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Report

Facial-Expression and Gaze-Selective Responses in the Monkey Amygdala

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Summary

The social behavior of both human and nonhuman primates relies on specializations for the recognition of individuals, their facial expressions, and their direction of gaze [1–5]. A broad network of cortical and subcortical structures has been implicated in face processing, yet it is unclear whether co-occurring dimensions of face stimuli, such as expression and direction of gaze, are processed jointly or independently by anatomically and functionally segregated neural structures. Awake macaques were presented with a set of monkey faces displaying aggressive, neutral, and appeasing expressions with head and eyes either averted or directed. BOLD responses to these faces as compared to Fourier-phase-scrambled images revealed widespread activation of the superior temporal sulcus and inferotemporal cortex and included activity in the amygdala. The different dimensions of the face stimuli elicited distinct activation patterns among the amygdaloid nuclei. The basolateral amygdala, including the lateral, basal, and accessory basal nuclei, produced a stronger response for threatening than appeasing expressions. The central nucleus and bed nucleus of the stria terminalis responded more to averted than directed-gaze faces. Independent behavioral measures confirmed that faces with averted gaze were more arousing, suggesting the activity in the central nucleus may be related to attention and arousal.

Results

Activation to Faces versus Scrambled Images

Awake monkeys were scanned in a 4.7 T magnet at 1 × 1 mm in-plane resolution covering the occipital and temporal lobes, and this produced widespread functional activation to the Face > Scrambled contrast (Figure 1, see Experimental Procedures). Activation included a large continuous section of the superior temporal sulcus (STS) extending along the inferotemporal (IT) cortex onto the ventral surface of the temporal lobe (Figure 2). Maximal activation was found on the anterior, lateral lip of lower-bank STS near AP +19 of both left and right hemispheres of the two monkeys examined (see Table S1 in the Supplemental Data online). In addition, significant bilateral activation was seen in the amygdala of both monkeys (Figure 2B and Table S1).

Effects of Facial Expressions and Gaze in the Amygdala

On the basis of the nuclear contours obtained from structural images, active voxels for the Threat >Appease contrast fell within the basal and accessory basal nuclei of the amygdala (Figure 3), which, combined with the lateral amygdala, will be referred to as the basolateral amygdaloid complex (BLA, see Supplemental Data). The active volumes filled 10%–38% of the BLA (16–60/160 mm^3), based on standardized estimates of BLA volume [6]. ROI analysis with all voxels that fell within the predetermined nuclear contours revealed that, although multiple regions in the amygdala were active for faces relative to scrambled controls, only the BLA showed an enhanced BOLD response for Threat faces compared to Appeasing faces, with no effect of head and eye gaze and no interaction (2 × 3 ANOVA, main effect of expression $F(2) = 10.35$, $p < 0.001$, Figure 3, inset; Table S2). No other expression contrasts showed consistent activation patterns in the amygdala, whether Appease > Threat or either-expression > Neutral.

The Averted > Directed contrast for head and eye direction, henceforth referred to simply as directed or averted gaze, produced a tight cluster of activation corresponding to and restricted to the central nucleus and the bed nucleus of the stria terminalis, termed the lateral extended amygdala (LEA). The activation in the LEA occupied approximately 32% (monkey 2) and 80% (monkey 1) of the volume of these nuclei (8, 20/25 mm^3; Figure 4). ROI analysis confirmed that, indeed, only the these nuclei showed a heightened BOLD response for averted compared to directed face stimuli, regardless of expression and with no significant interaction (Figure 4, inset; 2 × 3 ANOVA, main effect of gaze $F(1) = 6.84$, $p < 0.01$; Table S2). No consistent activation was seen for the Directed > Averted contrast.

Relation to Skin-Conductance Responses

The correlation between amygdala activity and measures of arousal [7, 8] led us to ask whether the face conditions showing the strongest amygdala activation would also show the greatest levels of arousal. The skin-conductance responses (SCRs) of two monkeys were monitored as they were presented with the same 72 face stimuli used in the fMRI experiment. On average, faces with averted gaze elicited stronger SCRs than did faces with gaze directed toward the viewer, regardless of expression (2 × 3 ANOVA, main effect of gaze $F(1) = 8.23$, $p < 0.01$; Table S2). This pattern of autonomic response was consistent with the activation profile in

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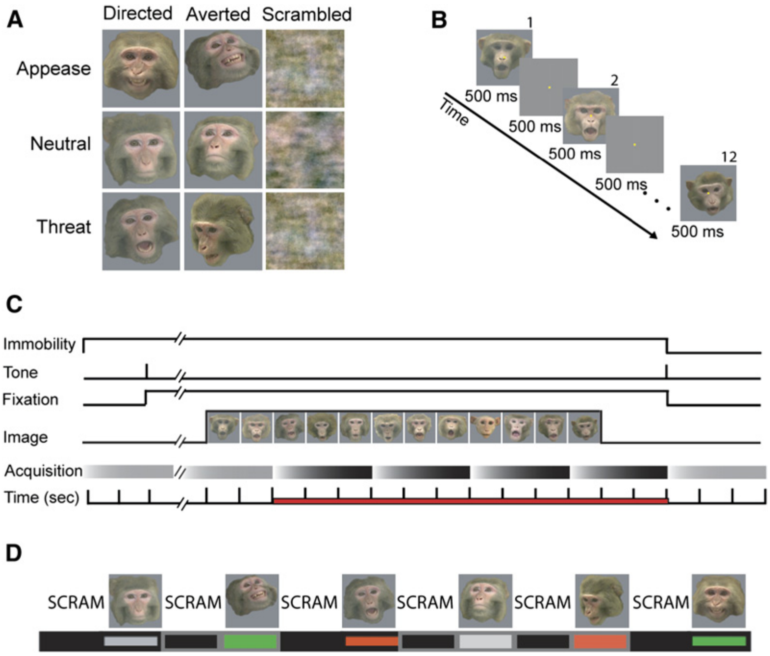

Figure 1. Stimulus Presentation and Task Design

(A) Example of the six face stimuli obtained from each monkey. Facial expressions were neutral, threatening, or appeasing (fear grimace shown) and could be either directed at the viewer or with gaze and head averted. A Fourier-phase-scrambled image was made from each face stimulus (far-right column).

(B) Presentation of stimulus blocks. During one stimulus block, presentations alternated between images and gray squares, each lasting 500 ms, for a total block duration of 12 s.

(C) Time course of one trial. Acquisition refers to the acquisition of scan volumes (TR = 3 s). The volumes extracted for analysis ("target volumes") are highlighted in red in the timeline.

(D) Schematic example of a pseudocontinuous time course concatenated from one continuous acquisition period ("scan"). Face conditions are indicated by the example face. Red, gray, and green indicate threat, neutral, and appease conditions, respectively; a black outline indicates directed gaze. Scrambled blocks always preceded their respective face conditions, but face conditions and presentation of individuals within a block were randomized across scans.

the LEA, which is connected to subcortical regions involved in autonomic regulation [9].

Neocortical Activation to Facial Expressions and Gaze

Activation in the STS was seen for all expressions relative to their scrambled controls (Figure 3, inset), but the location and the magnitude of activation were similar and overlapping for all facial expressions (Figure S1A, left, overlaps in white). No region of STS showed selective activation, for any Expression > Neutral contrast or for one expression relative to the other; however, there was one region within the occipitotemporal sulcus that was active for the Appease > Threat contrast, and for that contrast alone (Table S1 and Figure S1B).

When the stimuli were grouped according to gaze, both groups elicited strong, overlapping responses in STS/IT relative to those for scrambled images (Figure S1A, right, overlaps in white), but these stimuli produced no reliable activation in Directed > Averted or Averted > Directed contrasts (Figure 4, inset).

Coactivation with Other Structures

To examine possible task-dependent interactions between the amygdala clusters and the rest of the brain, we conducted an analysis termed the psychophysiological interaction separately for each cluster (see Supplemental Data). Fluctuations in BLA activity were significantly related to those in the posterior fundus of STS during the face blocks but not scrambled blocks. The coactivated region in STS was located at AP +6, (Figure S2; $T_{max} = 3.88$, 34 voxels at $p < 0.001$). The posterior STS interaction was specific to the BLA; no neocortical regions showed face-specific covariance in activity with LEA activity. Indeed, the BLA has strong bidirectional connections with the STS, whereas the LEA is connected to subcortical regions [9].

Discussion

The amygdala was responsive to faces, regardless of expression. This is consistent with a previous fMRI study of amygdala activation for Face > Scrambled stimuli in anesthetized monkeys [10], as well as findings from electrophysiological studies showing that all major nuclei contain face-selective neurons [11]. Here, the Face > Scrambled contrast resulted in a larger activated region in the amygdala than any expression or gaze contrasts, at equal thresholds. Although numerous studies in humans report preferential activation in the amygdala for emotion-laden as opposed to neutral faces (see [12] for review), other studies show that the amygdala is activated *primarily* to Face > Scrambled images, rather than to emotional faces per se [13–15].

In the present study, emotional faces produced heightened amygdala activation only for Threat > Appease contrasts and only in the BLA cluster of amygdaloid nuclei. Single-unit responses in the monkey amygdala to similar images showed a small but significant increase in the neural-population activity in response to threatening faces compared to neutral and appeasing faces [11]. This modest processing bias in favor of threatening facial expression is often interpreted as a specialization of the amygdala for stimuli with negative valence, but this interpretation is not supported by the reliable activation induced by neutral and appeasing faces compared to phase-scrambled controls (Figure 3B) or the large number of neurons in the amygdala that responded selectively to neutral and appeasing faces [11].

In contrast to the response selectivity of the BLA, the LEA showed stronger BOLD activation for averted than directed gaze, regardless of expression. Given the small size of the LEA relative to the BLA, and the lower spatial resolution afforded by earlier experiments, it is possible that differential activation of these groups of nuclei

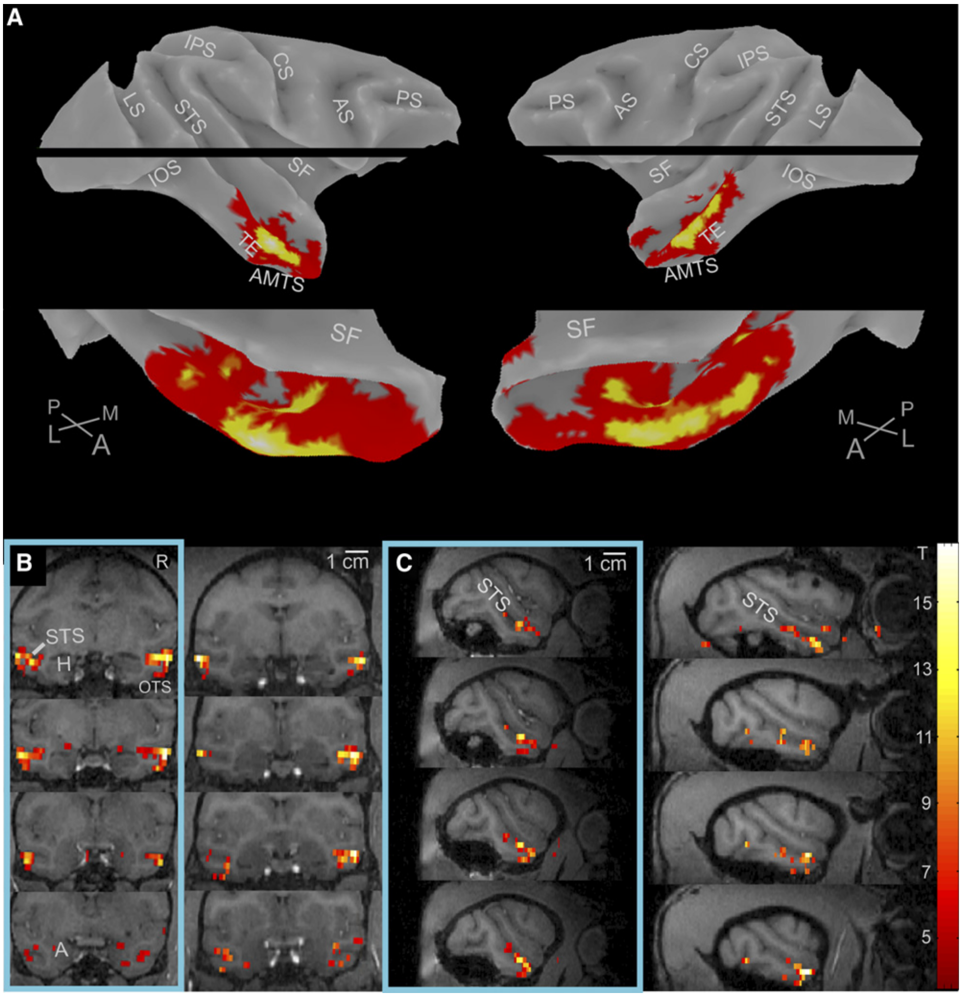

Figure 2. Activation for Faces versus Fourier-Phase-Scrambled Images

(A) The activation for one subject monkey, projected onto the gray-matter-segmented brain ($p < 0.001$, uncorrected, no clustering). The top panel shows the lateral view of each hemisphere; the right hemisphere shown on the left side, with a horizontal bar indicating the approximate dorsal limit of the slices. The bottom panel shows an enlarged perspective into the STS of both hemispheres, revealing the extension of activation into the lower bank of the STS. Temporal-lobe regions of activation described previously for Face > Scrambled or Face > Object contrasts [10, 48, 49] were subsumed by regions of activation shown here, with the present activation extending from about AP +6 to near the temporal pole.

(B) Coronal sections showing activation in both monkeys. Images from the monkey shown in (A) are bounded by a blue box; the right hemisphere is indicated by the "R."

(C) Sagittal sections, running medial to lateral progressing downward, shown for both monkeys. The color bar applies to all sections in this figure. Abbreviations of sulci are as follows: AMTS, anterior medial temporal; AS, arcuate; CS, central; IOS, inferior occipital; IPS, intraparietal; LS, lunate; PS, principal; SF, Sylvian fissure; STS, superior temporal; and OTS, occipitotemporal sulcus. Areas TE, the amygdala (A), and the hippocampus (H) are also labeled.

remained undetected in previous studies. As the main source of autonomic outputs of the amygdala, the LEA is expected to respond to the same stimuli that elicit the strongest skin conductance responses. Indeed, the SCRs for these stimuli were also stronger for gaze-averted faces, suggesting that averted faces are more arousing.

Why Is Averted Gaze More Arousing?

An important role for LEA activity is to initiate exploration of stimuli that are ambiguous and require attention for further evaluation [16]. Stimulation of the central nucleus leads to fast, desynchronized cortical EEG activity, associated with an increased state of attention and vigilance [17, 18]. Similarly, the most commonly reported behavioral consequence of central-nucleus stimulation is heightened attention and orienting behaviors [19], leading to the idea that the central nucleus plays a role in attention and vigilance, in particular, to ambiguous or uncertain stimuli [20, 21]. Whereas the target of facial expression with directed gaze is clear, facial expressions with averted head and eyes require more attention and exploration in order to determine the intended target and the possible consequences for the viewer. Indeed, both human and monkey viewers direct their gaze and attention toward the target of the gaze of the faces they encounter (i.e., joint attention) [22–24]. This type of directed attention in humans was shown to be stronger when viewing fearful or angry than happy or neutral faces [25–27]. These findings are generally consistent with an influence of gaze direction

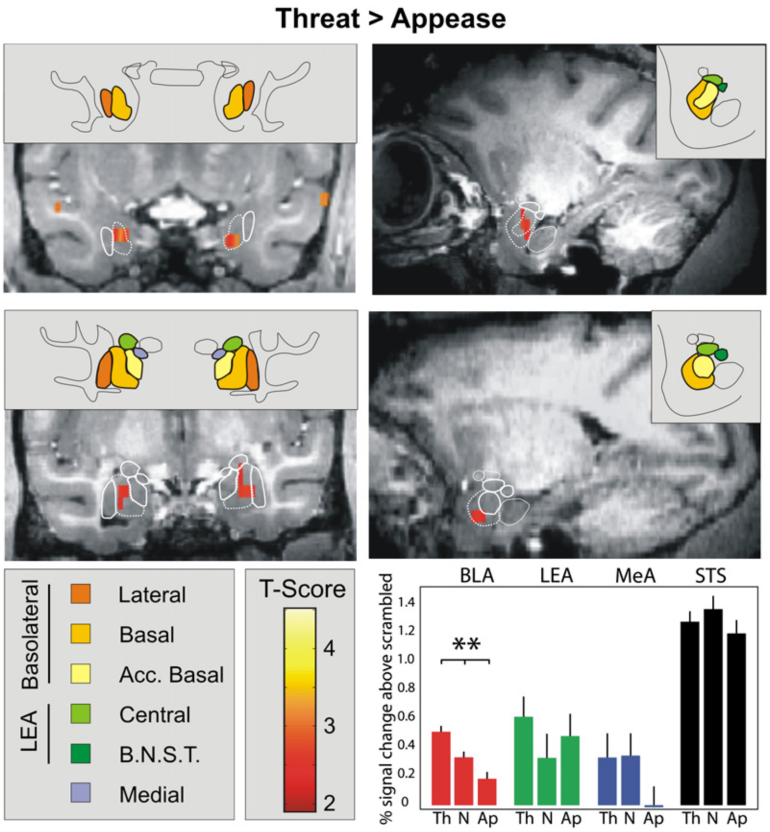

Figure 3. Selective Activation for Threat > Appease Conditions

Coronal (left) and sagittal (right) views from both monkeys, showing activation in amygdaloid nuclei. The legend for the color code is shown in the left inset, with the color map of T scores shown to the right. The color map applies to all images. The bar plot inset shows the percentage of signal change during the face conditions relative to their respective scrambled conditions. Error bars reflect the SEM, $^{**}p < 0.001$. Because BLA responses to face conditions were always stronger than the respective responses to scrambled conditions, the Threat > Appease activation could indicate a strong response to threatening faces or a relatively weak response—but not a deactivation—to appeasing faces. Note that the three amygdala ROIs are based on anatomical subdivisions; the STS ROI is taken from the peak of activation for the Face > Scrambled condition and is therefore expected to show a strong percentage of signal change to faces relative to the scrambled condition.

on processing certain facial expressions [28, 29], and such an influence has been shown to activate the amygdala [30]. Specific comparisons between these human studies and the present results require a better understanding of the significance of facial expressions across species.

Species-Specific Expressions

Macaque gestures are not typically characterized along a positive-negative valence axis, as in the human literature, but along an axis of dominance-submission ([31], see Supplemental Data). Thus, "negative" expressions of fear or anger, in macaques, would fall on opposite ends of the continuum. Although both may indicate some negative encounter, the implications to a perceiving monkey are dramatically different: Directed threat indicates aggression directed toward the perceiver, whereas directed-fear grimace signals a subordinate status and the lack of aggressive intentions toward the perceiver. Add to that the generally aggressive nature of direct gaze and the lack of a "happy" expression in adult macaques, and it becomes difficult to directly

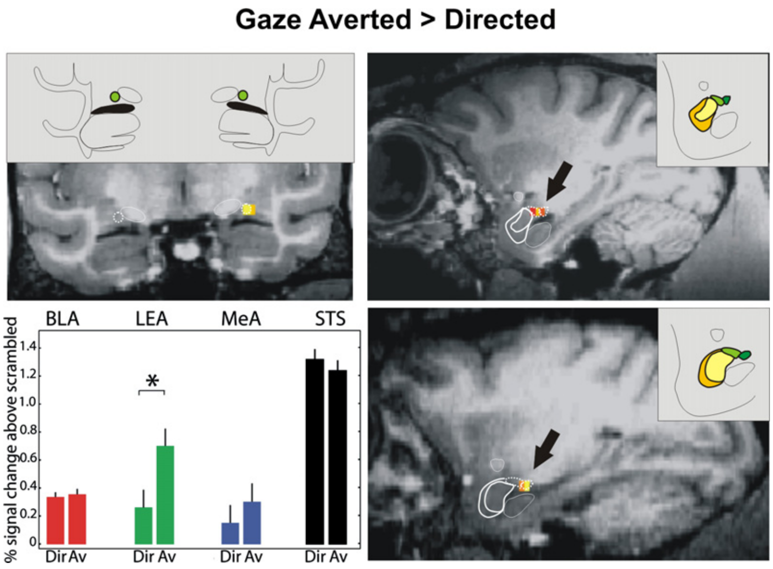

Figure 4. Selective Activation for Averted > Directed Gaze Conditions

Conventions and color map are as shown in Figure 3; error bars are SEM; $^{*}p < 0.01$.

compare the effect of gaze and the expression-specific influence of gaze seen in humans [30, 32, 33] with the present results in monkeys.

Despite the indirect or unknown mapping of expressions across species, factors influencing the salience of expressions may generalize across species. For example, frequently seen expressions may be less salient than infrequent ones [20]. Those regions showing heightened responses to dynamic gestures may also be conserved across species [34]. Finally, homologous structures in humans and monkeys may be involved in the processing of seen or attended compared to unseen or neglected stimuli [35, 36].

A clearer understanding is needed of the utility of expressions in macaques, their dependencies on sender versus receiver status in the group, as well as determinants of changes in salience. This would enable better comparisons to human facial expressions. Nevertheless, the observed dissociation between activity in the BLA and the LEA confirm functional differences in processing two main dimensions of face stimuli such as facial expression and gaze.

Neocortical Responses to Facial Expressions and Gaze

Relative to their scrambled controls, large regions of STS and IT were active for monkey faces bearing various expressions and gaze directions. Responses in these overlapping regions are of similar magnitude, generating no significant activation when any one expression or gaze condition was subtracted from another. This leaves open the following possibilities: (1) The underlying neural responses are not selective for gaze or expression; (2) neurons with similar selectivity are spatially distributed rather than clustered; or (3) neurons with similar response properties are clustered, but these clusters are too small to be detected with the present fMRI resolutions. Prior electrophysiological studies have reported neurons in the STS selective for gaze [37], head position [38–40], or expressions [38, 41]. Combined with the present results, this suggests that selectivity across conditions is distributed or that the clustering for a given condition would be at a submillimeter scale. Use of designs that are sensitive to multiple signal generators within a voxel, e.g., through adaptation designs [42], or algorithms for decoding or classification [43, 44] may prove useful in detecting spatially overlapping groups of selective cells.

The posterior region in the occipitotemporal sulcus (OTS), showed greater activity for the appeasing than threat conditions. This area, TEpv [45], has reciprocal connections with the STS [46] and is situated between the parahippocampal gyrus and lateral visual area TEO, similar to the location of the fusiform gyrus in humans.

Conclusions

Our findings verify electrophysiological observations of the monkey amygdala, reporting selective responses to facial expressions. Neural recording techniques, however, have yet to track simultaneously large numbers of neurons from multiple amygdaloid nuclei in order to establish functional specializations. Here, with high-resolution fMRI, we first confirm the processing bias associated with threatening faces and further localize that bias to the BLA region. Moreover, a dissociation of activation is seen between the BLA and the LEA, with the latter showing a greater BOLD response to averted-gaze than directed-gaze faces. Independent measures of arousal, in conjunction with studies on joint attention, indicate that the averted-gaze stimuli may trigger reallocation of attention. This functional dissociation might explain why the amygdala has been associated not only with the evaluation of threatening social stimuli but also with attention and arousal.

Experimental Procedures

Procedures are described in Figure 1 and in the Supplemental Data. In brief, two socially housed male rhesus macaques (*Macaca mulatta*) were implanted with custom-fitted cranial head posts under sterile surgical conditions [10] with the approval of local authorities (Regierungspräsidium) and in accordance with the guidelines of the European Community (EU VD 86/609/EEC) for the care and use of laboratory animals.

Static face images were obtained from video footage of 12 unfamiliar, socially housed monkeys at the California National Primate Research Center in Davis, CA [47]. The 12 monkeys were selected on the basis of their presentation of unambiguous threatening (open-mouth stare), appeasing (fear grimace or lipsmack), and neutral facial expressions in both directed and averted gaze and head positions. The criteria defining facial expressions were described previously [47] based on an extensive literature detailing the characteristic facial expressions of macaques. Each monkey contributed six face stimuli: one for each combination of gaze and expression condition (Figure 1A). Fourier-phase-scrambled images were then constructed from each face stimulus (Figure 1A). Blocks of scrambled images were interleaved with blocks of face images. Each stimulus monkey contributed one image per 12-image block, and all images in one face block were of the same condition.

Structural images (3D MDEFT images at 0.5 mm isotropic voxels) and functional images (eight-segment GE-EPI at 1 × 1 mm in-plane voxel resolution) were obtained from a vertical 4.7 T magnet (Bruker, Ettlingen, Germany). With statistical parametric mapping software (SPM2; Wellcome Department of Imaging Neuroscience, London, UK; http://www.fil.ion.ucl.ac.uk/spm), data from each monkey were analyzed separately in a fixed-effects analysis across all sessions. This included a separate set of regressors for each session (M1: five sessions; M2: two sessions; with 114 blocks completed per session, on average). Analyses used t contrasts between a given face condition against its respective scramble, with no constraints on cluster size. In addition, based on ROI time courses, 2 × 3 ANOVAs were run for the gaze and expression conditions, respectively. Note for each ROI, the activation across the scrambled conditions did not differ (2 × 3 ANOVA, $p > 0.40$ for gaze and expression main effects as well as for interactions in each ROI).

Skin conductance responses were recorded from two monkeys trained to passively view the 72 face stimuli. Data were pooled across 11 repetitions distributed over six recording sessions in monkey 1 and eight repetitions over seven recording sessions in monkey 2, producing an average SCR for each of the 72 images shown.

Supplemental Data

Supplemental Data include additional Experimental Procedures, two figures, and two tables and are available with this article online at http://www.current-biology.com/cgi/content/full/17/9/766/DC1/.

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