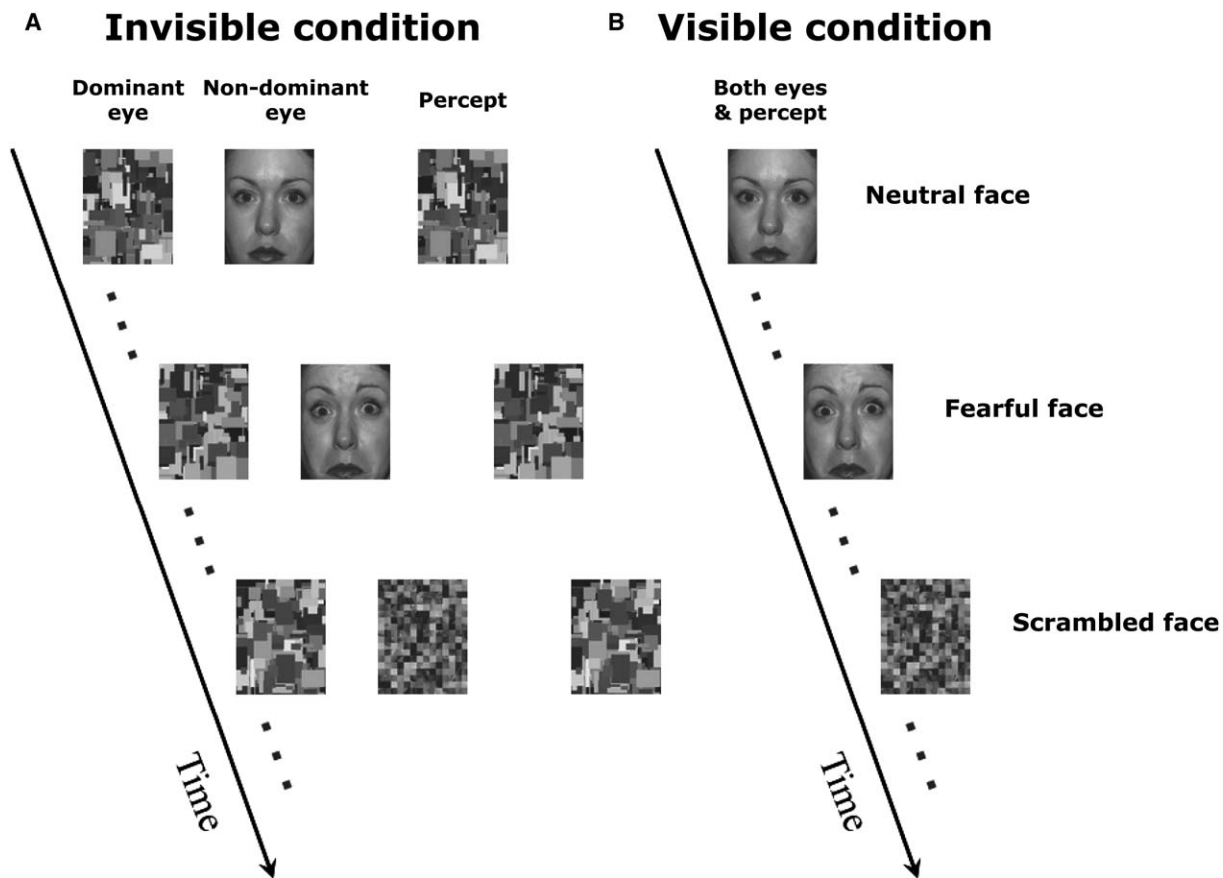## A **Invisible condition**

B **Visible condition**

Figure 1. Sample Stimuli and Procedure Used in the Current Study

(A) In the invisible condition, the intact face images with neutral and fearful expressions and the scrambled face images presented to the non-dominant eye can be completely suppressed from awareness by dynamic Mondrian patterns presented to the dominant eye because of inter-ocular suppression. The suppression effectiveness was verified by objective behavioral experiments.

(B) The visible condition was the same as the invisible condition except that the Mondrian patterns were not presented; instead, both eyes viewed the same face or scrambled face stimuli.

(2AFC) decision on which interval (first or second) the intact face was presented (see Experimental Procedures for details). Each observer performed at chance level in both prescan and postscan sessions. After each invisible condition scan, observers were also asked whether they saw any intact or scrambled faces or any parts of faces other than the Mondrian patterns. No observers reported seeing faces or parts of faces.

Regions of Interest (ROIs)
Face-selective ROIs were defined independently with a block-design scan. Observers passively viewed the images of faces and nonface objects. Face-selective ROIs were defined as areas that responded more strongly to faces than nonface objects ($p < 10^{-4}$, confirmed with a Bonferroni correction, p(Bonf) < .05). Three cortical areas, including the bilateral FFA and the right STS, were consistently found in all observers (Figure 2A). Significant face-specific activation in left STS was seen in four of the six observers. Because the pattern of results in the left FFA (all six observers) and the left STS (four of the six observers) are the same as the more robust ROIs on the right side, we decided to present the results from the right FFA and right STS only. More details about ROI information for each subject can be found in Table S1.

The amygdala could be activated by emotional information even when stimuli were not perceived by observers [15–19]. To assess the relationship between amygdala activity and activity in FFA and STS, we also identified each observer's bilateral amygdalae with an independent scan contrasting neutral and fearful faces to scrambled faces (Figure 3A). Amygdala locations were very consistent across the six individual participants, with the following mean Talairach coordinates: left amygdala (-20 ± 2, 0 ± 1, and -14 ± 1) and right amygdala (20 ± 2, -1 ± 2, and -16 ± 2).

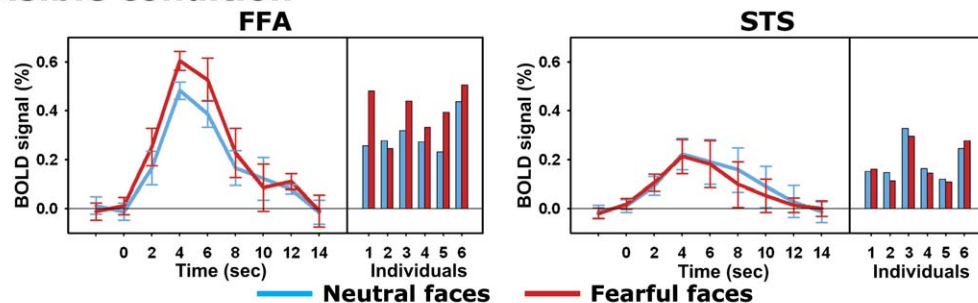**fMRI Responses to Visible and Invisible Face Images across ROIs**
The Effect of Awareness States and Facial Expressions
FFA had strong activations to the visible faces, for both the neutral ($t_5 = 10.5$ and $p < .0005$) and the fearful expression ($t_5 = 15.8$ and $p < .0005$), with scrambled faces as the baseline (Figure 2B). FFA activations from the fearful faces were slightly but significantly stronger than activation from the neutral faces ($t_5 = 2.83$ and $p < .04$). Although this enhanced response in the visible condition to the fearful faces could be due to increased attention to fearful faces compared to neutral faces, it is

A ROIs

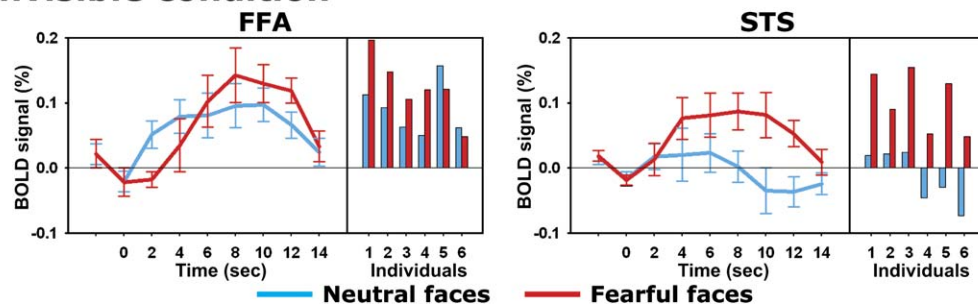## B Visible condition

C Invisible condition

Figure 2. fMRI Responses of Face-Selective Areas to Both Visible and Invisible Face Images

(A) Face-selective areas (FFA and STS) were identified with an independent scan and depicted on the inflated right hemisphere of a representative observer.

(B) Results for the visible condition. Each panel shows the time course averaged from six observers with scrambled faces as the baseline as well as the BOLD amplitude for each individual. Results from the left hemispheres are similar to the data shown here for the right hemispheres. Both the FFA and the STS had strong activations to visible neutral (blue curves and bars) and fearful (red curves and bars) faces.

(C) Results for the invisible condition. Each panel shows the time course averaged across six observers and BOLD amplitude for each individual. Even when observers were not aware of the nature of the pictures presented in this condition, the FFA still showed substantial activation for both invisible neutral and fearful faces, whereas the STS only responded to invisible fearful faces. Error bars stand for SE.
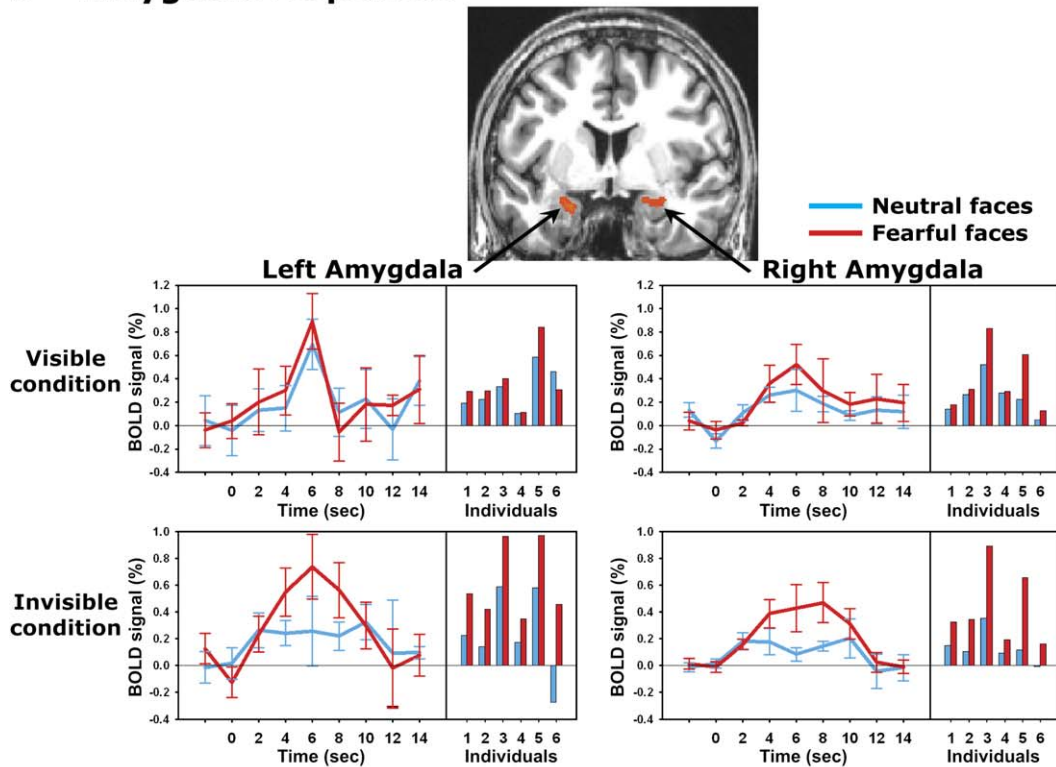
still consistent with recent functional imaging studies showing that the response in the fusiform gyrus was stronger to emotional faces than neutral faces [9, 12, 20, 21]. In the invisible (suppressed) condition where observers perceived the dynamic noise and were not aware of the face pictures presented, the FFA responses to faces were much reduced, consistent with previous findings [22]. However, the residual responses in FFA to faces were still reliable for both invisible neutral faces ($t_5 = 3.68$ and $p < .02$) and invisible fearful faces ($t_5 = 4.07$ and $p < .01$). Furthermore, no difference was found between the fMRI responses to the invisible neutral and fearful faces in FFA ($t_5 = 1.02$ and $p > .3$) (Figure 2C).

The STS was also significantly activated in response to the visible neutral faces ($t_5 = 2.90$ and $p < .04$) and the visible fearful faces ($t_5 = 3.25$ and $p < .03$) (Figure 2B). In contrast to the activation patterns in FFA, the STS showed similar fMRI signals between neutral and fearful face conditions ($t_5 = 0.84$ and $p > .4$). More surprisingly, the STS only responded to invisible fearful faces ($t_5 = 3.13$ and $p < .03$) but not to invisible neutral faces ($t_5 = -0.57$ and $p > .5$) (Figure 2C).

The bilateral amygdalae showed strong activation to both the visible neutral faces ($t_{11} = 5.93$ and $p < .0005$) and the visible fearful faces ($t_{11} = 5.40$ and $p < .0005$), with the fearful faces evoking a stronger signal than the neutral faces ($t_{11} = 2.40$ and $p < .04$). When the faces were suppressed and invisible, the bilateral amygdalae still responded significantly to the invisible neutral faces ($t_{11} = 2.72$ and $p < .02$) and the invisible fearful faces ($t_{11} = 6.26$ and $p < .0005$) (Figure 3A). The signal of the invisible fearful faces was significantly stronger than that of the invisible neutral faces ($t_{11} = 6.23$ and $p < .0005$), even though observers did not consciously perceive the faces at all; such findings are consistent with recent brain imaging studies [15–19].
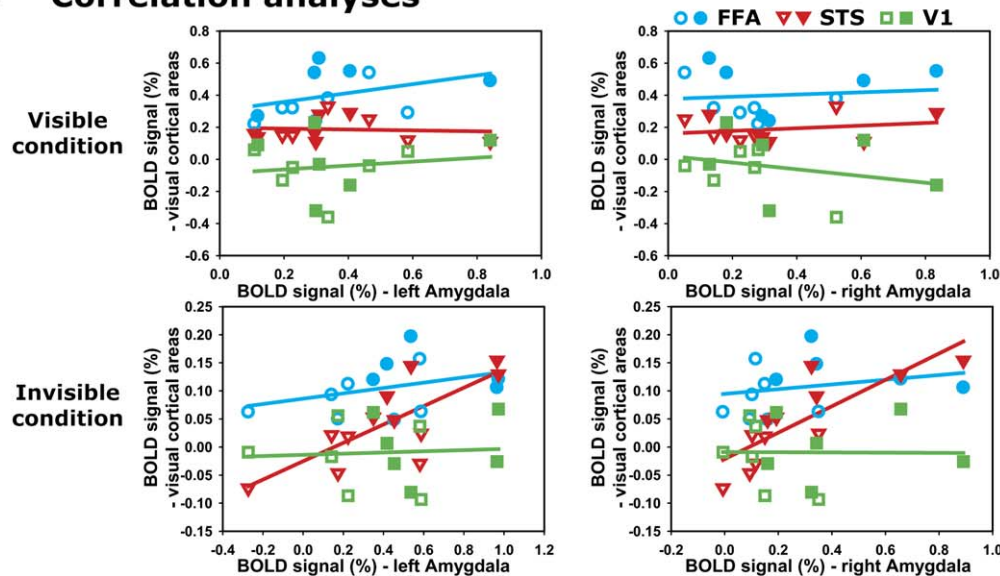
A Amygdala responses

Figure 3. fMRI Responses of Bilateral Amygdalae to Both Visible and Invisible Face Images

(A) The bilateral amygdalae were identified with an independent scan. The average time course and individual BOLD amplitude are shown in each panel. For both visible and invisible conditions, the amygdala showed stronger responses to fearful faces (red curves and bars) than neutral faces (blue curves and bars).

(B) Correlations of BOLD signals between amygdala and other visual areas (FFA: blue circles, STS: red triangles, and V1: green squares). Activities generated by the fearful faces are shown with the filled symbols, whereas activities from neutral faces are shown with the open symbols. There were highly significant correlations between activity in the amygdala and STS in the invisible condition only (red lines in the bottom panels). Error bars stand for SE.

The Interaction among Awareness States, ROIs, and Facial Expressions

Comparing the pattern of results across FFA and STS allowed us to test the validity of the idea that there are distinct pathways for facial-identity and facial-expression processing [1, 2]. A significant interaction among awareness state (visible versus invisible), ROI (FFA versus STS), and facial expression (neutral versus fearful)

was found ($F_{1,10}$ = 13.2 and p < .005). Further analyses revealed that the significant interaction was due to the changes in activity pattern across visibility states in STS ($F_{1,5}$ = 88.1 and p < .0005) but not FFA ($F_{1,5}$ = 1.89 and p > .2), suggesting dissociable functions of the FFA and the STS in facial processing. In addition to the interaction analysis, another way to highlight the differential sensitivity between different ROIs to the visibility of the stimuli is to quantify the suppression by a residual-activity index, RI, defined as the ratio of activity in the invisible condition compared to the visible condition, where 0 represents complete suppression and 1 represents no suppression. Specifically, there was an equal suppression of activity in FFA for both neutral and fearful faces (RI = 26% and RI = 27%, respectively), whereas there was a contrasting reduction of activity in STS for neutral (RI $\approx$ 0%) and fearful faces (RI = 57%). There was a mild reduction of amygdalae responses for neutral faces (RI = 66%) but no reduction at all for fearful faces (RI $\approx$ 100%).

A correlational analysis between the amygdala and both the FFA and the STS showed that bilateral amygdalae activity was highly correlated with STS activity in the invisible condition only (left amygdala: r = .767 and p < .005; right amygdala: r = .821 and p < .001). However, amygdala activity was not significantly correlated with FFA activity (left amygdala: r = .359 and p > .2; right amygdala: r = .236 and p > .4) (Figure 3B). To rule out the possibility that the significant correlations found here were due to a general pattern of brain activity, we also analyzed the correlation between the amygdala and the primary visual cortex (V1) but could not find any significant correlations (left amygdala: r = .064 and p > .8; right amygdala: r = −.008 and p > .9). It is worth emphasizing that all of the significant correlations were found in the invisible condition; there were no significant correlations in the visible condition.

Relationships to Other Studies

Our results show that in FFA, the fMRI signals were much reduced when faces were rendered invisible, for both the neutral and fearful faces. This result is consistent with earlier fMRI findings with similar binocular-rivalry techniques [14, 22]. On the other hand, FFA activity was still significantly greater for invisible faces than scrambled faces: Whereas observers could not tell whether a scrambled or a nonscrambled face was presented, their FFA reacted more strongly to the intact faces. The reliable residual activity seen in FFA when faces were invisible is consistent with Moutoussis and Zeki's discovery that invisible faces due to dichoptic color fusion could activate face-specific brain areas [23]. On the contrary, Pasley and colleagues used binocular suppression to render stimuli invisible, but they did not find significant brain activation in the object-selective inferior temporal cortex to unperceived fearful faces compared to unperceived nonface objects [19]. Because meaningful visual images (e.g., houses) were used to suppress face images, it is possible that the relatively weak brain responses to unperceived faces could not be distinguished from the fMRI signals to houses. We recently performed a psychophysical experiment showing that upright faces took less time to gain dominance compared to upside-down faces

against the identical suppression noise during binocular rivalry [24], and such a finding implies that the suppressed face images are processed at the level where the brain can tell the upright face from the inverted face, most likely FFA [25, 26].

In our view, the more surprising and novel aspect of the current finding is that STS showed a robust response to the invisible fearful faces but did not show a response to the invisible neutral faces. Contrasted with the FFA's similar responses to fearful and neutral invisible faces, this pattern of results supports a dissociation of function between FFA and STS. Such dissociation of function is highlighted by a significant interaction between ROI (the right FFA versus the right STS) and facial expression (neutral versus fearful) in the invisible condition ($F_{1,5}$ = 8.52 and p < .04). Our observation provides further support for the dissociable neural systems that are specialized for facial-structural encoding versus facial-expression analysis [1] or invariant versus changeable aspects of faces [2]. Why are the distinct functions for facial-information processing between FFA and STS only revealed in the invisible condition? We hypothesize that the absence of awareness of the facial information maximally reduced, if not abolished, cortical feedback modulations. Thus, the observed BOLD responses reflect more feed-forward visual-information processing without the influence of feedback modulation from a conscious representation of faces, and such an isolation of the feed-forward process made it possible for us to reveal the distinct functions of FFA and STS by using fMRI.

A remaining question is when face images were suppressed interocularly, how did the information arrive at the face-sensitive cortical sites? It is possible that interocular suppression is incomplete at the early cortical areas and face information leaks through at the site of interocular competition. This idea is consistent with the current belief that binocular rivalry is better characterized as a multistage process, occurring at multiple cortical regions [27]. Alternatively, face information could also travel through subcortical pathways and bypass the cortical site of interocular suppression to eventually reach FFA and STS. The amygdala is believed to play a critical role in processing threat-related stimuli, particularly facial expressions of fear and anger [20, 28–30]. It has been suggested that the amygdala receives visual inputs via both cortical and subcortical pathways with the subcortical pathway conveying crude but rapid signals before awareness and also facilitating early detection of threat [18]. Furthermore, studies with both blindsight patients and normal observers support the existence of a subcortical neural pathway (colliculo-thalamo-amygdala) capable of processing fear-related stimuli independent of both the striate cortex and visual awareness [15, 16, 31]. Our study provides further support that processing of emotional information in the amygdala is, to a large degree, automatic. However, although still controversial [9, 32], our findings do not exclude the possibility that deprivation of attentional resources (with a very heavy load) could still modulate the amygdala's response to emotional stimuli [33]. The observation that STS only responded to invisible fearful faces but not neutral faces and the strong correlation between STS and amygdala activity imply a close

relationship between STS and the amygdala. However, our data are consistent with communication in either direction between the amygdala and STS.

In summary, by rendering face images invisible through interocular suppression, we demonstrated distinct patterns of responses in FFA, STS, and the amygdala, with STS and the amygdala being selectively sensitive to the facial-expression information. Our results support the idea that face perception involves two functionally (identity versus expression or invariant versus changeable) and anatomically (FFA, STS, and amygdala) distinct pathways. The current study also highlights the usefulness of the interocular suppression paradigm, which we believe is effective in isolating the feed-forward processes for close examination.

Experimental Procedures

Participants
Six healthy observers (three male) participated in the current experiment. Observers had normal or corrected-to-normal vision and gave written, informed consent in accordance with procedures and protocols approved by the human-subjects review committee of the University of Minnesota.

Stimuli and Procedure
Stimuli were generated with MATLAB based on the NimStim face stimulus set (The Research Network on Early Experience and Brain Development) and presented through a LCD projector onto a rear projection screen located behind the participant's head inside the magnet bore. The screen was viewed with an angled mirror positioned on the head-coil. The scrambled faces were made by segmentation of the face images into 18×24 square grids and random rearrangement of the grid elements. A central point ($0.3° \times 0.3°$) was always presented to each eye and served as the fixation point. The presentation of a frame ($5.7° \times 7.5°$) that extended beyond the outer border of the stimulus and fixation point facilitated stable convergence of the two eyes' images. The viewing distance was 102 cm.

In the fMRI scanner, observers viewed the face images (neutral, fearful, and scrambled faces) through red-green anaglyph eyeglasses. The visible and invisible conditions were run in separate scans. In the invisible condition, dynamic Mondrian patterns (10 Hz) were presented to subject's dominant eye through the red filter, and the intact or the scrambled face was simultaneously presented to the other eye through the green filter for the same period. The faces and the Mondrian patterns extended $4.2° \times 5.7°$, and each trial was presented for 2 s followed by a 2 s intertrial interval (ITI) in which only the fixation and the outer frame were presented. The contrast of the face images was adjusted for each individual observer to ensure that the intact and scrambled faces were fully suppressed and truly invisible for the length of the experiment. After each scan of the invisible condition, observers were also asked whether they saw any faces or parts of faces other than the Mondrian patterns. Observers also performed a 2AFC test so that the effectiveness of the suppression could be checked (see below). The visible condition was exactly the same as the invisible condition except that the Mondrian patterns were replaced with the same face stimulus presented to the other eye so that observers could tell whether a neutral, fearful, or scrambled face was presented during the block.

In both conditions, neutral, fearful, and scrambled faces were presented randomly with one block consisting of 48 trials. Observers were asked to detect an occasional 3-fold size change of the fixation point. Functional scans in the visible and the invisible conditions were run two and four times, respectively, and the order of the visible and invisible scans was randomized. The order of the three test stimulus types was also counterbalanced within each scan with M sequences [34]. These are pseudorandom sequences that have the advantage of being perfectly counterbalanced among the three stimulus types so that trials from each kind of test stimulus were preceded equally often by trials for each of the other kinds of stimuli.

fMRI Data Acquisition and Analysis
MRI data were collected on a 3T Siemens Trio outfitted with an 8-channel phase-array coil. Echoplanar data were acquired with standard parameters (28 axial slices, 3.0 mm thick; field of view, 220×220 mm^2; matrix, 64×64; repetition time, TR, 2000 ms; echo time, TE, 30 ms; and flip angle, 75°). The first four volumes were discarded to allow for magnetization equilibration. The lowest slice of the 28 functional slices was positioned just beneath the ventral surface of the temporal lobes. This ensured coverage of most of the visual and temporal cortex. A T1-weighted anatomical volume (3D MPRAGE; $1 \times 1 \times 1$ mm^3 resolution) was acquired for localization and visualization of the functional data.

After motion correction (SPM99, http://www.fil.ion.ucl.ac.uk/spm), the functional data were coregistered with the anatomical scan with BrainVoyager QX (Brain Innovation). After regions of interest (ROIs) were defined (see below), time courses from each ROI were extracted and imported into MATLAB for further analyses. For each scan, we averaged the signal intensity across the 16 trials in each condition at each of 9 time points (from -2 s to 14 s). These event-related time courses of signal intensity were then converted to percent signal change by subtraction of the corresponding value for the scrambled face condition and then division by that value. The resulting time course for each condition was then averaged across scans and observers. The mean of three successive time points around the peak in the event-related averages served as the measured BOLD response for each condition and each individual.

Localizing Face-Specific Areas
A separate scan was used to localize face-processing areas in the occipital-temporal cortex. During the localizer scan, observers viewed alternating 20 s blocks of intact face images (both neutral and fearful faces with full contrast) and nonface object images. A boxcar response model smoothed with a hemodynamic response function was used so that voxels with a significantly higher signal ($p < 10^{-4}$, and the significance was further confirmed with Bonferroni correction for multiple comparisons, p(Bonf) < .05) could be identified in response to the face images compared to the nonface object images, and these brain areas were defined as regions of interest (ROIs). Because the amygdala is centrally involved in emotional-information processing even in the absence of awareness and is known to respond to faces [35], we further identified each observer's bilateral amygdalae with this independent face localizer scan contrasting neutral and fearful faces to scrambled faces.

Objective Measures of the Suppression Effectiveness
Because the interpretation of the study depends critically on the suppressed images being truly invisible, we also checked the suppression effectiveness in a criterion-free way. All participants underwent 2AFC experiments in separate sessions both before and after the fMRI experiment. The experimental situation (contrast, luminance, and viewing angle, etc.) was made to be fully comparable with that in the functional imaging experiments. The same set of intact face images and scrambled controls were used in this behavioral measurement. For each trial, there were two successive temporal intervals (2 s each, with a 500 ms blank gap between them). The intact face (either neutral or fearful expression) could be presented randomly in the first or the second interval, and the scrambled face was presented in the other interval. Observers pressed one of two buttons to indicate whether the face was presented in the first or the second interval. Each observer underwent 200 trials (100 trials before and 100 trials after the fMRI experiment), and all performed at chance level. To further test the possibility that the face stimuli could be fused with the Mondrian pattern during the initial brief period of stimulus presentation [36] but remain invisible due to the masking effect of the subsequent dynamic Mondrian patterns, we performed the same 2AFC experiment but with a brief presentation duration (100 ms). Observers still performed at chance level under this condition. Therefore, these 2AFC measurements confirmed that the suppressed images were truly invisible throughout the whole presentation.

Supplemental Data
Supplemental Data include one table and can be found with this article online at http://www.current-biology.com/cgi/content/full/16/20/2023/DC1/.

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