Perception of emotional expressions is independent of face selectivity in monkey inferior temporal cortex

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The ability to perceive and differentiate facial expressions is vital for social communication. Numerous functional MRI (fMRI) studies in humans have shown enhanced responses to faces with different emotional valence, in both the amygdala and the visual cortex. However, relatively few studies have examined how valence influences neural responses in monkeys, thereby limiting the ability to draw comparisons across species and thus understand the underlying neural mechanisms. Here we tested the effects of macaque facial expressions on neural activation within these two regions using fMRI in three awake, behaving monkeys. Monkeys maintained central fixation while blocks of different monkey facial expressions were presented. Four different facial expressions were tested: (*i*) neutral, (*ii*) aggressive (open-mouthed threat), (*iii*) fearful (fear grin), and (*iv*) submissive (lip smack). Our results confirmed that both the amygdala and the inferior temporal cortex in monkeys are modulated by facial expressions. As in human fMRI, fearful expressions evoked the greatest response in monkeys— even though fearful expressions are physically dissimilar in humans and macaques. Furthermore, we found that valence effects were not uniformly distributed over the inferior temporal cortex. Surprisingly, these valence maps were independent of two related functional maps: (*i*) the map of "face-selective" regions (faces versus non-face objects) and (*ii*) the map of "face-responsive" regions (faces versus scrambled images). Thus, the neural mechanisms underlying face perception and valence perception appear to be distinct.

amygdala | emotion | valence | fMRI

Faces are complex stimuli that convey information not only about an individual's identity, but also about the individual's emotional state. For instance, in monkeys a fearful expression could indicate a nearby predator, whereas a lip smack expression could reflect social submission. Thus, the interpretation of facial expressions is crucial for both individual and group survival. However, the neural bases underlying the recognition of facial expression remain unclear.

Lesion studies in both humans and monkeys suggest that the amygdala plays a key role in both the recognition of facial expressions (1) and the production of behavioral responses to emotional stimuli (e.g., refs. 2–4). Numerous functional MRI (fMRI) studies in humans have shown enhanced responses to faces with emotional valence (e.g., greater responses to fearful relative to neutral faces) in both the amygdala and visual cortex (e.g., refs. 5–9; for a review see refs. 10 and 11). As in the human fMRI studies, several single-unit studies in monkeys have reported modulation of amygdala responses by viewing facial expressions (e.g., refs. 12–15). A few single-unit studies also examined the effects of facial expressions in the inferior temporal (IT) cortex, including the superior temporal sulcus (STS) (16–18), and found that some neurons were also modulated by facial expression.

Surprisingly, a recent fMRI study in monkeys showed virtually no effect of facial expression within the ventral visual pathway, even though valence effects were found in the amygdala (19). Conceivably, this lack of effect in IT cortex could indicate that few neurons are modulated by facial expressions in monkey IT cortex, relative to its human counterpart. Alternatively, neurons showing valence effects in monkey IT cortex may be widely distributed and therefore not easily detectable using fMRI.

Thus, it was important to reexamine whether it is possible to use fMRI to reveal valence modulation in monkeys. A positive finding would resolve the currently discrepant fMRI results between humans and monkeys, thus allowing subsequent clarification of fMRI results using classical invasive techniques (e.g., ref. 20). A specific goal here was to reexamine valence effects within monkey IT cortex using fMRI, comparing regions selective for faces (relative to non-face objects) with those responsive for faces (relative to scrambled images). In both humans and monkeys, the former contrast is the standard measure for face selectivity (e.g., refs. 21–23) whereas the latter isolates only regions that are activated by objects versus non-objects. Of course, the object category includes faces, but, because most objects are non-faces, this comparison is much less functionally specific as compared with face selectivity (e.g., refs. 24–26). A further goal was to compare valence effects in monkey visual cortex with those observed in the amygdala.

Results

We scanned three awake, fixating monkeys while they viewed blocks of four different monkey facial expressions (neutral, threat, fear grin, and lip smack) and scrambled faces (Fig. 1*A*). The imaged region included the entire temporal lobe and the amygdala (e.g., Fig. 1*C*). Typically, posterior regions of visual cortex (including V1–V4) and the frontal lobe were not covered.

Perception of Faces: "Face-Responsive" Versus "Face-Selective" Regions. Relative to scrambled images, the images of neutral faces elicited widespread activation throughout the temporal cortex as well as in the amygdala in all three monkeys. As described above, these regions were defined as face-responsive. As illustrated in Fig. 2, this face-responsive activation extended bilaterally along IT cortex, including STS and the IT gyrus, as well as in the lunate and the inferior occipital sulci. In monkey E (in which the imaged volume included more anterior regions) face-responsive activation was also found in prefrontal cortex, within the left inferior bank of the arcuate sulcus, and in the lateral portion of the orbitofrontal cortex. In all monkeys, the strongest face-responsive activation was consistently elicited anteriorly within area TE, at the level of the anterior middle temporal sulcus, and posteriorly within STS, proximal to the anterior tip of the
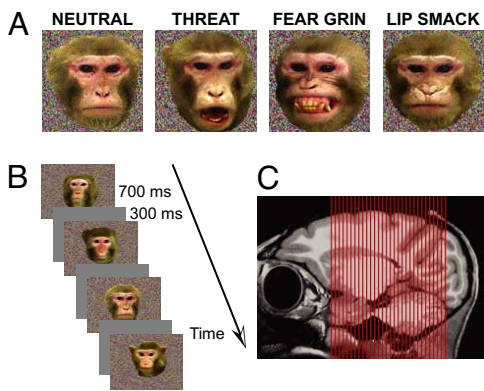
Fig. 1. Stimulus conditions and fMRI coverage. (*A*) Examples of the different facial expressions tested. (*B*) Within each block, each image was presented for 700 ms followed by a mask for 300 ms. Four facial expressions were presented from each of eight different monkeys. (*C*) Sagittal view of a monkey anatomical scan illustrating the typical location of the slices (in red).

posterior middle temporal sulcus (red regions in Fig. 2). Additionally in monkey E, strong face-responsive activation was found in the posterior visual cortex, within both the lunate and the inferior occipital sulci.

We also mapped the activation produced in monkeys E and R by the presentation of neutral faces relative to non-face objects [black outlines in Fig. 2, see supporting information (SI) Fig. 6]. These regions were defined as being face-selective. Consistent with prior fMRI studies (20–22), we found two face-selective regions ("patches") within IT cortex: (*i*) an anterior face patch, located in area TE, and (*ii*) a posterior face patch, located posteriorly, near/within area TEO (27). As in previous studies,

the anterior face patch was smaller and less robust than the posterior face patch; in two of four hemispheres mapped the anterior patch was not statistically significant.

Effect of Facial Expression in Face-Responsive and Face-Selective Regions Within IT Cortex. Within IT cortex we examined the effect of facial expression in both face-responsive and face-selective regions, using size-matched regions of interest (ROIs) in each region, independently in monkeys E and R (Fig. 3). Face-selective regions could not be mapped in monkey B for technical reasons. In each hemisphere, two face-selective ROIs were selected, one anterior and one posterior; as a control comparison two nearby face-responsive ROIs were also selected (see *Materials and Methods*). An ANOVA with repeated measures tested for the effects of (*i*) ROI selectivity (two levels corresponding to face-selective and face-responsive); (*ii*) ROI location (two levels corresponding to anterior and posterior); (*iii*) expression (four levels corresponding to the different expressions); and (*iv*) the interaction between the different factors. In both monkeys, a main effect was found for ROI selectivity [$F_{1-37} = 20.0$, $P < 0.001$; $F_{1-31} = 184.3$, $P < 0.001$ (for monkeys E and R, respectively)]; a stronger response was found to all faces within the face-selective ROIs as compared with the face-responsive ROIs. A main effect of ROI location was found only for monkey E ($F_{1-37} = 7.7$, $P = 0.009$); a stronger response was found for all faces in the anterior face-selective ROI compared with that in the posterior face-selective ROI. Additionally, a main effect of expression was found for both animals [$F_{3-111} = 5.6$, $P = 0.001$; $F_{3-93} = 3.0$, $P = 0.033$ (for monkeys E and R, respectively)]; the fear grin expressions consistently elicited a greater response relative to the neutral expressions. A significant interaction was also found between ROI selectivity and expression for both animals [$F_{3-111} = 3.6$, $P = 0.02$; $F_{3-93} = 5.4$, $P = 0.003$ (for
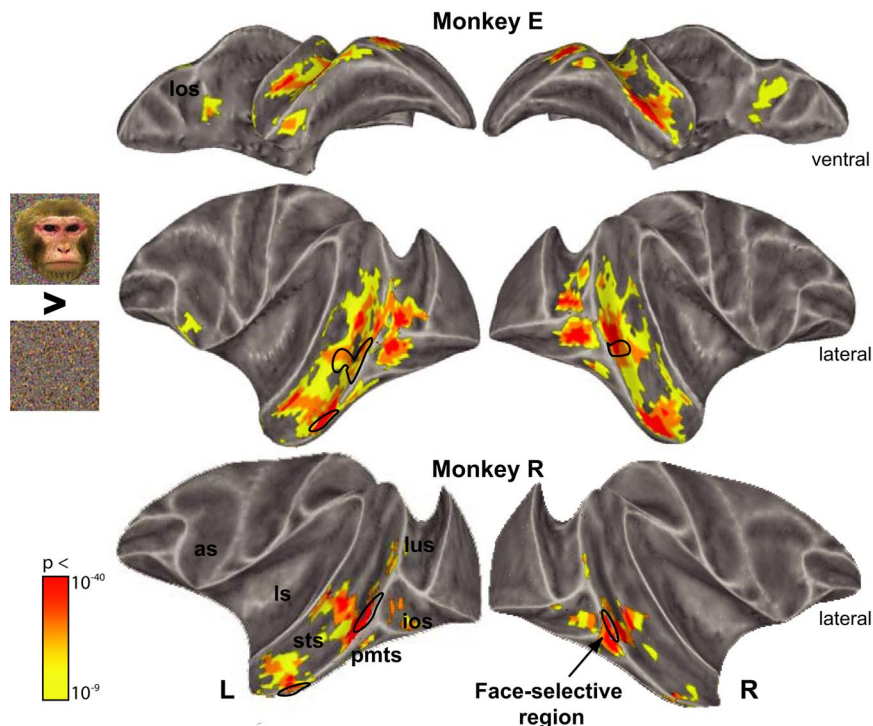
Fig. 2. Face-responsive versus face-selective regions. Lateral and ventral inflated views show face-responsive regions and face-selective regions in both hemispheres from monkeys E and R. Face-responsive regions were defined as those showing significantly greater activation for neutral faces relative to scrambled faces (shown in yellow/red), whereas face-selective regions were defined as those showing greater activation for neutral faces relative to non-face objects (outlined in black). The frontal lobe was imaged only in monkey E. as, arcuate sulcus; ios, inferior occipital sulcus; ls, lateral sulcus; los, lateral orbital sulcus; lus, lunate sulcus; pmts, posterior middle temporal sulcus; sts, superior temporal sulcus.

Fig. 3. Amplitude of valence effect within face-responsive and face-selective regions of IT cortex. The percent signal change is show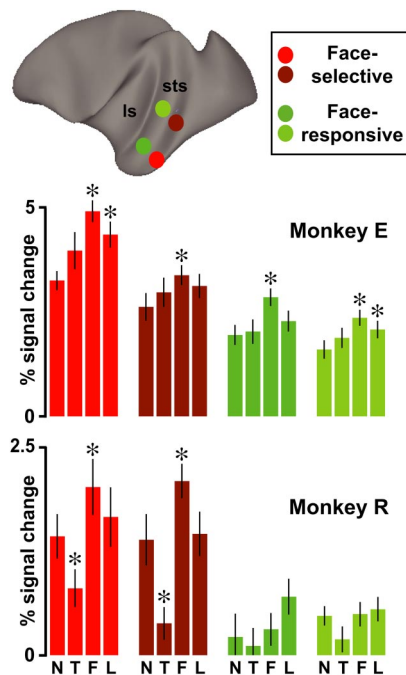n for the different facial expressions within two face-selective and two face-responsive ROIs in the left hemispheres of monkeys E and R. The lateral view illustrates the approximate location of the selected ROIs. For both the face-selective and face-responsive regions, the histograms on the left indicate activations in the anterior ROIs, whereas the histograms on the right indicate activations in the posterior ROIs. All ROIs were equated in size. Asterisks indicate significant differences relative to the neutral condition for each ROI ($P < 0.05$; errors bars indicate the SEM). N, neutral; T, threat; F, fear grin; L, lip smack.

monkeys E and R, respectively)]; the modulation by fear grin expressions was greater within the face-selective ROIs as compared with face-responsive ROIs. In addition, some idiosyncratic effects were found across animals; monkey R showed a significantly decreased response to open-mouthed threats (relative to neutral, $P < 0.05$), whereas monkey E did not. However, all six hemispheres in our sample showed the largest fMRI increase in response to fear grins relative to neutral expressions (see SI Fig. 7 for monkey B).

In addition to examining valence effects within these specific ROIs, we also mapped the distribution of valence effects across the full expanse of IT cortex. Specifically, we measured the difference in the fMRI signal evoked by any facial expression (e.g., threat, fear grin, or lip smack) relative to the neutral facial expression, within all face-responsive and face-selective regions. The resulting maps showed that the valence effect was not distributed uniformly across IT cortex (Fig. 4A). Moreover, although face-selective regions (black outlines in Fig. 4A) sometimes showed strong valence effects (e.g., the anterior face patch in the left hemisphere of monkey E), just as often they did not (e.g., the posterior face patches in the right hemispheres of both monkeys E and R).

To quantify this relationship further, we calculated the correlation between the magnitude of the valence effect relative to the magnitude of either (i) face selectivity (face > object) or (ii) face responsivity (face > scrambled) in a voxel-by-voxel manner, averaged across both animals (Fig. 4B). These tests revealed that none of the three maps (valence, face selectivity, or face responsivity) was significantly correlated with any of the other maps (Fig. 4B). Thus, the voxels showing the strongest face-selective or face-responsive variation did not correspond to the voxels with the highest valence modulation, except by chance covariation. Even when valence modulation was calculated based solely on fear grins (the expression that produced the strongest response), no correlation emerged. Thus, in IT cortex, the map of valence variations is apparently independent of the maps of variations in face selectivity and face responsivity.

Effect of Facial Expression Within the Amygdala. We also found face-responsive regions in the amygdala, located bilaterally within the dorsal portion of the basal and the lateral nuclei of the amygdala, in all three animals (Fig. 5 A and B). However, no statistically significant amygdala activation was found when using the more stringent standard of face selectivity.

Fig. 5C shows the amygdala responses to the different facial expressions from the right hemisphere of monkey B (see also SI Fig. 8). The fear grin expression evoked significantly greater activation than the neutral expression across all animals (significant effect within each hemisphere for each animal, $P < 0.05$). This response profile resembled that found in the visual cortex (described above), although the response magnitude was considerably smaller in the amygdala (see SI Fig. 8).

Discussion

Valence Effects in IT Cortex. Using fMRI in monkeys we demonstrated that the perception of facial expression modulates activity in some subregions of IT cortex, confirming fMRI findings in humans (5–9) and single-unit studies in monkeys (16–18). Our results extend recent findings from Hoffman et al. (19), who also used fMRI in monkeys; that earlier study showed a valence effect in amygdala but virtually none in the visual cortex. Although we cannot explain this discrepancy, it could be due to technical differences in the two studies (e.g., higher contrast/noise due to MION versus BOLD, different amounts of signal averaging).

Interestingly, we found that the valence modulation was not uniformly distributed; instead it varied across IT cortex. Furthermore, this valence modulation was not simply overlaid on previously described functional maps of either face selectivity (2, 21) or face responsivity (e.g., refs. 24–26). In other words, in IT cortex, the voxels that showed the greatest difference between faces and non-face objects or between faces and scrambled images were not necessarily those that showed the greatest valence modulation. Even the voxels that showed the highest selectivity for faces (faces > objects) were not simply the more activated voxels in the map of face responsivity (faces > scrambled images). The mutual independence of these maps strongly suggests that there are correspondingly independent neural mechanisms underlying face perception, valence perception, and object perception.

Does the Amygdala Modulate IT Activity? As reported previously (e.g., refs. 12, 15, and 19), we found face-responsive regions in the amygdala in the dorsal part of the lateral nucleus, extending into the basal nucleus. The fMRI signal in these nuclei was modulated by facial expressions, consistent with prior single-unit studies (e.g., refs. 12 and 15) and one recent fMRI study (19).

Neuroanatomical studies in monkeys have revealed that visual information reaches the amygdala through the ventral ("object recognition") pathway, which projects from the primary visual cortex (V1) through multiple extrastriate areas to area TE within the anterior IT cortex. Information from area TE then projects to the amygdala, mainly to the lateral nucleus (28, 29). Feedback projections from the amygdala arise mainly from the basal nucleus and terminate in virtually all areas of the ventral visual pathway, including V1.

It has been proposed that the valence effects evoked in human visual cortex by fearful faces reflect feedback signals generated in the amygdala (7, 30), and our results are consistent with this

NEUROSCIENCE

Fig. 4. Map of valence effects throughout IT cortex. (*A*) Lateral inflated views of the left and right hemispheres of monkeys E and R, showing the magnitude of the valence effect within the face-selective regions (outlined in black) and the more extensive face-responsive regions. The significance of the valence effect reflects the difference in the fMRI signal of any facial expression relative to the neutral expression (i.e., threat versus neutral or fear grin versus neutral or lip smack versus neutral). (*B*) Correlation between valence effect and either face responsivity (*Left*) or face selectivity (*Right*) across monkeys E and R.

model. First, the valence effect found in the visual cortex resembled that found in the amygdala, with fear grins producing the strongest response in all six hemispheres tested. Second, activation in the amygdala was localized within the nuclei receiving input from or projecting to the visual cortex (28, 29). Direct support for this view comes from a recent fMRI study showing that valence effects were absent within face-responsive regions of the visual cortex in patients with extended amygdala

Fig. 5. Valence effect within the amygdala. (*A*) Coronal section illustrating face-responsive regions within the amygdala for all three animals. (*B*) Magnified view of the amygdala activation and schematic representation of the amygdala nuclei. The face-responsive regions were found bilaterally in the basal and lateral nuclei of the amygdala in all animals. (*C*) Percent signal change within face-responsive regions in the amygdala in one hemisphere of one monkey, evoked by the perception of facial expressions. Asterisks indicate that fear grin elicited a greater response than the neutral expression. AB, accessory basal nucleus; B, basal nucleus; CE, central nucleus; L, lateral nucleus; M, medial nucleus; N, neutral; T, threat; F, fear grin; L, lip smack.

lesions (31). However, it remains unclear exactly how these valence effects influence visual cortical processing.

Social Cognition in Primates. Monkey studies of facial expression have compared the effects of open-mouthed threat versus "appeasing/submissive" expressions (e.g., refs. 16–19). In those earlier studies, fear grin expressions were not systematically tested (17, 18)—or, when tested, fear grins were averaged together with lip smack expressions (19). This is indeed appropriate if variations in macaque facial expression are graded along the axis of dominance–submission. However, lip smack could instead be considered an affiliative behavior, whereas fear grin could be an avoidance response, based on a classification along three axes: dominance, avoidance, and affiliation (32–34).

Here, open-mouthed threat produced varied responses across animals. Such individual differences in the pattern of "threat" modulation suggest that different animals may perceive distinct expressions according to their level in the social hierarchy. By contrast, fear grin consistently elicited the greatest response across animals, within both IT cortex and the amygdala—analogous to the consistently enhanced response to fearful faces in human fMRI. Although fear grins in monkeys and fearful human expressions are physically dissimilar, they presumably convey similar emotional states. Such increased activity in response to facial expressions could reflect the ambiguity related to the fear-inducing situations (35, 36). Angry human faces (as in open-mouthed threat in monkeys) provide information about both the presence and the source of a threat, whereas fearful faces provide information about the presence of threat but not its source. Thus, a stronger neural response to fearful faces would presumably reflect greater attentional engagement to select the most appropriate behavioral response (35, 36).

Materials and Methods

Subjects and General Procedures. Three male macaque monkeys were used (*Macaca mulatta*, 3–5 years, 3–5 kg). All procedures were in accordance with Massachusetts General Hospital guidelines and are described in detail elsewhere (37, 38). Briefly, each monkey was surgically implanted with a plastic head post under anesthesia. After recovery, monkeys were trained to sit in a sphinx position in a plastic restraint barrel (Applied Prototype) with their heads fixed, facing a screen on which visual stimuli were presented. During MR scanning, gaze location was monitored by using an infrared pupil tracking system (ISCAN).

Stimuli and Task. Stimuli were presented by using a custom Matlab (Mathworks) program, including PsychToolbox, and displayed via a LCD projector (Sharp model XG-NV6XU) onto a back-projection screen positioned within the magnet bore. All stimuli used in this experiment were colored images of macaque faces, ≈25° wide. Images were acquired from eight unfamiliar monkeys (i.e., eight identities), each with four different expressions in frontal view (Fig. 1*A*): (*i*) neutral, (*ii*) aggressive (open-mouthed threat), (*iii*) fearful (fear grin), and (*iv*) submissive (lip smack) (39).

Stimuli from each condition were presented in blocks of 40 s each. These block conditions included the four different emotional expression conditions listed above (equated for the eight identities), a fixation condition (gray background), and scrambled faces (mosaic scrambled and Fourier phase scrambled). Each stimulus was presented for 700 ms and was followed by a 300-ms mask period (Fig. 1*B*). Each image was presented five times per block, with a total of 40 images presented per block. The order of blocks was randomized across runs. Each stimulus was overlaid with a small (0.2°) central fixation point, which the monkeys were required to fixate to receive a liquid reward. In the reward schedule, the frequency of reward increased as the duration of fixation increased (e.g., refs. 21, 37, and 38).

We also mapped the location of face-selective regions in two animals (monkeys E and R) in a separate study. In those experiments, each block was devoted to one of four visual stimulus categories: neutral faces, body parts, objects, and places. Each block lasted 32 s, during which each of 16 images (≈22 × 22°) was presented for 2 s.

Scanning. Before each experiment, an exogenous contrast agent [monocrystalline iron oxide nanocolloid (MION)] was injected into the femoral vein (7–11 mg/kg) to increase the contrast/noise ratio and to optimize the localization of fMRI signals (37, 38). Imaging data were collected by using a 3-T Allegra scanner (Siemens) and a single-loop, send/receive surface coil. Functional data were obtained by using a multiecho gradient echo sequence, i.e., using two echoes with alternating phase-encoding direction: TR, 4 s; TE, 30/71 ms; flip angle, 90°; field of view (FOV), 96 mm; matrix, 64 × 64; voxel size, 1.5 mm isotropic; 28 coronal slices (no gap). For monkey E, the FOV was reduced to 80 mm to increase the spatial resolution (1.25 mm isotropic), but all other scanning parameters remained constant.

In separate scan sessions, high-resolution anatomical scans were obtained from each monkey under anesthesia (3D MPRAGE; TR, 2.5 s; TE, 4.35 ms; flip angle, 8°; matrix, 384 × 384; voxel size, 0.35 mm isotropic). These anatomical scans were used as an underlay for the functional data and to create anatomical ROIs. Inflated cortical surfaces were also created from these scans by using FreeSurfer (40, 41).

Data Analysis. Functional data were analyzed by using AFNI (42). Images were realigned to the first volume of the first session, for each subject, and spatially smoothed by using a 2-mm full-width half-maximum Gaussian kernel. Signal intensity was normalized to the mean signal value within each run. A total of 3,720, 3,360, and 3,720 volumes were collected and analyzed for monkeys E, R, and B, respectively, across two scan sessions per monkey. Data were analyzed by using a general linear model and a MION kernel to model the hemodynamic response function (35). The different facial expressions and the scrambled conditions were used as regressors of interest. Regressors of no interest included baseline, movement parameters from realignment corrections, and signal drifts (linear as well as quadratic). Note that all fMRI signals throughout the article have been inverted so that an increase in cerebral blood volume is represented by an increase in signal intensity. We identified brain regions that responded more strongly to neutral faces compared with scrambled images (face-responsive regions) or compared with objects (face-selective regions). Statistical maps were thresholded to at least $P < 10^{-9}$ uncorrected and overlaid onto anatomical scans and/or inflated cortical surfaces.

Analysis of Activity in Face-Responsive and Face-Selective Regions of Interest. One main goal was to compare the activity produced by different expressions within face-responsive and face-selective ROIs. We defined ROIs of ≈30 (±5) voxels each within both face-responsive and face-selective regions. Within the face-selective regions, the ROIs corresponded to a spherical mask surrounding the peak activation. For the face-responsive regions, we chose regions medial to both face-selective regions (one anterior and one posterior) within the STS and generated an ROI of the same size. The percent signal change was extracted from these ROIs. Specifically we calculated a response for each block and averaged these values over the ≈35 presentation blocks for each condition. We performed an ANOVA with three levels, testing for the effect of ROI selectivity (responsive/selective), ROI location (anterior/posterior), and expression (neutral, threat, fear grin, and lip smack), followed by multiple paired *t* tests and tests for interactions. Analogous tests were performed in the amygdala by using only a single ROI (the face-responsive region in the anatomically defined amygdala).

Valence Effects Within Face-Responsive and Face-Selective Regions. To further examine the effect of valence across face-responsive and face-selective regions, statistical maps were created for monkeys E and R, which reflected any difference in the fMRI signal between neutral versus threat, neutral versus fear grin, or neutral versus lip smack expressions. We then tested the relationship between valence effects and either face responsivity or face selectivity on a voxel-by-voxel basis using Pearson correlations. Valence effects corresponded to the sum of any absolute difference of any expression (threat, fear grin, or lip smack) relative to neutral expressions. Data from both animals were equated for the number of voxels sampled and grouped together for this analysis.

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