Activation of the Visual Cortex in Motivated Attention

Margaret M. Bradley, Dean Sabatinelli, Peter J. Lang, Jeffrey R. Fitzsimmons,
Wayne King, and Paramtap Desai
University of Florida

Functional activation (measured with fMRI) in occipital cortex was more extensive when participants view pictures strongly related to primary motive states (i.e., victims of violent death, viewer-directed threat, and erotica). This functional activity was greater than that observed for less intense emotional (i.e., happy families or angry faces) or neutral images (i.e., household objects, neutral faces). Both the extent and strength of functional activity were related to the judged affective arousal of the different picture contents, and the same pattern of functional activation was present whether pictures were presented in color or in grayscale. It is suggested that more extensive visual system activation reflects "motivated attention," in which appetitive or defensive motivational engagement directs attention and facilitates perceptual processing of survival-relevant stimuli.

In a recent functional magnetic resonance imaging (fMRI) study, we found that viewing affective pictures (either pleasant or unpleasant) resulted in more extensive activity in visual cortex, compared with viewing neutral pictures (Lang, Bradley, Fitzsimmons et al., 1998). These effects were particularly clear in secondary association areas (Brodmann Areas 18 and 19) and in fusiform gyri. Similar blood oxygen level-dependent (BOLD) effects in the visual system—greater for emotional than neutral stimuli—have also been found by others using fMRI (Breiter et al., 1996; Knight, Smith, Stein, & Helmstetter, 1999; LaBar et al., 2001; Sprengelmeyer, Rausch, Eysel, & Przuntek, 1998), as well as positron emission tomography (PET; Fredrikson et al., 1993; Fredrikson, Wik, Annas, Ericson, & Stone-Elander, 1995; Lane et al., 1997; Reiman et al., 1997; Taylor, Liberzon, & Koeppe, 2000). Increased activation in visual cortex also occurs when participants are simply asked to imagine, rather than view, emotional stimuli, suggesting that these effects are primarily mediated by affective factors, rather than by sensory or perceptual differences (Kosslyn, Shin, Thompson, & McNally, 1996; Pietrini, Guazzelli, Brasso, Jaffe, & Grafman, 2000).

Blood flow-based effects are consistent with data from electroencephalographic (EEG) studies of cortical activity during picture processing. Event related potentials (ERPs) measured during viewing of affective and neutral pictures clearly vary with emotional arousal (Cacioppo, Crites, & Gardner, 1996; Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000). When source localization techniques were conducted on data from dense electrode EEG arrays, greater dipole strength was found for picture stimuli judged to be high in emotional arousal, compared with less affectively engaging pictures (Junghoefer, Bradley, Elbert, & Lang, 2001). The primary dipole sources defining these electrophysiological differences were in occipital and occipital–parietal cortical areas, and these effects were independent of formal factors of the picture stimuli, such as color, brightness, and various measures of stimulus complexity.

One explanation for these findings is that increased functional activity in the visual cortex is a direct effect of emotional engagement. Here, we consider emotion to be fundamentally organized by two motivational systems, one appetitive and one defensive, that have evolved to mediate transactions in the environment that either promote or threaten physical survival (Lang, Bradley, & Cuthbert, 1997). These systems are presumed to be evolutionarily old, shared across the mammalian species, and implemented by neural circuits in the brain with common outputs to structures mediating the somatic and autonomic physiological systems involved in emotion and attention (see Davis, 1998; Davis & Lang, 2003; Fanselow, 1994; LeDoux, 1990). The defense system is primarily activated in contexts involving threat, with a basic behavioral repertoire built on withdrawal, escape, and attack. Conversely, the appetitive system is activated in contexts that promote survival, including sustenance, procreation, and nurturance, with a basic behavioral repertoire of ingestion, copulation, and care-giving.

Multivariate studies have consistently shown that the principal variance in emotional meaning is accounted for by two factors: hedonic valence (pleasure) and arousal (Mehrabian & Russell, 1974; Osgood, Suci, & Tannenbaum, 1957; Smith & Ellsworth, 1985). In the current view, these factors are seen as parameters of motivational activation. Thus, judgments of hedonic valence (e.g., pleasure/displeasure) indicate which motivational system is active

(e.g., appetitive or defensive), and judgments of arousal indicate the intensity of motivational activation.

Motivationally relevant stimuli (i.e., those that strongly activate either the appetitive or defensive system) initially engage attentional processes, which facilitates perceptual encoding and recognition in sensory systems. A considerable body of research with animal subjects supports this view: For example, when exposed to a predator or other aversive cue, an animal normally stops moving ("freezes"), orients toward the threat stimulus, and shows a variety of reflex behaviors—autonomic and somatic—that appear to facilitate sensory intake. According to several investigators (Davis, 1998; Kapp, Whalen, Supple, & Pascoe, 1992; LeDoux, 1990), this response complex is orchestrated by a neural circuit initiated when relevant sensory input activates the basolateral nuclei of the amygdala. Furthermore, as Amaral and colleagues (Amaral, Price, Pitkanen, & Carmichael, 1992, pp. 44–45) have noted, the amygdala in primates "projects to virtually all levels of the visual cortex," and amygdalopedal projections reciprocate, closing a potentially reverberating "processing loop." Given this neural circuit, once an organism is motivationally engaged, heightened and sustained activation could be expected to occur widely in the visual system.

Measures of the peripheral physiology (autonomic and somatic) during affective perception in humans are similar to those evoked in the motive states of animals, suggesting that the same motivational circuits are activated. For example, "fear bradycardia" (associated with amygdala activation, Kapp, Frysinger, Gallagher, & Haselton, 1979) is observed in most animals when they attend to a threatening, aversive cue. A similar bradycardia is found in humans viewing emotionally unpleasant picture stimuli (Bradley, Codispoti, Cuthbert, & Lang, 2001). Furthermore, when abrupt acoustic probes are presented to animals during exposure to an aversively conditioned stimulus, the defensive startle reflex is potentiated (mediated by projections from the central nucleus of the amygdala; Davis, 1989). A similar enhanced startle response is found in aversively conditioned humans (e.g., Greenwald, Bradley, Cuthbert, & Lang, 1998) and in humans viewing emotionally arousing, unpleasant pictures (e.g., Bradley et al., 2001).

In the present research, we assessed the extent to which stimuli that strongly engage the primary motivational states (e.g., arousing images of viewer-directed threat and sexually evocative scenes) might be responsible for the broad activation of the visual system previously observed in participants viewing emotional pictures. Thus, picture contents were selected that varied in rated arousal, presumably reflecting the strength of activation in either appetitive or defensive systems. Scenes of threat, mutilation, and erotica prompt the strongest emotional reactions in cardiovascular, electrodermal, and reflex responses (Bradley et al., 2001), and they were compared here to less emotionally arousing pictures depicting families, angry faces, neutral faces, and objects. These picture contents allowed us to assess a number of specific comparisons related to motivational intensity:

1. Erotic pictures are generally rated higher in emotional arousal (a theoretical correlate of motivational intensity) than pictures of happy families, but these contents are essentially equivalent in judged hedonic valence (based on normative ratings data; Lang, Bradley, & Cuthbert, 1999). Presuming that it is the intensity of motivational activation that determines increased perceptual processing, it was predicted that erotic scenes would prompt more

extensive activation of the visual system than pictures of happy families.

2. Attack by a predator and evidence of the death and mutilation of a species member are both expected to strongly engage defensive motivation. Pictures depicting attack by an animal or human have consistently prompted startle reflex potentiation similar to that observed when animals or humans are exposed to stimuli that augur electric shock or other painful consequences (Balaban & Taussig, 1994; Bradley et al., 2001). Hebb (1949) early noted that primates react to a representation of mutilation (i.e., a model of a severed monkey head) with fear, agitation, and avoidance. When viewing pictures of mutilated bodies, humans show marked psychophysiological reactions, and report strong negative affective arousal (Bradley et al., 2001). Thus, greater visual system activation was anticipated for these threatening stimuli compared with other, less arousing unpleasant input (e.g., angry faces).

3. Assuming that both strong appetitive and strong defensive system engagement similarly enhance goal-oriented attention and perceptual processing, it was anticipated that functional activity when viewing erotica and attack–mutilation pictures would not differ but would both show similar, broad activation of visual cortex that was greater than that shown for less arousing picture contents.

4. To determine the extent to which the presence of color might account for increased visual system activation to motivationally relevant stimuli (e.g., the predominance of red in pictures of mutilated bodies and erotica), the pictures were presented in grayscale for one group of participants and in color for a second group. If color enhances the BOLD effect of individual picture contents, effects of emotional content would be minimal when viewing pictures in grayscale.

For comparison and replication purposes, activity in the visual cortex was assessed with the same blocked design used in a previous study (Lang et al., 1998), in which picture viewing periods were interspersed with periods involving no visual stimulation. Functional activity was examined on a voxel-by-voxel basis, in which the strength of the fMRI signal during picture processing in each block of trials was compared with signal strength when no visual stimulus was present. Voxels that were reliably active during picture processing (using a t statistic as threshold) were subsequently examined for both the extent and strength of their activation during viewing of each of the seven different picture contents.

Considerable data support the view that the ventral visual brain, extending from the posterior pole forward along a path through the fusiform gyri, is primarily active in object definition and semantic categorization, whereas a more dorsal path through the parietal region is most active in spatial location (Felleman & Van Essen, 1991; Ungerleider & Haxby, 1994). A number of studies have also found that, in general, the right hemisphere may be more involved in visual processing than the left hemisphere (Benton, 1979; Junghoefer et al., 2001; Lang et al., 1998; Posner & Petersen, 1990). Furthermore, on the basis of neurological findings (Heilman, 1979) and EEG studies (Heller, 1990), it has been proposed that emotional arousal might be specifically associated with the right hemisphere and posterior parietal activation.

Considering these views, our region analysis assessed the extent and strength of functional activity for eight volumes, composed of the left and right ventral and dorsal regions of the visual cortex,
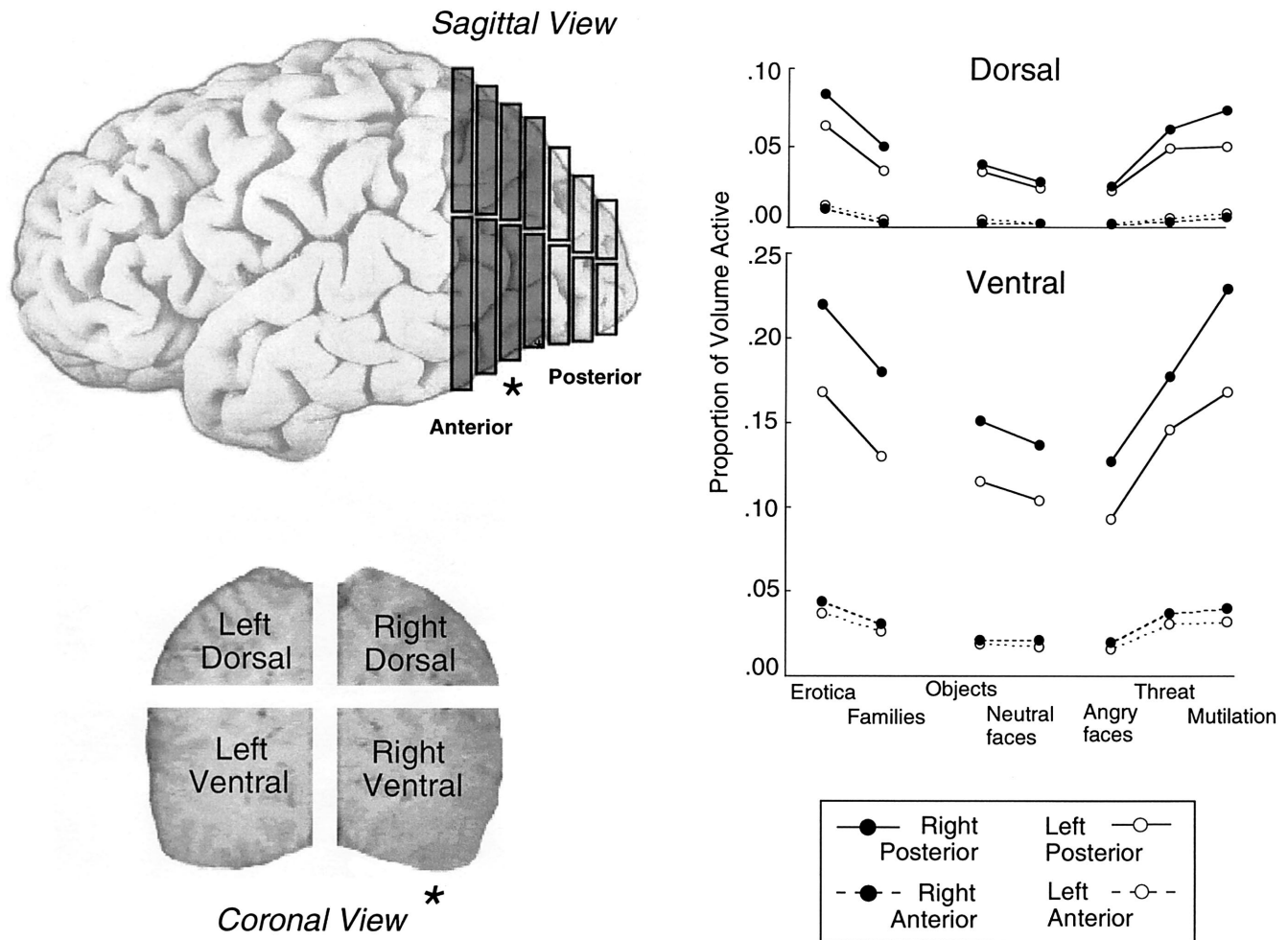
Figure 1. Top left: Sagittal view illustrating the slice selection and the dorsal and ventral regions in each of the anterior and posterior regions. Bottom left: A coronal view of the regions of interest, in which each coronal image was divided into four regions defined by hemisphere (left, right) and extent along a superior–inferior axis (dorsal, ventral). Right: Extent of functional activity in each of the eight regions of interest as a function of picture content.

with each volume further subdivided into anterior and posterior portions (see Figure 1). Other than striate cortex (Brodmann Area 17), which extends along the banks of the calcarine fissure, the visual cortex is primarily differentiable on functional, rather than strictly anatomical, grounds. Thus, the current design focused first on the extent of visual cortex that is functionally active when processing affective input (the presumed breadth of neural activity within each region) and, second, on the strength of local input.

Striate cortex represents only a small section of the total brain volume sampled, which was largely the unimodal association cortex (i.e., functional sites for processing color, shape, objects, faces, letters, and spatial targets), with a smaller portion including medial parietal cortex (Mesulam, 2000). Our sampled volume extended from 10 mm anterior to the occipital pole to a point 54 mm anterior, covering the entire coronal plane. The defined regions allowed us to assess functional activity in the ventral and dorsal streams, both in the posterior region adjacent to striate cortex and farther forward as their paths diverge, and to determine

if this activity is laterally biased. In a second analysis, we averaged the functional maps for each picture condition across subjects, using transformation based on the Talairach–Tournoux atlas (Talairach & Tournoux, 1988). This analysis complemented the primary region analysis, specifying specific neural structures activated on the basis of a standardized coordinate space.

As the experimental task did not involve the location of the objects in different parts of the visual field (i.e., all stimuli were presented foveally), a preponderance of activation was anticipated in posterior ventral areas, where the central visual field is represented (Wurtz & Kandel, 2000). A general right-hemisphere bias caused by visual processing was also anticipated, as we found previously (Lang et al., 1998), and given the predictions of Heller (1990), there was also an expectation of greater activation for emotional, compared with neutral, pictures in the right than in the left occipital/parietal region. In general, we expected to replicate our previous findings that emotional (pleasant or unpleasant) pictures prompt more extensive functional activity in visual cortex

than neutral stimuli. We hypothesized that this functional activity would be primarily related to the level of emotional arousal, with the most extensive activity for pictures that cue events primitively important for species and individual survival. We expected that greater activation would be a consequence of the motivational content of the pictures and would not mediated by perceptual features such as color, or content features not intrinsic to affect (e.g., the presence of human faces).

Method

Participants

Eighteen male volunteers (mean age = 18.6 years) from a University of Florida general psychology course participated to fulfill a course requirement. Potential participants were contacted by phone and screened for claustrophobia and physical restrictions (e.g., height, weight). Those participants with corrected vision were asked to wear contact lenses. Nine participants viewed the picture stimuli in color, and 9 viewed the pictures in grayscale.

Materials and Design

Stimuli consisted of 56 pictures representing eight exemplars in seven different content categories, including pictures of erotica, families, household objects, neutral faces, angry faces, threat, and mutilation. Pictures were selected from the International Affective Picture System (IAPS;[1] Center for the Study of Emotion and Attention, 1999) and from the Japanese and Caucasian Facial Expressions of Emotion set (Matsumoto & Ekman, 1989). In the IAPS norms for men (Lang et al., 1999), bipolar valence ratings (1–9 scale: 1 = *most unpleasant*; 9 = *most pleasant*) for erotica, families, household objects, threat, and mutilation were 7.6, 7.2, 4.9, 3.3, and 1.8, respectively, and arousal ratings (1–9 scale: 1 = *calm*; 9 = *most aroused*) were 6.8, 4.2, 2.3, 6.8, and 6.5, respectively. Although valence and arousal ratings were not available for the Matsumoto and Ekman faces, these values were estimated from ratings of IAPS pictures of faces, which were 4.7 (valence) and 2.7 (arousal) for neutral faces, and 4.0 (valence) and 4.4 (arousal) for angry faces.

There were seven blocks in the experiment, with each block presenting pictures from one of the seven picture contents. Each block consisted of eight cycles of a 12-s intertrial interval (off) and a 12-s picture presentation period (on), with one of the eight exemplars in each content displayed during the 12-s picture presentation period on each cycle. A picture was presented for 12 s, flickering at a 3-Hz rate throughout the 12-s picture presentation period.[2] During the intertrial interval (off) period, the screen was dark (i.e., no illumination from the slide projector). Order of picture content was counterbalanced across subjects such that, across participants, each content was seen equally often in the first or second half of the session, as well as in the first, second, or third position within the half. Picture presentation was time-locked to image acquisition by a PC-compatible computer interfaced to the scanner, running VPM stimulus control software (Cook, Atkinson, & Lang, 1987).

Images were acquired with a specially built quadrature head coil (Fitzsimmons et al., 1997) that was seated in a football helmet, with an attached bitebar[3] to stabilize the head. An adjustable mirror, mounted on top of the helmet, allowed visual stimuli that were rear-projected on a white screen located at the participant's feet to be viewed, and a red fixation dot was illuminated in the center of the screen throughout the session. The screen size was 57 cm × 57 cm, with the centrally presented stimuli 57 cm wide × 37 cm high when projected on the screen, subtending a visual angle of 20°.

The fMRI scanning sequence began with the acquisition of a 60-image (ear-to-ear) sagittal scout set, using a standard T1-weighted sequence. This volume was used to prescribe the location of seven coronal functional

slices, with the first slice placed 10 mm anterior to the occipital pole. Thus, the most posterior image was nearly centered on the calcarine fissure in primary visual cortex. Subsequent images extended anteriorly, with the superior portion of the final image generally including substantial tissue anterior to the occipital–parietal fissure. High-resolution anatomical images for use in overlaying the functional maps were acquired at each of seven coronal locations before the functional series began, also using a standard T1-weighted scanning sequence.

The functional images were acquired with a four-shot multislice spiral scan technique (Noll, Cohen, Meyer, & Schneider, 1995) on a 3T Signa scanner (General Electric, Fairfield, CT). Seven 5-mm thick (1.5 mm gap), 128 × 128 matrix functional images were acquired in the coronal plane, across an 18 cm field of view (1.4 mm in-plane resolution). Echo time (TE) was 35 ms, repeat time (TR) was 720 ms, and a flip angle of 45° was used. A set of seven coronal images was collected four times during each of the 12-s picture presentation (i.e., approximately 3 s acquisition time per set of images) and 12-s interpicture interval, resulting in a 196-s series of 68 images at each coronal location for each of the seven blocks in the experiment.

After the functional series were complete, areas of large venous flow were identified by acquiring a series of vascular time-of-flight (TOF) spoiled gradient echo images that corresponded in anatomical location to the seven coronal slices. Voxels in areas with large venous flow were later used as a mask in the functional maps, in order to minimize large vascular contribution to the activation maps.

In a passive viewing task, each participant was instructed that pictures would be presented on a screen, and that their eyes should remain comfortably focused on a red dot (laser pointer) in the center of the screen. The entire scanning session lasted from 45 to 50 min.

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[1] The International Affective Picture System (Center for the Study of Emotion and Attention, 1999) is available on CD-ROM and as photographic slides. The IAPS and technical manuals can be obtained on request from the authors at the NIMH Center for the Study of Emotion and Attention, Box 100165 HSC, University of Florida, Gainesville, FL 32610-0165. IAPS catalog numbers for the pictures used in this study are Mutilations: 3053, 3110, 3000, 3010, 3102, 3060, 3080, 3130; Attack: 1120, 3530, 6350, 1050, 1930, 6260, 1300, 6510; Household Objects: 7235, 7080, 7040, 7009, 7175, 7010, 7002, 7030; Families: 2080, 2311, 2050, 2360, 2341, 2160, 2070, 2165; and Erotica: 4680, 4652, 4658, 4670, 4651, 4660, 4664, 4650.

Pictures used from the Japanese and Caucasian Facial Expression of Emotion (Matsumoto & Ekman, 1989) set are Angry Faces: 1RH 1C24, NM 2C14, 1KG 1C21, BM 1C22, 1LR 1C24, 1AL 1C21, 1ES1 2C17, AF 1C30; Neutral Faces: CF 2C01, NH1 1C01, ES2 1C04, SW1 1C02, WW 1C02, GO 1C01, JC 1C02, AK2 1C02.

[2] Each picture was presented for 12 s. A 3-Hz flicker rate was used during each 12-s picture presentation, which results perceptually in the presentation of a single picture that is flashing; this rate replicates that used by Lang et al. (1998) and allowed us to assess our current hypothesis without changing stimulation conditions. Schneider, Casey, and Noll (1994) demonstrated increasing activation in visual cortex with increases in presentation rate. Current fMRI studies in our laboratory indicate that similar patterns of modulation by emotion in visual cortex occur in the absence of the flickering pictures, however, indicating that this presentation rate is not essential to the pattern of effects.

[3] The participant was instructed to "hang" from the bitebar using the upper palate, rather than actively biting down on the bitebar, and all subjects easily understood this instruction. Each participant was able to drop the lower jaw, swallow, talk, and breathe while the upper jaw was firmly attached to the bitebar apparatus, which greatly assisted in restricting head movement.

Data Reduction and Analyses

For each block of the experiment for each participant, the difference in mean signal intensity during the picture presentation periods and during the interpicture interval for each voxel was computed. A phase lag of two images (approximately 6 s) was used for all participants. A t statistic was used to evaluate the mean difference in signal intensity between averaged epochs for each voxel. Functional t statistic maps were thresholded for each subject and condition at a level of $p < .01$, and constrained to include four contiguous voxels in the final map, which effectively reduces the rate of false positives (to $p < .00001$, Forman et al., 1995). Active voxels in areas dominated by flow in large vessels (identified in the TOF images) were removed (i.e., recoded to zero).

Eight regions were determined by manually dividing each of the seven high-resolution coronal images into right and left hemisphere regions at the longitudinal fissure, including only cortical tissue in each region. Dorsal and ventral regions were determined by assigning 40% of the total area from superior to inferior to a dorsal region and 60% to a ventral region (see Figure 1, left). Data were averaged over the three most posterior images to form a single estimate of posterior activation and averaged over the four most anterior images to create a single estimate of anterior activation, resulting in eight regions of interest. In general, the ventral regions in this analysis included the primary visual cortex along the calcarine fissure, particularly in the posterior images. It also included the pathways to the inferior temporal cortex concerned with the analysis of color and form and crucial to object recognition. The dorsal regions encompassed the dorsal stream to the caudal parietal lobe, which is involved in spatial recognition (Nieuwenhuys, Voogd, & van Huijzen, 1988). The anterior region included fusiform gyri and parietal visual association areas, whereas the posterior region included Areas V1, V2, and V3.

The extent of functional activity in each of these eight regions was calculated as the proportion of active voxels (determined by the t test procedure described above) in each region, relative to the number of voxels in that region. The strength (percent change in signal intensity) of functional activity in each region of interest was calculated as the mean signal intensity for active voxels during picture presentation minus the mean signal intensity for these voxels during the interpicture interval, divided by the mean signal intensity during the interpicture interval.

A mixed analysis of variance was computed separately for extent and strength of functional activity, using a between-subject variable of picture presentation mode (2: color or grayscale) and 4 within-subject variables that involved the factorial combination of anterior–posterior region (2), ventral–dorsal region (2), left–right hemisphere (2) and picture content (7: erotica, families, household objects, neutral faces, angry faces, threat, mutilation).

The anatomical and functional scans for each subject were also normalized into the standard stereotaxic space as defined by Talairach and Tournoux (1988), using the Medical College of Wisconsin AFNI software package (Cox, 1996). Functional t-statistic maps were averaged across participants (following Binder et al., 1997, who opted for averaging statistics to avoid problems of heteroscedasticity), excluding voxels with negative or zero values. A 2-mm full width at half maximum spatial filter was applied to the averaged data, and active areas were identified by thresholding the resulting data at $t > 2.5$ and defining a cluster on the basis of nearest-neighbor connectivity and a minimum size of 50 microliters.[4]

Results

Figure 1 (right) illustrates the extent of functional activity for each picture content in each region, as defined by the primary region analysis (untransformed data). The picture contents are ordered on the abscissa according to their mean IAPS arousal ratings. The most arousing pleasant and unpleasant contents are at the ends, with ratings progressively diminishing to the neutral pictures in the middle.

Across all picture contents, more extensive activation was found in posterior, compared with anterior, regions: anterior–posterior region, $F(1, 16) = 45.27$, $p < .01$, as well as in ventral, compared with dorsal, regions: Anterior–Posterior $\times$ Ventral–Dorsal, $F(1, 16) = 69.09$, $p < .01$; ventral: anterior–posterior, $F(1, 16) = 61.53$, $p < .01$; dorsal: anterior–posterior, $F(1, 16) = 16.40$, $p < .01$. Within the ventral posterior region, there was more activity in the right, compared with the left, hemisphere: Anterior–Posterior $\times$ Ventral–Dorsal $\times$ Hemisphere, $F(1, 16) = 9.20$, $p < .01$; hemisphere, $F(1, 16) = 33.36$, $p < .01$ (see Figure 2). Thus, replicating our previous study (Lang et al., 1998), the most extensive functional activity occurred in the right ventral posterior area, which includes the object identification pathway proposed for primary visual cortex.

A main effect of picture content, $F(6, 96) = 7.56$, $p < .01$, supported the predicted effect of differences in functional activity as a function of emotional content. As Figure 2 (top) illustrates, the U-shaped function indicates more extensive activity as picture content became more emotionally arousing, and was supported by a significant quadratic trend when contents were ordered as depicted in Figure 1, $F(1, 16) = 21.45$, $p < .01$, and a significant linear trend when ordered by emotional arousal, $F(1, 16) = 14.78$, $p = .01$. Thus, emotionally arousing pictures, regardless of affective valence, prompted more extensive functional activity in visual cortex.

Regional differences in the extent of functional activity were suggested by multiple interactions involving picture content and brain region: Anterior–Posterior $\times$ Content, $F(6, 96) = 7.03$, $p < .01$; Ventral–Dorsal $\times$ Content, $F(6, 96) = 4.33$, $p < .01$; Hemisphere $\times$ Content, $F(6, 96) = 4.93$, $p < .01$; Anterior–Posterior $\times$ Ventral–Dorsal $\times$ Content, $F(6, 96) = 2.80$, $p < .05$; Anterior–Posterior $\times$ Hemisphere $\times$ Content, $F(6, 96) = 5.39$, $p < .01$. Simple main effects tests of picture content in each of the eight regions indicated significant main effects of picture content in each region, however, with more extensive activation elicited when viewing emotional (i.e., pleasant or unpleasant), compared with neutral, stimuli in each of the regions, quadratic $F(1, 16) =$ posterior: 26.55, 17.20, 21.22, 9.40 for right ventral, right dorsal, left ventral, and left dorsal regions, respectively; anterior: 9.40, 16.23, 14.07, 14.20, 7.19 for right ventral, right dorsal, left ventral, and left dorsal regions, respectively. Figure 1 (right) illustrates these data.

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[4] The averaged data were inspected at thresholds varying from $t = 2.4$ to $t = 3.0$, with the number of clusters appearing varying from 20 ($t > 2.4$) to 7 ($t > 3.4$) in the unpleasant picture condition, for example. The selected criteria of $t > 2.5$ together with a cluster size of 50 was selected because (a) this threshold adequately represented clusters that were consistently identified at various levels of thresholding without including those that were only apparent at lower levels of thresholding, and (b) this cluster size identified relatively smaller, as well as larger, clusters that consistently appeared across different levels of thresholding. Nonetheless, it should be remembered that particular structures that are not implicated in analyses using the current thresholding might appear if the thresholding level were changed. In the absence of a known distribution for determining the appropriate threshold for averaged t-maps (Binder et al., 1996), our criteria were determined by an in-depth assessment of the data at multiple thresholding levels and a conservative judgment regarding the reliability of clusters on the basis of these analyses.
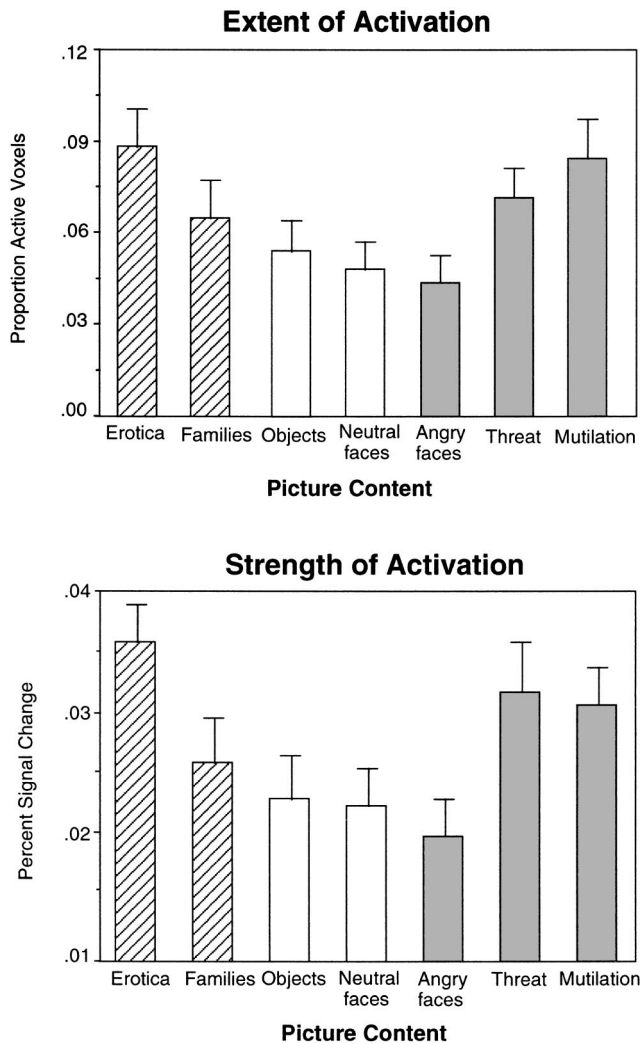
Extent of Activation

Strength of Activation

Figure 2. Top: Extent of functional activity produced by viewing pictures with different affective content (hatched bars, pleasant pictures; open bars, neutral pictures; gray bars, unpleasant pictures), expressed as a proportion of the total number of voxels sampled in this experiment. Bottom: Strength of signal change produced by viewing pictures with different affective content in voxels that reached threshold. Error bars represent *SEM.*

The main effect of picture content was subsequently followed up by specific tests that addressed a priori hypotheses and questions.

1. Stimuli with clear, appetitive motivational relevance showed greater extent of functional activity than other affective and neutral contents. Thus, sexually evocative erotic pictures led to more extensive activation than the other similarly rated pleasant pictures (i.e., families), $F(1, 16) = 5.25$, $p < .05$. This effect was general across all regions (i.e., no interactions).

2. Similarly, for unpleasant pictures, the most arousing contents of threat and mutilation led to significantly more activation than angry faces, which are unpleasant pictures rated lower in arousal: threat vs. angry faces, $F(1, 16) = 11.75$, $p < .01$; mutilation vs. angry faces, $F(1, 16) = 13.36$, $p < .01$. Furthermore, these differences were significant in each of the eight regions ($ps < $

.015). Significant interactions with brain region indicated slight differences in the size of these significant effects. For threat versus angry faces, a Content $\times$ Anterior–Posterior interaction, $F(1, 16) = 10.93$, $p < .01$, indicated a slightly stronger effect in the posterior region. For mutilations versus angry faces, there were interactions involving region: Content $\times$ Anterior–Posterior $\times$ Hemisphere, $F(1, 16) = 19.46$, $p < .01$; Content $\times$ Ventral–Dorsal $\times$ Anterior–Posterior, $F(1, 16) = 12.04$, $p < .01$, which indicated the largest difference was in the right posterior ventral region.

When threat pictures were compared with pictures of mutilation, the main effect of picture content was only marginal, $F(1, 16) = 3.73$, $p = .07$, but a four-way interaction of picture content, anterior–posterior, ventral–dorsal, and hemisphere was significant, $F(1, 16) = 7.32$, $p < .05$. Separate comparisons in each anatomical region indicated that threat and mutilation pictures were reliably different in the extent of activity only in the right posterior ventral cortex, with mutilation scenes eliciting slightly more extensive functional activity than pictures depicting threat.

3. If strong appetitive and defensive activation similarly orient attention and enhance sensory processing, we expected no differences in functional activity in response to motivationally relevant stimuli, whether pleasant (e.g., erotica) or unpleasant (e.g., mutilation or threat) contents. Consistent with this view, there were no significant differences between these pleasant and unpleasant contents in extent of functional activity.

4. Whether pictures were presented in color or grayscale had no effect on the pattern of functional activity as a function of emotional content, as indicated by the lack of any main or interaction effects involving mode of picture presentation in any of the analyses.

When functional activity was assessed for neutral and angry faces, no differences were obtained in the extent of activation, as evidenced by a lack of main effects or interactions involving these two picture contents.

Strength of Signal Change

Table 1 lists the mean signal change in each of the regions of interest for each picture content. The mean change in signal intensity for voxels meeting threshold was higher in the ventral, compared with dorsal, regions: ventral–dorsal, $F(1, 16) = 98.8$, $p < .01$. And, whereas signal change in the ventral region was equivalent in both the anterior and posterior regions, in the dorsal region, changes in the anterior were somewhat lower than in the posterior region: Ventral–Dorsal $\times$ Anterior–Posterior, $F(1, 16) = 12.19$, $p < .01$.

As Figure 2 (bottom) illustrates, a main effect of picture content, $F(6, 96) = 12.17$ $p < .01$, indicated similar differences as a function of emotional content in the intensity of signal change. The same U-shaped function was obtained as found with extent of functional activity: quadratic, $F(1, 16) = 40.75$, $p < .01$, suggesting that the differences in extent were, for the most part, related to differences in the strength of the BOLD signal. A three-way interaction of category, anterior–posterior, and ventral–dorsal, $F(6, 96) = 2.88$, $p < .05$, indicated that modulation by emotional arousal was significant in all regions except for the posterior–ventral region, $Fs(6, 102) = 8.72, 4.77, 7.96$, for posterior–dorsal, anterior–dorsal, and anterior–ventral, respectively. In the posterior–

Table 1

Mean (SD) Signal Change in Percent for Each Region of Interest as Elicited by a Block of Eight Pictures Representing a Specific Affective or Neutral Content

Region	Erotica	Families	Objects	Neutral faces	Angry faces	Threat	Mutilation
Dorsal posterior							
Left	.039 (.02)	.026 (.01)	.022 (.01)	.016 (.01)	.017 (.01)	.030 (.01)	.033 (.02)
Right	.039 (.02)	.029 (.01)	.022 (.01)	.023 (.01)	.020 (.01)	.038 (.03)	.031 (.02)
Anterior							
Left	.023 (.03)	.008 (.04)	.006 (.02)	.006 (.02)	.004 (.02)	.014 (.03)	.017 (.03)
Right	.029 (.01)	.009 (.02)	.007 (.02)	.008 (.02)	.005 (.02)	.025 (.02)	.019 (.02)
Ventral posterior							
Left	.033 (.02)	.031 (.02)	.029 (.02)	.029 (.02)	.026 (.02)	.032 (.02)	.032 (.02)
Right	.033 (.01)	.031 (.01)	.029 (.02)	.033 (.02)	.029 (.01)	.032 (.01)	.034 (.03)
Anterior							
Left	.053 (.01)	.040 (.01)	.039 (.01)	.033 (.01)	.032 (.01)	.042 (.01)	.041 (.01)
Right	.035 (.01)	.031 (.01)	.025 (.01)	.028 (.01)	.025 (.01)	.034 (.01)	.038 (.01)

ventral region, where striate cortex is most prominently represented, all picture contents prompted an equivalent (and relatively large) change in signal strength (see Table 1).

Anatomical Normalization and Localization

In an analysis which transformed all images into a standardized brain space based on the Talairach–Tournoux method, functional activity was averaged across participants to determine more specific brain areas activated when viewing different picture contents. Table 2 lists the location and size of active clusters for each picture content. As expected, the total number of voxels occurring in active clusters when averaged across subjects generally agreed with the data reported above that was assessed on a subject-by-subject basis. For instance, the number of active voxels appearing in significant clusters was largest for the most highly arousing pleasant pictures, such as erotica (i.e., 7,524 mm^3)—more than

double the cluster size for pleasant pictures of families (i.e., 3,065 mm^3). Similarly, cluster size was considerably larger when viewing these emotionally engaging pictures compared with viewing neutral faces (i.e., 1,526 mm^3) or household objects (i.e., 661 mm^3).

As Table 2 indicates, functional activity was generally found in a right posterior region centered on or near the calcarine fissure and in a bilateral, more anterior region that included the fusiform gyrus. These two regions were active to some extent when viewing pictures of any content. On the other hand, extent of functional activity in these regions varied systematically with picture content, and the pattern was generally consistent with those previously reported. For instance, in the calcarine fissure, cluster size was largest for mutilation pictures, the unpleasant content rated most arousing in the IAPS. Similarly, erotic pictures prompted more extended activation than the less arousing pleasant pictures (e.g.,

Table 2

List of Active Clusters (Center) in Talairach Coordinates and Cluster Volume in Parentheses for Each Picture Content

Picture	Calcarine fissure				Inferior occipital gyrus				Fusiform gyrus Right				Left				Total volume
Erotica	−12	−89	−3	(2,798)	26	−92	6	(895)	−16	−77	−17	(1,603)	34	−72	−18	(1,330)	7,524
					18	−94	23	(395)									
					41	−81	−3	(145)									
Families	−17	92	7	(125)					−14	−79	−17	(1,108)	33	−74	−16	(699)	3,065
	5	−86	14	(125)													
	−10	−90	−8	(70)													
Neutral objects	−13	−89	−3	(278)					−19	−78	−18	(89)	31	−73	−19	(158)	661
	−2	−91	−7	(136)													
Neutral faces	−8	−90	−6	(216)					−22	−76	−19	(379)	33	−74	−18	(512)	1,526
Angry faces	5	−85	−12	(70)					−18	−78	−19	(77)	32	−73	−20	(101)	257
Threat	−10	−90	−2	(238)	22	−91	0	(147)	−19	−75	−17	(378)	35	−72	−17	(1,266)	2,266
Mutilation	−9	−84	−9	(6,817)	28	−93	7	(576)	−24	−65	−17	(181)[a]	29	−74	−16	(1,797)	9,371

Note. Cluster volumes are in cubic millimeters. Larger clusters were found for emotionally arousing, compared with neutral, pictures. In addition to the clusters listed above, six additional clusters were found. Of these, two were clusters for neutral faces located near the same right fusiform gyrus site noted above (−8 −80 −14 [307], −20 −83 −12 [112]). Clusters not occurring in the three regions noted above included a common cluster in the left medial fusiform gyrus that was obtained for erotica (16 −79 −14 [86]) and for families (18 −80 −13 [138]), and two remaining clusters found for erotica in the right lateral fusiform gyrus at a posterior (−39 68 −13 [76]) and more anterior (−35 52 −15 [96]) site. Empty cells indicate that the specific anatomical region was not active when that picture content was viewed.

[a] Inspection of the data indicates that the size of this cluster as noted here is misleadingly small. Activation in this region was subsumed into the very large cluster whose center was in the calcarine fissure for this picture content.

families), as well as compared with all other pictures, except for scenes of mutilation.

Active sites were found in both the left and right fusiform areas of participants viewing pictures, and activity in these sites was greater when participants were viewing emotional, compared with neutral, pictures. As Figure 3 illustrates, the most highly arousing picture contents—erotica and mutilation—involved the most extensive activity in fusiform gyrus, and the least arousing pictures—faces and household objects—resulted in the least amount of functional activity in fusiform gyrus. Although Table 2 suggests that right fusiform activity was more anterior for pictures of mutilation than for other contents, this is due to the fact that activity in the more posterior fusiform region merged into a single, very large cluster centered on the calcarine fissure for the mutilation pictures. In fact, as Figure 3 illustrates, active clusters in the fusiform region were very similar in participants viewing pictures of erotica and mutilated bodies.

In a previous study (Lang et al., 1998), viewing emotional pictures resulted in bilateral activity in the inferior occipital gyrus (Brodmann Area 18) that was absent when viewing neutral pictures. In the current study, viewing the most arousing emotional stimuli, including pictures of erotica, mutilation, or threat, again produced activity in these regions. Whereas separate clusters were identified in the left inferior occipital gyrus for each of these arousing picture contents, the cluster occurring in the right inferior occipital gyrus was generally subsumed in the large cluster centered on the calcarine fissure for each content. Use of a more stringent threshold (e.g., $t > 2.7$) results in two separately identifiable clusters for each content that are located bilaterally in the inferior occipital gyrus. For picture contents rated lower in arousal—families, household objects, neutral or angry faces—there was no significant activity at these bilateral sites.

Discussion

The present research found more extensive visual cortex activity in participants viewing emotional, compared with neutral, pictures, confirming previous findings (e.g., Lang et al., 1998). The new data show, furthermore, that this functional activity is closely related to the rated intensity of emotion, as reported in the IAPS standardization sample (Lang et al., 1999). The most affectively arousing pictures generally prompted more extensive cortical activation than other picture contents. In specific tests, functional activity was greater for erotic pictures than for the less arousing happy families, even though these contents were equivalent in rated affective valence. Functional activity was also more extensive for pictures of threat and mutilation, compared with angry faces. Thus, the three picture contents that most intensely activate the primary motive systems—erotica, mutilation, and threat—all elicited significantly different activation than neutral, and less arousing affective, pictures. These systematic fMRI differences in the visual cortex, observed when subjects viewed pictures, follow the same general pattern previously obtained in measures of sympathetic activation (Bradley, 2000; Lang, Greenwald, Bradley, & Hamm, 1993) and in the late positive potential of the ERP (Cuthbert et al., 2000; Keil et al., 2001). That is, in both measures, one finds greater reactivity for emotional, compared with neutral, content, and the largest responses for the highly arousing contents that are presumed to be relevant to primary motivational systems.

Picture viewing evoked, as expected, reliable functional activity in the primary visual processing areas of occipital cortex for all picture contents, compared with no stimulus processing. In nearly all of the regions we sampled, both the extent and strength of activation were greatest for contents with high motivational relevance—erotica, threat, and mutilation. One exception was for the strength of activation in the posterior ventral region, perhaps because all visual stimuli similarly activated a retinal map in striate cortex, which constitutes a major proportion of this region's cortical tissue. Nevertheless, erotica, mutilation, and threat stimuli clearly engaged more functional activity than other picture contents in secondary processing regions, including the inferior occipital gyrus (Figure 3).

The posterior fusiform area was also specifically implicated in processing affective stimuli, with more extensive activity elicited for the most arousing pictures: erotica, threat, and mutilation. Although a number of previous studies have explored activity in the fusiform gyrus as it varies during face perception, using affectively neutral stimuli (Gauthier et al., 2000; Halgren et al., 1999; McCarthy, Puce, Gore, & Allison, 1997), in the current study, few differences were found in participants viewing neutral faces, compared with viewing household objects. It should be noted, however, that the fusiform region that is held to be face sensitive is more anterior (e.g., approximately 54 mm posterior to the anterior commissure; Halgren et al., 1999) than the prescription used here (i.e., 65 mm posterior to the anterior commissure) and that data indicate the fusiform region is also activated by many classes of visual stimuli, including objects (Chao, Weisberg, & Martin, 2002).

Differences in functional activity for emotionally arousing pictures are unlikely to rely strongly on the formal perceptual properties of the pictures. The present experiment clearly shows that color (e.g., the blood red in some of the mutilation pictures) is not a relevant factor. Furthermore, in a recent ERP study (Junghoefer et al., 2001), we found two main dipole sources indicating greater activity for emotionally arousing pictures in occipital cortex that were independent of formal perceptual features of the pictures, including spatial frequency, brightness, and others. It is also unlikely that functional differences are an artifact of heightened scanning. Not only were participants in the current study instructed to maintain central fixation, but in a previous study utilizing the same design and instructions (including replication in an MRI simulator, Lang et al., 1998), there were no confounding differences in eye movement between emotional and neutral pictures. Whereas future studies should continue to pursue these issues, the data strongly suggest that during emotional picture viewing, the visual system is engaged in more extensive, sustained processing than is found for affectively less arousing stimuli.

When the strength of activation in voxels meeting threshold was assessed, a similar pattern of modulation by emotional arousal was obtained: Emotionally arousing pictures prompted significantly larger changes in signal strength than did pictures that were of lower arousal. More extensive activation of visual cortex, in this case, probably reflects the stronger signal changes induced by processing emotionally arousing pictures, as increased differentiation will result in more voxels reaching threshold. Consistent with this interpretation, areas activated during picture processing were generally similar across all picture types, with both the extent and strength of activation greater for emotionally arousing stimuli.
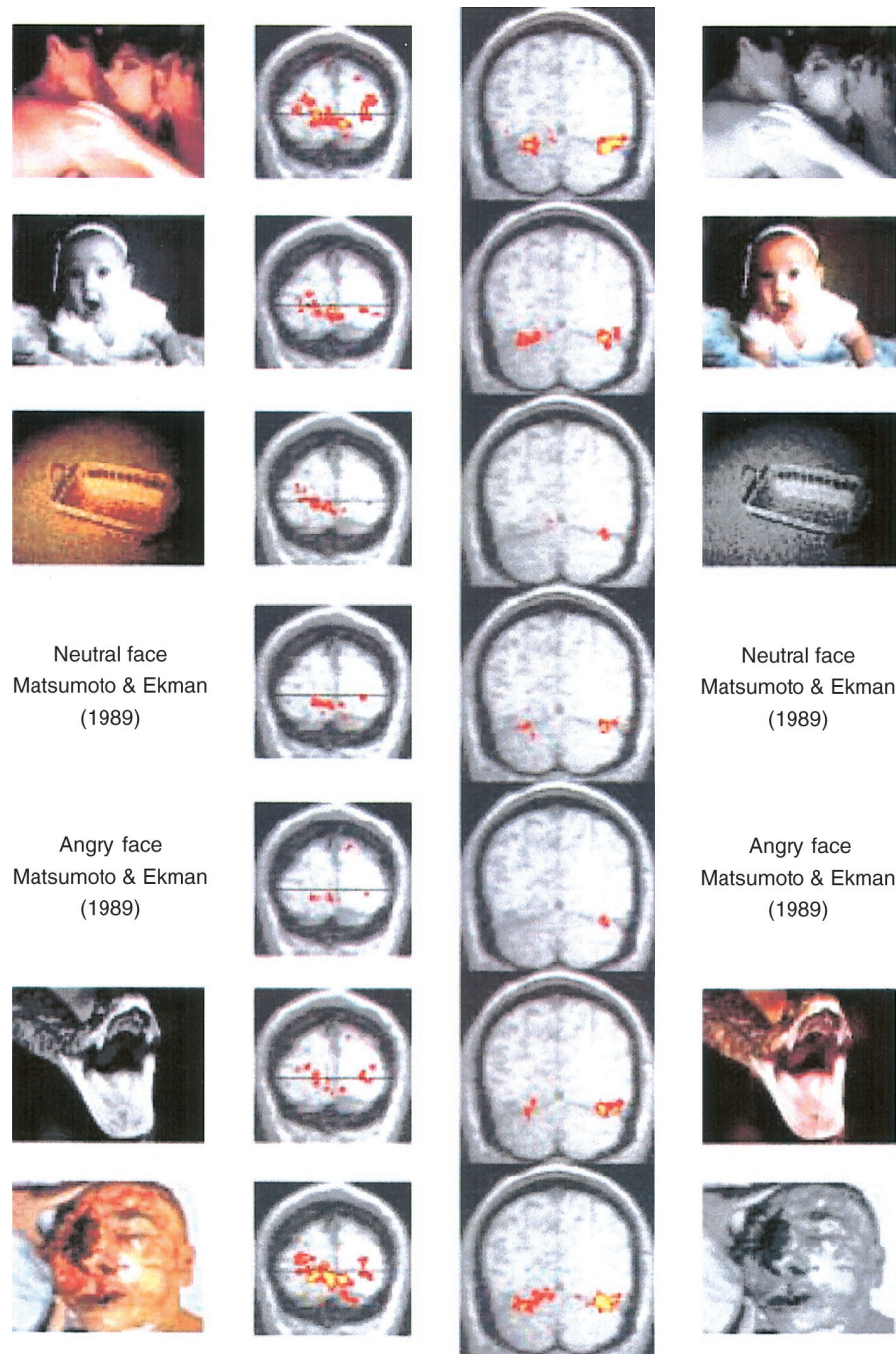
Figure 3. Sites of functional activity during processing of pictures with different affective content, compared with the interpicture interval, as determined from averaging functional maps across subjects. Clusters meeting criteria are depicted in red and yellow, with yellow indicating a larger difference. First and fourth columns: Examples of color and grayscale versions of exemplars in each of the picture contents presented in this study. Second column: All picture contents show activity centered on the calcarine fissure ($z = -90$), whereas only emotionally arousing pictures (e.g., erotica, threat, mutilation) also show bilateral activity in the occipital gyrus. Third column: The extent of functional activity in the bilateral fusiform gyrus ($z = -73$) varies, with emotionally arousing pictures prompting more activity than pictures rated lower in arousal.

In the posterior–ventral visual cortex, differences in the size of signal change as a function of picture content did not reach significance, although content differences in the extent of functional activity were the largest of all regions. These data are consistent with the idea that more extensive functional activity may also reflect differential recruitment of visual cortex (Haxby, Courtney, & Clark, 1998). For instance, Karni et al. (1995) found that practice in a motor task systematically increased the extent of functional activity over motor cortex, suggesting that learning resulted in more extensive neural activity. Considering this finding in terms of the visual system suggests that affectively arousing materials may prompt more extensive activity because they more frequently involve elaborative associations in secondary visual areas. The lack of difference in signal strength uniquely in posterior–ventral visual cortex may reflect the predominance of striate cortex in this region, which is highly activated by all visual stimulation.

Differential recruitment of visual cortex could also reflect differences in attentional engagement for stimuli of primary emotional relevance. Many data support the notion that emotional pictures differentially engage attentional processes. Physiological systems sensitive to attentional allocation, including cardiac orienting, electrodermal responding, and the P3 component of ERPs show heightened activity when people view pictures depicting erotica, threat, and mutilation (Bradley et al., 2001; Keil et al., 2002). Moreover, ratings of interest and voluntary viewing time are also accentuated when people view highly arousing pictures.

We have previously suggested that motivational activation drives attention: Cues that activate primary motivational system (i.e., appetitive or defensive) initially direct attention to the stimulus for further processing (Lang et al., 1997). We further presume that the attentional engagement prompted by motivationally relevant stimuli involve the same neural circuits as those that modulate attentional resource allocation more broadly, e.g., by task or instructional requirements. Supporting this, Lane, Chua, and Dolan (1999), using PET, found that extrastriate cortex, particularly in the right hemisphere, was similarly activated by emotion or attention. In their study, attention was manipulated by requiring the performance of an easy or hard secondary task during viewing of IAPS pictures. They conclude that both emotion and attention heighten sensitivity to visual cues.

One interesting possibility is that motivated attention reflects re-entrant processing, possibly based on reciprocal projections between the amygdala and the visual system (Amaral et al., 1992). As noted previously, there are extensive interconnections between subcortical areas associated with emotional processing, such as the amygdala, and the visual cortex, providing a potential mechanism whereby motivational activation could modulate perceptual processing. On the other hand, in their PET study, Lane et al. (1999) found increased activity in medial prefrontal cortex when more attention was available for processing emotional pictures (i.e., low distraction condition), raising the possibility that back-projections could be of cortical origin. Consistent with this, in the monkey, lesions of orbitofrontal cortex impair visual recognition, particularly the ability to form associations between objects and reward (Meunier, Bachevalier, & Mishkin, 1997). Alternatively, Posner and Petersen (1990) have emphasized the role of the anterior cingulate as an executive attention center that may direct processing in sensory systems. Taken together, an important goal of subsequent research is to extend the present functional analysis to the whole brain, combined with better methods for evaluating the covariation between occipital sites and more anterior cortical and subcortical structures, in an effort the trace the circuit of emotional processing. A recent study reported in this journal has already shown that emotional picture processing (using the IAPS) may prompt differential activation of anterior brain structures, associated with individual differences in emotionality (Canli et al., 2001).

Analysis of the relationship between cortical and subcortical structures and visceral systems should, however, proceed cautiously. For example, whereas some fMRI research suggests that amygdala activation may occur when participants view posed face stimuli (Breiter et al., 1996; Morris, Öhman, & Dolan, 1999; Whalen et al., 1998), such stimuli do not normally evoke either palpable verbal report or autonomic indications of an affective response, even when the faces have emotional expressions (Lang et al., 1999; van Honk et al., 2001). The current data furthermore indicate that pictures of angry expressions did not prompt more activation of visual cortex than pictures of household objects. These data highlight the need to distinguish activation that might be related to stimulus discrimination from functional brain activity that reflects the actual engagement of an emotional response. Motivationally relevant pictures of erotica, mutilations, and threat evoke strong, measurable responses in a host of physiological systems (Bradley et al., 2001), and it is these stimuli that are responsible for the broad activation of visual cortex that occurs when emotional pictures are viewed. In a broader sense, it will be increasingly important to validate emotionality in brain imaging studies. Although standardized stimuli facilitate this task, it will also require coincident measures of the reflex physiology of emotion (e.g., "fear bradycardia," electrodermal orienting, startle reflex modulation), as it covaries with the brain's functional activity that mediates motivated attention and affective perception.

References

Amaral, D. G., Price, J. L., Pitkanen, A., & Carmichael, S. T. (1992). Anatomical organization of the primate amygdaloid complex. In J. P. Aggleton (Ed.), *The amygdala: Neurobiological aspects of emotion, memory, and mental dysfunction* (pp. 1–66). New York: Wiley-Liss.

Balaban, M. T., & Taussig, H. N. (1994). Salience of fear/threat in the affective modulation of the human startle blink. *Biological Psychology, 38,* 117–131.

Benton, A. (1979). Visuoperceptive, visuospatial, and visuoconstructive disorders. In K. M. Heilman & E. Valenstein (Eds.), *Clinical neuropsychology* (pp. 186–232). New York: Oxford University Press.

Binder, J. R., Frost, J. A., Hammeke, T. A., Cox, R. W., Rao, S. M., & Prieto, T. (1997). Human brain language areas identified by functional magnetic resonance imaging. *Journal of Neuroscience, 17,* 353–362.

Bradley, M. M. (2000). Emotion and motivation. In J. T. Cacioppo & L. G. Tassinary (Eds.), *Handbook of psychophysiology* (2nd ed., pp. 602–642). New York: Cambridge University Press.

Bradley, M. M., Codispoti, M., Cuthbert, B. N., & Lang, P. J. (2001). Emotion and motivation: I. Defensive and appetitive reactions in picture processing. *Emotion, 1,* 276–299.

Breiter, H. C., Etcoff, N. L., Whalen, P. J., Kennedy, W. A., Rauch, S. L., Buckner, R. L., et al. (1996). Response and habituation of the human amygdala during visual processing of facial expression. *Neuron, 17,* 1–13.

Cacioppo, J. T., Crites, S. L., Jr, & Gardner, W. L. (1996). Attitudes to the

right: Evaluative processing is associated with lateralized late positive event-related brain potentials. *Personality and Social Psychology Bulletin, 22,* 1205–1219.

Canli, T., Zhao, Z., Desmond, J. E., Kang, E., Gross, J., & Gabrieli, J. D. (2001). An fMRI study of personality influences on brain reactivity to emotional stimuli. *Behavioral Neuroscience, 115,* 33–42.

Center for the Study of Emotion and Attention. (1999). *The international affective picture system* [photographic slides]. Gainesville, FL: The Center for Research in Psychophysiology, University of Florida.

Chao, L. I., Weisberg, J., & Martin, A. (2002). Experience-dependent modulation of category-related cortical activity. *Cerebral Cortex, 12,* 545–551.

Cook, E. W., III, Atkinson, L., & Lang, K. G. (1987). Stimulus control and data acquisition for IBM PCs and compatibles. *Psychophysiology, 24,* 726–727.

Cox, R. W. (1996). AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical Research, 29,* 162–173.

Cuthbert, B. N., Schupp, H. T., Bradley, M. M., Birbaumer, N., & Lang, P. J. (2000). Brain potentials in affective picture processing: Covariation with autonomic arousal and affective report. *Biological Psychology, 52,* 95–111.

Davis, M. (1989). Neural systems involved in fear-potentiated startle. In M. Davis, B. L. Jacobs, & R. I. Schoenfeld (Eds.), *Annals of the New York Academy of Sciences: Vol. 563. Modulation of defined vertebrate neural circuits* (pp. 165–183). New York: New York Academy of Sciences.

Davis, M. (1998). Anatomic and physiologic substrates of emotion in an animal model. *Journal of Clinical Neurophysiology, 15,* 378–387.

Davis, M., & Lang, P. J. (2003). Emotion. In M. Gallagher & R. J. Nelson (Eds.), *Handbook of psychology: Vol. 3. Biological psychology* (pp. 405–439). New York: Wiley.

Fanselow, M. S. (1994). Neural organization of the defensive behavior system responsible for fear. *Psychonomic Bulletin and Review, 1,* 429–438.

Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex, 1,* 1–47.

Fitzsimmons, J. R., Scott, J. D., Peterson, D. M., Wolverton, B. L., Webster, C. S., & Lang, P. J. (1997). Integrated RF coil with stabilization for fMRI in human cortex. *Magnetic Resonance in Medicine, 38,* 15–18.

Forman, S. D., Cohen, J. D., Fitzgerald, M., Eddy, W. F., Mintun, M. A., & Noll, D. C. (1995). Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): Use of a cluster-size threshold. *Magnetic Resonance in Medicine, 33,* 636–647.

Fredrikson, M., Wik, G., Annas, P., Ericson, K. A. J., & Stone-Elander, S. (1995). Functional neuroanatomy of visually elicited simple phobic fear: Additional data and theoretical analysis. *Psychophysiology, 32,* 43–48.

Fredrikson, M., Wik, G., Greitz, T., Eriksson, L., Stone-Elander, S., Ericson, K. A. J., et al. (1993). Regional cerebral blood flow during experimental phobic fear. *Psychophysiology, 30,* 126–130.

Gauthier, I., Tarr, M. J., Moylan, J., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). The fusiform "face area" is part of a network that processes faces at the individual level. *Journal of Cognitive Neuroscience, 12,* 495–504.

Greenwald, M. K., Bradley, M. M., Cuthbert, B. N., & Lang, P. J. (1998). Startle potentiation: Shock sensitization, aversive learning, and affective picture modulation. *Behavioral Neuroscience, 112,* 1069–1079.

Halgren, E., Dale, A. M., Sereno, M. I., Tootell, R. B., Marinkovic, K., & Rosen, B. R. (1999). Location of human face-selective cortex with respect to retinotopic areas. *Human Brain Mapping, 7,* 29–37.

Haxby, J. V., Courtney, S. M., & Clark, V. P. (1998). Functional magnetic resonance imaging and the study of attention. In R. Parasuraman (Ed.), *The attentive brain* (pp. 123–142). Cambridge, MA: MIT Press.

Hebb, D. O. (1949). *The organization of behavior: A neuropsychological theory.* New York: Wiley-Liss.

Heilman, K. M. (1979). Neglect and related disorders. In K. M. Heilman & E. Valenstein (Eds.), *Clinical neuropsychology* (pp. 268–307). New York: Oxford University Press.

Heller, W. (1990). The neuropsychology of emotion. In N. Stein, B. Leventhal, & T. Trabasso (Eds.), *Psychological and biological approaches to emotion* (pp. 167–211). Hillsdale, NJ: Erlbaum.

Junghoefer, M., Bradley, M. M., Elbert, T. R., & Lang, P. J. (2001). Fleeting images: A new look at early emotional discrimination. *Psychophysiology, 38,* 175–178.

Kapp, B. S., Frysinger, R. C., Gallagher, M., & Haselton, J. R. (1979). Amygdala central nucleus lesions: Effect on heart rate conditioning in the rabbit. *Physiology & Behavior, 6,* 1109–1117.

Kapp, B. S., Whalen, P. J., Supple, W. F., & Pascoe, J. P. (1992). Amygdaloid contributions to conditioned arousal and sensory information processing. In J. P. Aggleton (Ed.), *The amygdala: Neurobiological aspects of emotion, memory, and mental dysfunction.* New York: Wiley-Liss.

Karni, A., Meyer, G., Jezzard, P., Adams, M. M., Turner, R., & Ungerleider, L. G. (1995, September 14). Functional MRI evidence for adult motor cortex plasticity during motor skill learning. *Nature, 377,* 155–158.

Keil, A., Bradley, M. M., Hauk, O., Rockstroh, B., Elbert, T., & Lang, P. J. (2001). *Event-related brain potentials in affective picture viewing: A high-density EEG study.* Manuscript submitted for publication.

Keil, A., Bradley, M. M., Hauk, O., Rockstroh, B., Elbert, T., & Lang, P. J. (2002). Large-scale neural correlates of affective picture processing. *Psychophysiology, 39,* 641–649.

Knight, D. C., Smith, C. N., Stein, E. A., & Helmstetter, F. J. (1999). Functional MRI of human Pavlovian fear conditioning: Patterns of activation as a function of learning. *NeuroReport, 10,* 3665–3670.

Kosslyn, S., Shin, L. M., Thompson, W. L., & McNally, R. J. (1996). Neural effects of visualizing and perceiving visual stimuli: A PET investigation. *NeuroReport, 7,* 1569–1576.

LaBar, K. S., Gitelman, D. R., Parrish, T. B., Kim, Y. H., Nobre, A. C., & Mesulam, M. M. (2001). Hunger selectively modulates corticolimbic activation to food stimuli in humans. *Behavioral Neuroscience, 115,* 493–500.

Lane, R. D., Chua, P. M.-L., & Dolan, R. J. (1999). Common effects of emotional valence, arousal and attention on neural activation during visual processing of pictures. *Neuropsychologia, 37,* 989–997.

Lane, R. D., Reiman, E. M., Bradley, M. M., Lang, P. J., Ahern, G. L., Davidson, R. J., & Schwartz, G. E. (1997). Neuroanatomical correlates of pleasant and unpleasant emotion. *Neuropsychologia, 35,* 1437–1444.

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1990). Emotion, attention, and the startle reflex. *Psychological Review, 97,* 377–398.

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1997). Motivated attention: Affect, activation and action. In P. J. Lang, R. F. Simons, & M. T. Balaban (Eds.), *Attention and orienting: Sensory and motivational processes* (pp. 97–135). Hillsdale, NJ: Erlbaum.

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1999). *International affective picture system (IAPS): Instruction manual and affective ratings, technical report A-4.* Gainesville: The Center for Research in Psychophysiology, University of Florida.

Lang, P. J., Bradley, M. M., Fitzsimmons, J. R., Cuthbert, B. N., Scott, J. D., Moulder, B., & Nangia, V. (1998). Emotional arousal and activation of the visual cortex: An fMRI analysis. *Psychophysiology, 35,* 199–210.

Lang, P. J., Greenwald, M. K., Bradley, M. M., & Hamm, A. O. (1993). Looking at pictures: Affective, facial, visceral, and behavioral reactions. *Psychophysiology, 30,* 261–273.

LeDoux, J. E. (1990). Information flow from sensation to emotion plasticity in the neural computation of stimulus values. In M. Gabriel & J.

Moore (Eds.), *Learning and computational neuroscience: Foundations of adaptive networks* (pp. 3–62). Cambridge, MA: Bradford Books/MIT Press.

Matsumoto, D., & Ekman, P. (1989). American-Japanese cultural differences in intensity ratings of facial expressions of emotion. *Motivation and Emotion, 13,* 143–157.

McCarthy, G., Puce, A., Gore, J. C., & Allison, T. (1997). Face-specific processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience, 9,* 605–610.

Mehrabian, A., & Russell, J. A. (1974). *An approach to environmental psychology.* Cambridge, MA: MIT Press.

Mesulam, M. M. (2000). *Principles of behavioral and cognitive neurology.* New York: Oxford.

Meunier, M., Bachevalier, J., & Mishkin, M. (1997). Effects of orbital frontal and anterior cingulate lesions on object and spatial memory in rhesus monkeys. *Neuropsychologia, 35,* 999–1015.

Morris, J. S., Öhman, A., & Dolan, R. J. (1999). A subcortical pathway to the right amygdala mediating "unseen" fear. *Proceedings of the National Academy of Sciences, 96,* 1680–1685.

Nieuwenhuys, R., Voogd, J., & van Huijzen, C. (1988). *The human central nervous system: A synopsis and atlas.* Berlin: Springer-Verlag.

Noll, D. C., Cohen, J. D., Meyer, C. H., & Schneider, W. (1995). Spiral K-space MR imaging of cortical activation. *Journal of Magnetic Resonance Imaging, 5,* 49–56.

Osgood, C. E., Suci, G. J., & Tannenbaum, P. H. (1957). *The measurement of meaning.* Urbana: University of Illinois Press.

Pietrini, P., Guazzelli, M., Brasso, G., Jaffe, K., & Grafman, J. (2000). Neural correlates of imaginal aggressive behavior assessed by positron emission tomography in healthy subjects. *American Journal of Psychiatry, 157,* 1772–1781.

Posner, M. I., & Petersen, S. E. (1990). The attention system in the human brain. *Annual Review of Neuroscience, 13,* 25–42.

Reiman, E. M., Lane, R. D., Ahern, G. L., Schwartz, G. E., Davidson, R. L., Friston, K. J., et al. (1997). Neuroanatomical correlates of externally and internally generated human emotion. *American Journal of Psychiatry, 154,* 918–925.

Schneider, W., Casey, B. J., & Noll, D. C. (1994). Functional MRI mapping of stimulus rate effects across visual processing stages. *Human Brain Mapping, 1,* 117–133.

Smith, C. A., & Ellsworth, P. C. (1985). Patterns of cognitive appraisal in emotion. *Journal of Personality and Social Psychology, 48,* 813–838.

Sprengelmeyer, R., Rausch, M., Eysel, U. T., & Przuntek, H. (1998). Neural structures associated with recognition of facial expressions of basic emotions. *Proceedings of the Royal Society of London: Biological Sciences, 265,* 1927–1931.

Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain.* New York: Thieme Medical Publishers.

Taylor, S. F., Liberzon, I., & Koeppe, R. A. (2000). The effect of graded aversive stimulation on limbic and visual activation. *Neuropsychologia, 38,* 1415–1425.

Ungerleider, L. G., & Haxby, L. V. (1994). 'What' and 'where' in the human brain. *Current Opinion in Neurobiology, 4,* 157–165.

van Honk, J., Tuiten, A., Hermans, E., Putman, P., Koppeschaar, H., Thijssen, J., et al. (2001). A single administration of testosterone induces cardiac accelerative responses to angry faces in healthy young women. *Behavioral Neuroscience, 115,* 238–242.

Whalen, P. J., Rauch, S. L., Etcoff, N. L., McInerney, S. C., Lee, M. B., & Jenike, M. A. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *Journal of Neuroscience, 18,* 411–418.

Wurtz, R. H., & Kandel, E. R. (2000). Central visual pathways. In E. R. Kandel, J. H. Schwartz, & T. M. Jessel (Eds.), *Principles of neural science* (pp. 523–547). New York: McGraw-Hill.