



## Neural correlates of social and nonsocial emotions: An fMRI study

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Common theories of emotion emphasize valence and arousal dimensions or alternatively, specific emotions, and the search for the underlying neurocircuitry is underway. However, it is likely that other important dimensions for emotional neurocircuitry exist, and one of them is sociality. A social dimension may code whether emotions are addressing an individual's biological/visceral need versus more remote social goals involving semantic meaning or intentionality. Thus, for practical purposes, social emotions may be distinguished from nonsocial emotions based in part on the presence of human forms. In the current fMRI study, we aimed to compare regional coding of the sociality dimension of emotion (nonsocial versus social) versus the valence dimension of emotion (positive versus negative). Using a novel fMRI paradigm, film and picture stimuli were combined to induce and maintain four emotions varying along social and valence dimensions. Nonsocial emotions of positively valenced appetite and negatively valenced disgust and social emotions of positively valenced joy/amusement and negatively valenced sadness were studied. All conditions activated the thalamus. Appetite and disgust activated posterior insula and visual cortex, whereas joy/amusement and sadness activated extended amygdala, superior temporal gyrus, hippocampus, and posterior cingulate. Activations within the anterior cingulate, nucleus accumbens, orbitofrontal cortex, and amygdala were modulated by both social and valence dimensions. Overall, these findings highlight that sociality has a key role in processing emotional valence, which may have implications for patient populations with social and emotional deficits.

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### Introduction

Emotions are often social, but a social dimension of emotional processing is seldom addressed. Common theories of emotion emphasize different dimensions (e.g., valence, arousal, approach/withdrawal); however, given the obvious role of emotion in transacting social behavior, sociality may be another important dimension of emotional functioning. Along an affective valence dimension, positive and negative emotions occupy two ends of the spectrum. Emotions also can vary along a sociality dimension, varying between either nonsocial or social.

The sociality dimension may reflect the differences between basic biological drives (nonsocial) and complex social interaction (social), where the main difference relies on the presence of human forms interacting in cognitively complex ways involving language, meaning and social intentionality to activate the emotion. In the nonsocial domain, emotions often promote individual survival by directing immediate physiological and behavioral responses to biologically significant stimuli (Darwin, 1998) such as approach behavior to food or sexual stimuli and aversive/avoidance behavior including fighting or fleeing (Frijda, 1988). On the other hand, in the social domain, emotions are motivated to direct long-term social goals and are embedded in semantic and thematic meaning. Thus, nonsocial emotions (e.g., appetite/food desire and disgust) are often elicited by incentive or aversive stimuli that have direct physiological relevance, while social emotions (e.g., joy/humor and sadness) emerge in social interactions with other individuals and are typically embedded in structures of social relationship, intentionality, and meaning. Experimentally, stimuli aimed to trigger emotions in the social domain might rely on the presence or absence of human forms and figures, or depict social scenes to elicit emotions. Using a newly developed behavioral paradigm, we differentiated nonsocial and social emotions, as well as positive and negative emotions, based on subjective and psychophysiological responses. Four distinct response profiles for appetite, disgust, joy/amusement, and sadness indicated sociality influences emo-

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tional responses, even to emotions of the same valence (Britton et al., in press). In this study, we asked whether sociality versus valence dimensions of emotion can be distinguished with neuroanatomical specificity?

Sociality includes processing human faces, understanding body language, and making inferences about the intentions of others; thus, it is not surprising that sociality may be processed by a dedicated network of brain regions including fusiform gyrus, superior temporal gyrus, medial prefrontal cortex, amygdala, and posterior cingulate. Face processing has been associated with fusiform and superior temporal gyrus activation. Fusiform gyrus is involved in the perception and recognition of faces (Kanwisher et al., 1997) and processing emotional pictures with human forms and social interactions (Geday et al., 2003). Superior temporal gyrus is involved in understanding complex social signals in eye gaze, mouth movements, and body language (Grossman and Blake, 2002; Pelphrey et al., 2005; Puce et al., 2003). In addition, regions such as medial prefrontal cortex, amygdala, and posterior cingulate have been implicated in self-reflection and assessing others intentions. The medial prefrontal cortex has been implicated in representing states of self versus others, theory of mind, and empathy (Frith and Frith, 2003; Kelley et al., 2002; Phan et al., 2004; Shamay-Tsoory et al., 2004). The amygdala has been associated with processing general salience or meaningfulness of emotional stimuli (Liberzon et al., 2003) and, in particular, social salience evidenced by the deficits in recognizing social emotions and making trustworthiness judgments associated with amygdalar lesions (Adolphs et al., 1998, 2002). Posterior cingulate responded to self-reflection and judgments about others (Johnson et al., 2002; Ochsner et al., 2004). Even though these regions may process social features of stimuli, do these regions respond to social dimension of emotional stimuli, independent of valence?

Neuroimaging studies have identified key brain structures involved in processing appetite, disgust, joy, and sadness. For example, appetite ratings during food presentation have been reported to correlate with blood flow in the right posterior orbitofrontal cortex, suggesting that reward processes are involved (Morris and Dolan, 2001). Humorous film clips have activated the nucleus accumbens (Mobbs et al., 2003; Moran et al., 2004). In addition, amygdala, commonly associated with fear processing (LeDoux, 1998), has been also implicated in processing of happy faces and positive stimuli (Breiter et al., 1996; Liberzon et al., 2003; Somerville et al., 2004). Disgust perception typically activates insular regions (Phillips et al., 1997; Sprengelmeyer et al., 1998), which are also associated with visceral functions, or so-called “gut reactions” (Critchley et al., 2000). Sadness has been associated with subcallosal cingulate (BA25) activation (Phan et al., 2002), and subcallosal cingulate hypometabolism has been reported in depressed patients (Drevets et al., 1997; Mayberg et al., 2000; Mayberg et al., 1999). Although the research on neuroanatomy of emotions (appetite, joy, disgust, and sadness) has been growing, only few studies have compared these emotions across valence (Lane et al., 1997a,b), and in particular, the sociality dimension has been relatively neglected.

To examine whether sociality modulates brain coding of valenced emotions, we used a novel behavioral paradigm, combining film to induce particular emotions and static picture stimuli to maintain those emotions under appropriate conditions for neuroimaging studies (Britton et al., in press). In the current fMRI study, we aimed to (1) identify regions that are involved in processing the sociality dimension of emotions (i.e., regions

responsive to social emotions versus nonsocial emotions), (2) identify regions processing emotional valence (i.e., regions responsive to positive emotions versus negative emotions). We used a paradigm that aimed to manipulate sociality (nonsocial, social) and valence (positive, neutral, negative) as independent factors. Nonsocial conditions used images of physical stimuli, such as an appetizing pizza to elicit a nonsocial positively valenced emotion (appetite) and amputation procedures to elicit a nonsocial negatively valenced emotion (disgust). Social conditions had human actors in scripted situations featuring direct interpersonal engagement, using either humor to elicit a positively valenced social emotion (joy/amusement) or social bereavement to elicit a negatively valenced social emotion (sadness). We examined BOLD activation patterns for both main effects of sociality and valence and interactions effects between these two independent factors (sociality  $\times$  valence). We hypothesized that regions would be more responsive to the social dimension (nonsocial: insula and hypothalamus, social: amygdala, superior temporal gyrus, fusiform, and ventromedial prefrontal cortex); whereas another set of regions may be more responsive to the valence dimension (positive: orbitofrontal cortex, positive/negative: nucleus accumbens, and negative: subgenual anterior cingulate). In addition, some regions may respond to the interaction between social and valence dimensions (e.g., nonsocial negative, disgust: insula).

## Materials and methods

### Participants

Twelve healthy volunteers (6 male, 6 female; age range 19–29 years, mean age  $23.6 \pm 0.96$  years) were recruited from advertisements placed at local universities. All participants were right-handed, English speaking and had normal or corrected-to-normal visual acuity and normal hearing. Participants did not have a history of head injury, learning disability, psychiatric illness, or substance abuse/dependence (>6 months) assessed by Mini-SCID (Sheehan et al., 1998). After explanation of the experimental protocol, all participants gave written informed consent, as approved by the University of Michigan Institutional Review Board. Participants were paid for their participation.

### Apparatus

After completing a practice session, volunteers were placed comfortably within the scanner. A light restraint was used to limit head movement during acquisition. While lying inside the scanner, stimuli were presented to participants via a shielded LCD panel mounted on the RF head coil. From a laptop computer (Macintosh Powerbook), film segments were shown using QuickTime (Apple Computer, Inc.) and participants listened to each film using headphones. Picture and fixation segments were displayed using Eprime software (Psychology Software Tools, Inc., Schneider et al., 2002a,b). In addition, Eprime recorded participants' subjective responses via right-handed button-glove.

### Procedure

Short film segments (~2 min) were shown to induce discrete emotional states. Immediately following each film, participants were asked to maintain the emotion evoked for a 30-s period, while

ten static frames extracted from the previous film were shown in a chronological sequence. Each frame/picture was shown for 3 s with no interstimulus interval. Following the static pictures, another 30-s period of control images (i.e., gray screens with a central fixation cross matched with equivalent brightness as the preceding picture segment) was viewed to control for visual properties of the stimulus and scanner drift across conditions. Subjective ratings were obtained following each film–picture pair by showing a series of adjectives. fMRI acquisition coincided with the 60-s picture presentation period (Fig. 1).

### Stimuli

To dissociate emotions, stimuli varied in sociality (nonsocial, social) and valence (positive, neutral, negative). Nonsocial stimuli included footage from a pizza commercial (Pizza Hut, Inc.) to induce appetite in the sense of a positive urge to eat and footage of wounded bodies, amputation procedures and burn victims (Gross and Levenson, 1995) to induce bodily disgust. Social stimuli included stand-up comedy routines from Robin Williams (An Evening with Robin Williams, 1982) to induce humor and movie clips of poignant bereavement scenes from *Steel Magnolias* (Columbia/Tristar Studios, 1989) and *The Champ* (Warner Home Video, 1979) to induce sadness. To control for human forms and figures in nonsocial and social situations, nonemotional/neutral stimuli were viewed. These nonemotional/neutral stimuli included clips from home-improvement films of deck building, vinyl flooring, chair caning, and jewelry making (Do-It-Yourself, 1985; IBEX, 1990; Nelson et al., 1991; TauntonPress, 1993). Two variants of each stimulus condition were shown.

To avoid carry over effects, similarly valenced blocks were viewed in succession. Positive, joy/amusement and pizza, stimuli were shown sequentially, and negative, disgust and sadness, stimuli were shown sequentially. The two variants of each stimulus were also shown in blocked fashion. The order of sociality (social, nonsocial), order of valenced blocks (positive, neutral, negative), and two variants of each stimuli were counterbalanced across subjects. Each valenced block was flanked by a blank stimulus condition, consisting of a series of gray fixation screens. No film was shown before the blank stimulus condition.

### Measures

#### On-task performance

To monitor task performance during scan acquisition, participants were instructed to respond via button press using the right index finger when a new image appeared on the screen. The reaction time of this response was recorded.

### Subjective response

Subjective responses were obtained after each film–picture pair to verify that the target emotional state was elicited. A series of adjectives were displayed on the screen one at a time. On a 1–5 scale (“1” = not at all, “5” = extremely), participants rated, via button-press, the extent each adjective described their emotional experience during the preceding stimulus presentation. The adjective list included words such as hungry, desire, disgusted, happy, joyful, sad, depressed, upset, relaxed, and interested. The ratings of several descriptors were averaged together to represent four emotion rating types corresponding to each condition (joy/amusement for social positive, sadness for social negative, appetite for nonsocial positive, and disgust for nonsocial negative). In addition, ratings of relaxed were used to measure subjective arousal. Similarly, baseline mood was measured prior to the induction procedure to assess their current emotional state upon entering the study.

### fMRI image acquisition

Scanning was performed on a 3.0-T GE Signa System (Milwaukee, WI) using a standard radio frequency coil. A T1-weighted image was acquired for landmark identification to position subsequent scans. After initial acquisition of T1 structural images, functional images were acquired. To minimize susceptibility artifact (Yang et al., 2002), whole-brain functional scans were acquired using T2\*-weighted reverse spiral sequence with BOLD (blood oxygenation level dependent) contrast (echo time/TE = 30 ms, repetition time/TR of 2000 ms, frequency of 64 frames, flip angle of 80°, field of view/FOV of 20 cm, 40 contiguous 3 mm oblique axial slices/TR approximately parallel to the AC–PC line). Each functional run corresponded to one condition (nonsocial positive, nonsocial neutral, nonsocial negative, social positive, social neutral, social negative or blank). Each run began with 6 ‘dummy’ volumes (subsequently discarded) to allow for T1 equilibration effects. Functional acquisition corresponded to the picture and control images, i.e., scan acquisition did not occur during film segment viewing or during subjective ratings. Thus, each functional run corresponded to 60 s of acquisition or 30 TR volumes (15 volumes per picture segment, 15 volumes per control segment). Two variants of each condition were acquired. After 16 functional runs were collected, a high-resolution T1 scan was also acquired to provide precise anatomical localization (3D-SPGR, TR of 35 ms, min TE, flip angle of 35°, FOV of 24 cm, slice thickness of 2.5 cm, 60 slices/TR). Coimages were reconstructed off-line using the gridding approach into a 128 × 128 display matrix with an effective spatial resolution of 3 mm isotropic voxels.

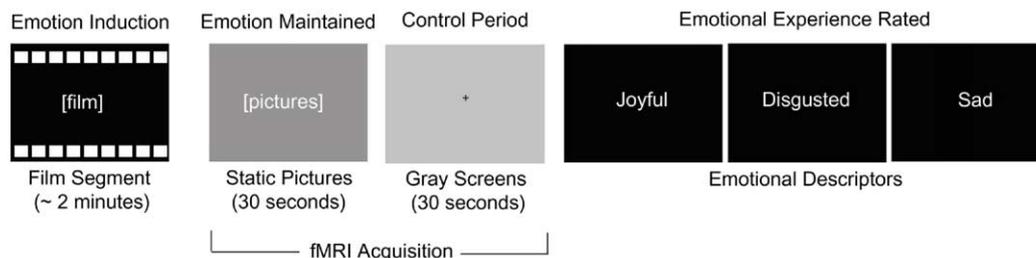


Fig. 1. Time line of events. The sequence of events included (1) a film segment to induce discrete emotional states, (2) static pictures to maintain the emotional state, (3) luminance-matched fixation screens to control for visual properties and scanner drift, (4) a series of adjectives to obtain subjective ratings. fMRI acquisition coincided with the 60-s picture presentation period.

### Statistical analyses

#### Behavioral data

To test on-task performance during fMRI acquisition, the accuracy in responding to the images (i.e., identifying a new image appeared) and the reaction time of a response were examined. The accuracy of response to both picture and control images was examined in a two-tailed paired *t* test. The reaction times were examined using 2 (modality: picture, control image)  $\times$  2 (sociality: nonsocial, social)  $\times$  3 (valence: positive, neutral, and negative) repeated measures ANOVA and post hoc analysis.

The subjective response data were examined using a 2 (sociality: social, nonsocial)  $\times$  3 (valence: positive, neutral, and negative)  $\times$  4 (emotion rating type: appetite, disgust, joy, and sadness) repeated measures ANOVA. Post hoc analysis determined significant changes in subjective response within each condition (social positive–comedy routines, social negative–bereavement scenes, nonsocial positive–pizza scenes, nonsocial negative–wounded bodies). Paired *t* tests were used to determine significant changes in subjective ratings in each emotional condition as compared to the appropriate neutral condition, which controlled for the effect of human forms and figures. Nonsocial positive and nonsocial negative conditions were compared to nonsocial neutral conditions. Social positive and social negative conditions were compared to social neutral condition. One-factor (emotion rating type: appetite, disgust, joy, and sadness ratings) repeated measures ANOVA and Bonferroni post hoc analysis tested whether the targeted emotion was elicited selectively during each respective condition. In addition, paired *t* tests were used to directly compare subjective ratings of arousal between social and nonsocial dimensions within each valence type.

#### fMRI data analysis

Images were slice-time corrected, realigned, coregistered, normalized, and smoothed according to standard methods. Scans were slice-time corrected using sinc interpolation of the eight nearest neighbors in the time series (Oppenheim and Schafer, 1989) and realigned to the first acquired volume using AIR 3.08 routines (Woods et al., 1998). Additional preprocessing and image analysis of the BOLD signal were performed with Statistical Parametric Mapping (SPM99; Wellcome Institute of Cognitive Neurology, London, UK; [www.fil.ion.ucl.ac.uk/spm](http://www.fil.ion.ucl.ac.uk/spm)) implemented in MATLAB (Mathworks, Sherborn, MA). Images were coregistered with the high-resolution SPGR T1 image. This high-resolution image was then spatially normalized, and transformation parameters were then applied to the coregistered functional volumes, resliced, and spatially smoothed by an isotropic 6 mm full-width-half-maximum (FWHM) Gaussian kernel to minimize noise and residual differences in gyral anatomy. Each normalized image set was band pass filtered (high pass filter = 100 s) (Ashburner et al., 1997; Friston et al., 1995) and analyzed using a general linear model with parameters corresponding to run and stimuli type (emotional pictures and control images). Each stimulus block was convolved with a canonical hemodynamic response function (HRF).

For each participant, parameter estimates of block-related activity were obtained at each voxel within the brain. Contrast images were calculated by applying appropriate linear contrasts to the parameter estimates of each block to produce statistical parametric maps of the *t* statistic (SPM{*t*}), which were transformed to a normal distribution (SPM{*Z*}). Since each run

of the scanner included only a single condition and we were interested in comparisons between conditions, it was necessary to control for differences in signal intensity occurring between runs. To do so, we subtracted the 30-s control period from the 30-s maintenance period. All subsequent contrasts compared this maintenance–control difference between conditions. Using the appropriate neutral as the reference condition, relevant linear contrasts included valence main effects (e.g., positive: [social positive + nonsocial positive] – [social neutral + nonsocial neutral]) and “sociality” main effects (e.g., social: [social positive + social negative] – [social neutral]), and valence  $\times$  sociality interaction effects. To account for inter-individual variability, an additional 6-mm smoothing on the contrast images before incorporating the individual contrasts in a random effect analysis.

A second-level random effects analysis used one-sample *t* tests on smoothed contrast images obtained in each subject for each comparison of interest, treating subjects as a random variable (Friston, 1998). This analysis estimates the error variance for each condition of interest across subjects, rather than across scans, and therefore provides a stronger generalization to the population from which data are acquired. In this random effect analysis, resulting SPMs ( $df = 11$ ) were examined in a priori regions of interest known to be involved in emotion processing, medial prefrontal cortex (MPFC), orbitofrontal cortex (OFC), anterior cingulate (ACC), posterior cingulate (PCC), insula, amygdala, sublentiform extended amygdala (SLEA), hippocampus, nucleus accumbens (NAC). Whole-brain analysis conducts comparisons in a voxel-wise manner, increasing the possibility of false positives unless an appropriate correction for multiple comparisons is used. To restrict the number of comparisons, a Small Volume Correction (SVC) also was applied for all activations in a priori regions. SVC was implemented in SPM across three volumes of interest [rectangular box 1:  $x = 0 \pm 70$  mm,  $y = -10 \pm 30$  mm,  $z = -5 \pm 25$  mm, rectangular box 2:  $x = 0 \pm 20$  mm,  $y = -35 \pm 35$  mm,  $z = 15 \pm 45$  mm, rectangular box 3:  $x = 0 \pm 20$  mm,  $y = -40 \pm 30$  mm,  $z = -30 \pm 30$  mm]. Within each SVC, a false discovery rate [FDR] correction of 0.005 was used to ensure that on average no more than 0.5% of activated voxels for each contrast are expected to be false positive results (Genovese et al., 2002). In addition, a cluster size/extent threshold of greater than 5 contiguous voxels was used.

## Results

### On-task performance

Using reaction time as a measure, participants were on-task during the experiment. Participant's responded via button press to 96.5% of the images, missing an equal number of responses to pictures and blanks [ $t(11) = 1.603$ ,  $P > 0.137$ ].

The reaction times showed differences among conditions (Table 1). The reaction time to pictures ( $577.7 \pm 24.6$  ms) was greater than the reaction time to control images ( $451.6 \pm 11.6$  ms) [modality effect:  $F[1,11] = 4.695$ ,  $P < 0.052$ ]. The reaction time to social pictures ( $609.5 \pm 38.5$  ms) was greater than reaction time to nonsocial pictures ( $545.9 \pm 37.9$  ms) [sociality effect:  $F[1,11] = 7.204$ ,  $P < 0.021$ ]. The reaction times to neutral pictures ( $580.6 \pm 41.9$  ms,  $P < 0.031$ ) and negative pictures ( $620.4 \pm 47.5$  ms,  $P < 0.055$ ) were greater than reaction times to positive pictures ( $532.1 \pm$

Table 1  
Reaction Times (RT) show differences for sociality and valence

	Picture (mean RT in ms $\pm$ SEM)	Control (mean RT in ms $\pm$ SEM)
<i>Social</i>		
Positive	557.4 $\pm$ 10.5	450.3 $\pm$ 29.8
Neutral	613.4 $\pm$ 68.0	461.1 $\pm$ 31.3
Negative	657.8 $\pm$ 78.9	457.9 $\pm$ 25.0
<i>Nonsocial</i>		
Positive	506.9 $\pm$ 56.2	452.3 $\pm$ 29.3
Neutral	547.9 $\pm$ 49.4	426.2 $\pm$ 27.3
Negative	583.0 $\pm$ 53.7	462.0 $\pm$ 30.5

37.9 ms) [valence effect:  $F(2,10) = 3.503$ ,  $P < 0.048$ ]. No interaction effects were detected ( $P > 0.684$ ).

### Subjective response

The targeted emotion was elicited by each film–picture condition as intended, and each of the conditions elicited appropriate valenced emotional ratings (Fig. 2). In subjective ratings, a significant sociality  $\times$  valence  $\times$  emotion rating type interaction [ $F(6,54) = 7.815$ ,  $P < 0.001$ ] was detected, prompting further post hoc analysis. Nonsocial positive, pizza, stimuli elicited the target emotion (appetite) more than nontarget emotions (disgust, joy/amusement, sadness). Specifically, pizza scenes elicited appetite [ $t(11) = 4.039$ ,  $P < 0.002$ ] and joyful ratings [ $t(11) = 2.532$ ,  $P < 0.028$ ]. A trend towards significant difference was detected between appetite, the target emotion, and happy/joy, the positive nontarget emotion [pairwise comparison:  $P < 0.113$ ]. Social positive, comedy, stimuli elicited the target emotion (joy/amusement) more than nontarget emotions (sadness, appetite, disgust). Comedy routines elicited joy [ $t(11) = 3.324$ ,  $P < 0.007$ ], while nontarget emotions were unchanged. Nonsocial negative, amputation, stimuli elicited the target emotion (disgust) more than nontarget emotions (appetite, joy/amusement, sadness). Wounded bodies elicited disgust [ $t(11) = 5.026$ ,  $P < 0.001$ ] and sadness [ $t(10) = 4.640$ ,  $P < 0.001$ ] and decreased joy [ $t(11) = -2.264$ ,  $P < 0.045$ ]. A trend towards significant difference was detected between disgust, the target emotion, and sadness, the negative nontarget emotion [pairwise comparison:  $P < 0.131$ ]. Similarly, social negative, bereavement, stimuli elicited the target emotion (sadness) more than nontarget emotions (joy/amusement, appetite, disgust). Bereavement scenes elicited both sadness [ $t(11) = 3.006$ ,  $P < 0.012$ ] and disgust ratings [ $t(11) = 3.684$ ,  $P < 0.004$ ] and decreased joy ratings [ $t(11) = -4.011$ ,  $P < 0.002$ ]; however, no significant difference between target and negative nontarget ratings was detected. This pattern of subjective ratings is consistent with our previous behavioral study; however, in that larger sample ( $n = 40$ ), all conditions elicited the target emotion significantly more than all nontarget emotions (Britton et al., in press).

Nonsocial and social neutral stimuli did not differ from blank on any rating (minimum  $t(11) = 0.488$ ,  $P > 0.635$ , maximum  $t(11) = 1.365$ ,  $P > 0.137$ ). In addition, nonsocial neutral conditions did not differ from social neutral conditions (minimum  $t(11) = -0.2$ ,  $P > 0.845$ , maximum  $t(11) = 1.483$ ,  $P > 0.166$ ). Finally, arousal ratings in social and nonsocial conditions did not significantly differ for any valence [positive:  $t(11) = 0.000$ ,  $P > 1.000$ , neutral:  $t(10) = 1.614$ ,  $P > 0.138$ , negative:  $t(10) = 0.796$ ,  $P > 0.796$ ].

### fMRI results

#### Social dimension

Nonsocial and social emotions, collapsed across valence and compared to neutral conditions, showed a different pattern of regional activation. Nonsocial emotions activated insula and visual cortex (Table 2), while social emotions activated the thalamus, amygdala/SLEA, superior temporal gyrus, hippocampus, and posterior cingulate (Table 3). Insula, visual cortex, and dorsomedial prefrontal cortex activated more during nonsocial emotional stimuli compared to social emotional stimuli; whereas the superior temporal gyrus, posterior cingulate, hippocampus, and nucleus accumbens activate more during social emotional stimuli than nonsocial emotional stimuli (Table 4).

#### Nonsocial emotions

*Appetite (positive) and disgust (negative).* Both nonsocial positive and nonsocial negative stimuli activated thalamus; however, the thalamic activation in the nonsocial negative condition was detected at a subthreshold cluster level [ $(6, -6, 0)$ ,  $Z = 2.76$ ,  $k = 4$ ]. Nonsocial positive and nonsocial negative stimuli

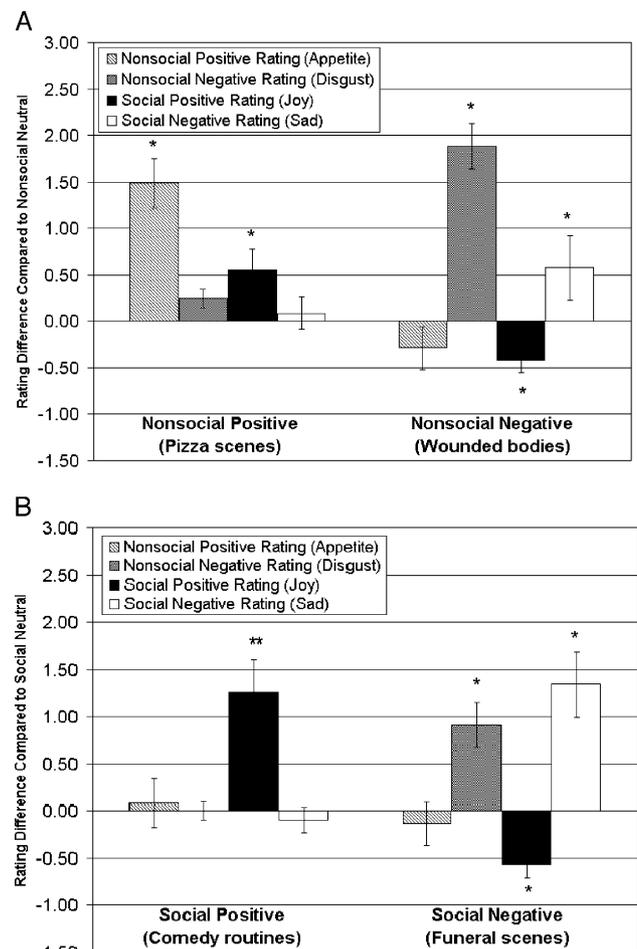


Fig. 2. Ratings partially dissociate nonsocial and social emotions. Ratings in nonsocial (A) and social emotions (B). \*\*Significant difference from neutral (paired  $t$  test,  $P < 0.05$ ) and all nontarget emotions (Bonferroni-adjusted pairwise comparison,  $P < 0.05$ ). \*Significant difference from neutral only (paired  $t$  test,  $P < 0.05$ ).

Table 2

Nonsocial conditions: Activation to nonsocial emotion conditions relative to nonsocial neutral conditions

Region		Nonsocial (positive + negative)			Nonsocial positive (appetite)			Nonsocial negative (disgust)		
		(x, y, z) <sup>a</sup>	Z <sup>b</sup>	k <sup>c</sup>	(x, y, z)	Z	k	(x, y, z) <sup>a</sup>	Z	k
Occipital	Visual	(18, -75, -15)	4.06	154	(24, -75, -18)	4.25	600	(21, -99, 3)	3.30	19
		(18, -99, 6)	3.01	48	(-3, -81, -6)	3.89				
Paralimbic	Insula	(-36, -24, 0)	3.56	13	(-36, -24, 0)	3.00	19	(33, -15, 15)	3.44	17
		(24, -9, 15)	3.35	53	(33, -15, 6)	3.99	55			
Limbic	Anterior cingulate				(-12, 21, 33)	3.09	6			
	Thalamus				(-9, -9, 12)	3.21	14			
	L. amygdala							(-18, -9, -21)	2.66	13

<sup>a</sup> Stereotactic coordinates from MNI atlas, left/right (x), anterior/posterior (y), and superior/inferior (z), respectively. R = right, L = left.

<sup>b</sup> Z score, significant after small volume correction using a false discovery rate [FDR] of 0.005.

<sup>c</sup> Spatial extent in cluster size, threshold ≥5 voxels.

activated the insula and visual cortex. Nonsocial positive appetite stimuli (pizza) activated the anterior cingulate. On the other hand, nonsocial negative disgust stimuli (wounded bodies) activated amygdala (Table 2, Fig. 3).

*Social emotions*

*Joy/humor (positive) and sadness (negative).* Both social positive and social negative stimuli activated thalamus. Social positive stimuli and social negative stimuli activated amygdala/SLEA, superior temporal gyrus, hippocampus, and posterior cingulate. SLEA activation in the social positive condition was at subthreshold cluster level [(-24, 3, -15), Z = 2.83, k = 4]. Social positive joy/amusement stimuli (comedy) activated the orbitofrontal cortex and the nucleus accumbens, a peak within the large thalamic cluster activation. On the other hand, social negative sadness (bereavement) stimuli activated the anterior cingulate (Table 3, Fig. 3).

*Valence-independent and valence-dependent effects.* The insula (Fig. 4A) and visual cortex activated more during both nonsocial positive and nonsocial negative stimuli compared to social stimuli.

The amygdala (Fig. 4B), posterior cingulate, and visual cortex activated more during both social positive and social negative stimuli compared to nonsocial stimuli. Furthermore, the nucleus accumbens and hippocampus activated more during social positive stimuli compared to nonsocial positive stimuli. The anterior cingulate activated more during social negative stimuli compared to nonsocial negative stimuli (Table 4).

*Valence dimension*

Positive and negative emotions, independent of sociality, showed a different pattern of activation. Both positive and negative emotions activated thalamus and visual cortex. Positive emotions activated superior temporal gyrus, hippocampus, and posterior cingulate. Negative emotions activated amygdala/SLEA (Table 5).

**Discussion**

In the current study, four emotions (appetite, disgust, joy, and sadness) induced by film–picture pairs elicited neural activation patterns associated with both sociality and valence dimensions. Nonsocial emotions, appetite and disgust, activated regions

Table 3

Social conditions: Activation to social emotion conditions relative to social neutral conditions

Region		Social (positive + negative)			Social positive (joy)			Social negative (sadness)		
		(x, y, z) <sup>a</sup>	Z <sup>b</sup>	k <sup>c</sup>	(x, y, z)	Z	k	(x, y, z)	Z	k
Occipital	Visual cortex	(-33, -87, -18)	3.47	12	(36, -90, -15)	3.45	120			
		(39, -87, -18)	3.94	60	(-33, -87, -15)	3.19	16			
Temporal	Superior temporal gyrus	(-48, -12, -12)	3.37	20	(42, 6, -21)	3.10	11	(-48, -12, -9)	3.17	43
		(45, -27, -9)	3.29	30						
Frontal	Orbitofrontal cortex				(15, 60, -12)	2.91	5			
Paralimbic	Anterior cingulate							(9, 18, 33)	3.30	10
	Posterior cingulate	(15, -24, 45)	3.87	113	(15, -18, 42)	3.93	54	(15, -24, 45)	3.07	34
Limbic	Thalamus	(3, -3, 3)	3.76	61	(-9, 6, 0)	3.10	23	(3, -3, 3)	3.73	87
					(0, -3, 3)	3.02				
	L. amygdala/SLEA	(-21, 9, -15)	3.16	*				(-15, 3, -12)	3.19	*
	R. amygdala/SLEA	(21, -9, -6)	2.97	**	(30, -6, -15)	3.62	**			
	Hippocampus	(33, -15, -18)	3.63	67	(33, -18, -21)	3.87	98	(39, -12, -27)	3.07	8
	Nucleus accumbens	(-33, -12, -21)	3.12	26	(6, 12, 3)	2.58	**			

\*Part of thalamic cluster, \*\*part of hippocampus, SLEA = sublenticular extended amygdala.

<sup>a</sup> Stereotactic coordinates from MNI atlas, left/right (x), anterior/posterior (y), and superior/inferior (z), respectively. R = right, L = left.

<sup>b</sup> Z score, significant after small volume correction using a false discovery rate [FDR] of 0.005.

<sup>c</sup> Spatial extent in cluster size, threshold ≥5 voxels.

Table 4

Nonsocial and social comparisons: Activation to emotion conditions relative to neutral conditions

Region		Emotion (positive + negative)			Positive			Negative		
		(x, y, z) <sup>a</sup>	Z <sup>b</sup>	k <sup>c</sup>	(x, y, z)	Z	k	(x, y, z)	Z	k
<i>Social &gt; Nonsocial</i>										
Occipital	Visual				(36, -87, -15)	2.98	9	(-9, -81, -9)	3.58	15
					(51, -57, -3)	3.43	48			
Temporal	Superior temporal gyrus	(57, -21, -15)	3.73	87				(-9, 30, 21)	2.89	6
Paralimbic	Anterior cingulate							(-9, -18, 36)	3.50	16
	Posterior cingulate	(15, -27, 36)	3.05	9	(12, -24, 36)	3.20	8	(15, -9, -18)	3.5	16
Limbic	R. amygdala	(18, -12, -18)	3.00	13	(30, -3, -15)	3.2	8	(-9, 3, -6)	3.09	8
	Nucleus accumbens	(-9, 3, -6)	3.91	33	(-6, 6, -6)	3.90	18	(18, -21, -21)	3.34	13
	Hippocampus				(24, -21, -24)	2.95	8			
<i>Nonsocial &gt; Social</i>										
Occipital	Visual	(15, -75, -15)	4.51	423	(15, -75, -15)	4.86	658	(18, -102, -9)	2.97	9
					(-9, -90, -9)	4.73		(15, -99, 6)	2.88	9
					(-18, -63, -9)	3.16	8	(-15, -66, -9)	3.19	7
Frontal	Dorsomedial Prefrontal	(-6, 15, 51)	3.08	6						
		(6, 33, 42)	2.82	6						
Paralimbic	Insula	(-36, -24, 0)	2.91	6	(-39, -9, 12)	3.30	18	(33, 18, 0)	3.45	8
		(54, -18, 12)	2.89	5	(54, -15, 15)	3.34	8			

<sup>a</sup> Stereotactic coordinates from MNI atlas, left/right (x), anterior/posterior (y), and superior/inferior (z), respectively. R = right, L = left.

<sup>b</sup> Z score, significant after small volume correction using a false discovery rate [FDR] of 0.005.

<sup>c</sup> Spatial extent in cluster size, threshold  $\geq 5$  voxels.

involved in visceral response: insula and visual cortex. Nonsocial appetizing pizza also activated anterior cingulate cortex, and nonsocial disgusting wounds also activated amygdala. Social emotions, joy and sadness, activated amygdala/sublenticular extended amygdala, superior temporal gyrus, hippocampus, and posterior cingulate. Positive social joy/amusement also activated reward-associated structures, orbitofrontal cortex and nucleus accumbens. Negative social sadness also activated anterior cingulate cortex. Thus, both sociality and valence exerted powerful effects on brain activation, with some activations related distinctly to a particular social or valence dimension, and other activation patterns jumping complexly across dimensions (for example, anterior cingulate activated by social negative and by nonsocial

positive emotion). Finally, all emotions activated the thalamus regardless of valence or sociality. Behavioral results confirmed on-task performance, and subjective responses indicated that the manipulation elicited targeted emotions.

Our findings suggest that the social dimension of emotion may be as neurobiologically distinct and meaningful as the dimension of valence. As Fig. 5 graphically depicts, positive and negative stimuli activated similar networks; however, in a number of regions, sociality determined more powerfully than valence which brain regions were activated. In addition, some regions responded to specific emotions that appeared to code a complex interaction between positive/negative valence and sociality dimension.

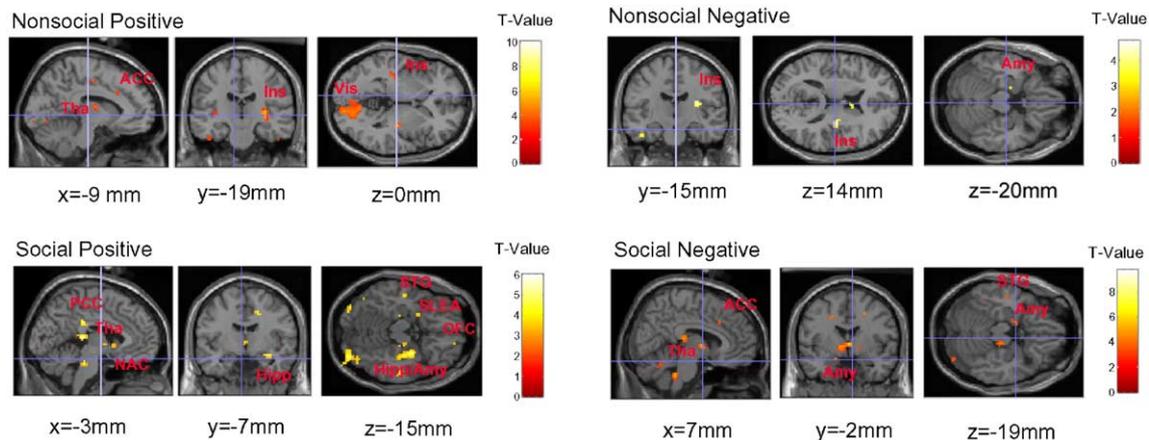
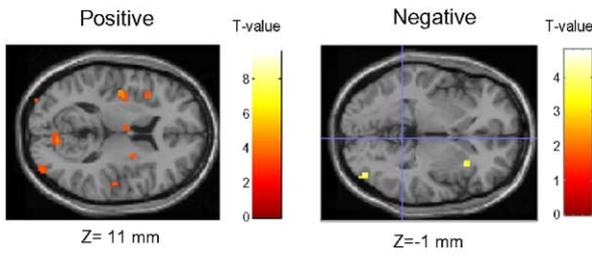


Fig. 3. Differential activation patterns to nonsocial and social emotions. Nonsocial dimension of emotion activates thalamus (Tha), insula (Ins), visual cortex (Vis). Positively valenced nonsocial emotion also activates anterior cingulate (ACC). Negatively valenced nonsocial emotion also activates amygdala (Amy). Social dimension of emotion activates thalamus, amygdala/sublenticular extended amygdala (SLEA), hippocampus (Hipp), posterior cingulate (PCC), and superior temporal gyrus (STG). Positively valenced social emotion also activates nucleus accumbens (NAC) and orbitofrontal cortex (OFC). Negatively valenced social emotion also activates anterior cingulate. Figure threshold  $P < 0.005$ , uncorrected,  $k \geq 5$  voxels. Note: Each set of figures has a different significance scale indicated by T value legend.

A. Insula Activation Greater in Nonsocial Conditions



B. Amygdala Activation Greater in Social Conditions

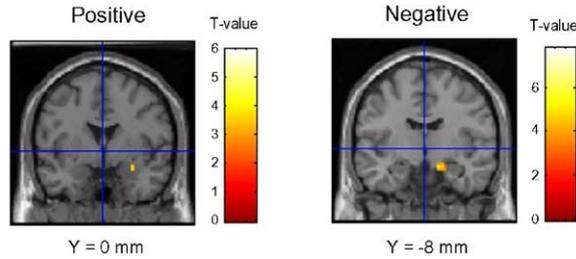


Fig. 4. Nonsocial dimension activates insula and social dimension activates amygdala. SPM *t* maps show greater insula activation in nonsocial emotions [positive: (−39, −9, 12), *Z* = 3.30, [*k*] = 18 and (54, −15, 15), *Z* = 3.34, [*k*] = 8, negative: (33, 18, 0), *Z* = 3.45, [*k*] = 8] and greater amygdala activation in social emotions [positive: (30, −3, −15), *Z* = 3.20, *k* = 8, negative: (15, −9, −18), *Z* = 3.50, [*k*] = 16]. Display threshold: *P* < 0.005, uncorrected, [*k*] ≥ 5 voxels. Note: Each set of figures has a different significance scale indicated by *T* value legend.

Nonsocial

Nonsocial emotions particularly activated regions involved in visceral response. Insular cortex activation to nonsocial emotions is consistent of responses involving monitoring of autonomic changes to maintain homeostasis (Reiman et al., 1997). For example, the insula responds to the interoceptive awareness of one’s own heartbeat (Critchley et al., 2004). In addition, insula may monitor emotional awareness (Craig, 2003).

Since the insula serves as an extension of the gustatory cortex and perceives pain information, it is not surprising that the insula captures the visceral response to appetizing pizza and to bodily disgust (Augustine, 1996). With respect to positive valence, insula responds to food and gustatory stimuli (Craig, 2003; LaBar et al.,

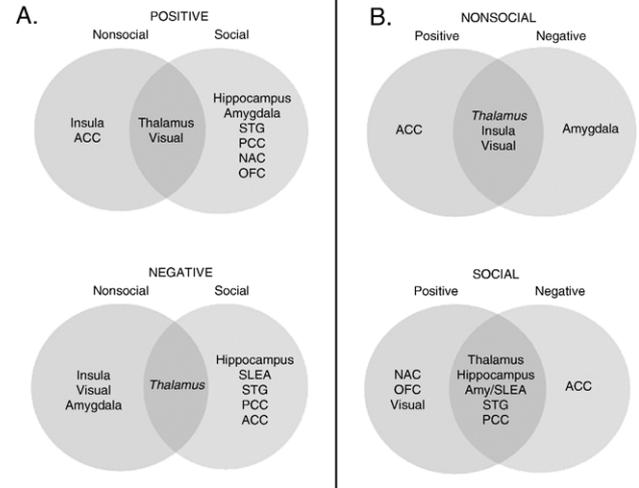


Fig. 5. Social dimension of emotion may be as neurobiologically distinct and meaningful as the dimension of valence. (A) Positive and negative dimensions of emotion activate a similar emotion network; however, little overlap exists along the social dimension within each valence. This emotional network includes thalamus, insula, anterior cingulate (ACC), hippocampus, amygdala (Amy), sublenticular extended amygdala (SLEA), superior temporal gyrus (STG), posterior cingulate (PCC), and visual cortex. In addition, positive conditions activate the nucleus accumbens (NAC) and orbitofrontal cortex (OFC). (B) Differential activation patterns correspond to social dimensions of emotion. Both nonsocial and social emotions activated the thalamus. Nonsocial positive and nonsocial negative emotions activate insula and visual cortex. In addition, ACC activates to nonsocial positive emotions and amygdala activates to nonsocial negative emotions. Social positive and social negative emotions activate amygdala/sublenticular extended amygdala, hippocampus, superior temporal gyrus, and posterior cingulate. In addition, nucleus accumbens and orbitofrontal cortex respond to social positive emotions and ACC respond to social negative emotions. Note: Regions in italics were activated at a subthreshold cluster level, *k* = 4.

2001; Pelchat et al., 2004) and is activated during hunger and satiated states (Hinton et al., 2004; LaBar et al., 2001). Anterior insula has been reported to be associated especially with hunger, while posterior insula has been associated with satiety (Morris and Dolan, 2001). In this study, a more posterior insular region was activated by the appetizing pizza stimulus, which elicited increased hunger ratings, although the participants had not actually been fasted or deprived of food. With respect to negative valence, the insula also has been implicated in disgust and pain. Insular lesions

Table 5  
Valence conditions: Activation to emotion conditions relative to neutral conditions

Region	Positive			Negative			
	( <i>x</i> , <i>y</i> , <i>z</i> ) <sup>a</sup>	<i>Z</i> <sup>b</sup>	<i>k</i> <sup>c</sup>	( <i>x</i> , <i>y</i> , <i>z</i> )	<i>Z</i>	<i>k</i>	
Occipital	Visual	(18, −93, 9)	3.15	21	(−18, −84, 9)	3.65	12
Temporal	Superior temporal gyrus	(−48, −3, −18)	2.91	5			
Paralimbic	Posterior cingulate	(21, −24, 48)	3.51	52			
Limbic	Thalamus	(3, −6, 6)	3.09	11	(6, −3, 0)	3.10	12
	L. amygdala/SLEA				(−21, −6, −21)	2.85	8
	Hippocampus	(33, −6, 15)	3.24	9	(−15, 3, −12)	3.04	13

SLEA = sublenticular extended amygdala.

<sup>a</sup> Stereotactic coordinates from MNI atlas, left/right (*x*), anterior/posterior (*y*), and superior/inferior (*z*), respectively. R = right, L = left.

<sup>b</sup> *Z* score, significant after small volume correction using a false discovery rate [FDR] of 0.005.

<sup>c</sup> Spatial extent in cluster size, threshold ≥5 voxels.

impair disgust recognition (Calder et al., 2000), and functional studies have found insula activations to unpleasant odors (Anderson et al., 2003), disgust pictures (Wright et al., 2004), disgust faces (Phillips et al., 1997), and self-induced disgust (Fitzgerald et al., 2004). Thus, one possibility is that insula activation in our participants may have reflected somatic responses triggered by appetizing and disgusting stimuli. These results are also consistent with greater insular activation found in response to nonsocial negative pictures compared to socially moral pictures (Moll et al., 2002).

This study detected insula activation in nonsocial conditions but not in social conditions; although other studies on amusement and sadness have detected insula activation. For example, those studies have found humor appreciation of films (Moran et al., 2004) and personal recall of a negative event to activate the anterior insula (Lane et al., 1997a,b; Reiman et al., 1997). In this study, however, the emotions of amusement and sadness were externally generated and maintained, which may have made a difference if the inclusion of a maintenance period reduced recruitment of insula activation. That possibility is consistent with findings that internally generated emotion activates the anterior insula more robustly than externally generated emotion (Reiman et al., 1997). In addition, those other studies activated a different region of the insula, anterior insula; whereas our study reports activation of posterior insula, a region thought to be involved in visceral responses, in nonsocial conditions (Augustine, 1996). Thus, the discrepancies in insula activation across studies may be due to partly differences in internally versus externally generated emotion and in regional location within insula cortex.

Nonsocial stimuli also preferentially activated visual cortex, possibly reflecting heightened attention related to motivation in response to the appetizing pizza and disgusting images. Increased activation in the visual cortex may reflect the stimulus' significance to organism (Anderson and Phelps, 2001; Pessoa et al., 2002) or increased attention (Lane et al., 1999). Recently, other investigators also have found that appetizing food stimuli activate the visual cortex (Simmons et al., 2005). Negative disgust facial expressions and immediate threat are reported to elicit increased extrastriate visual cortical activation (Bradley et al., 2003; Simmons et al., 2005).

Amygdala was activated by disgust in this study. Although it is most notably associated with fear (LeDoux, 1998), the amygdala responds to other emotional stimuli including disgust pictures (LeDoux, 1998; Liberzon et al., 2003; Stark et al., 2003; Whalen et al., 1998). In some studies, insula and amygdala activations have been detected using disgust and fearful faces, where insular activation preferentially responded to disgust faces and amygdalar activation preferentially responded to fearful faces (Phillips et al., 1997). It is also possible that the amygdala activation to wounded bodies reflects more nonspecific emotional response similar to that seen with horror films, a combination of innate fear (another nonsocial negative emotion) and disgust.

### Social

Amygdala/sublenticular extended amygdala was activated to social positive and negative conditions. This result is consistent with our previous findings that this region is involved in processing emotional salience (Liberzon et al., 2003). Amygdala/SLEA responds to salient properties of emotional stimuli, and faces are highly salient cues, given their importance in conveying

social meaning (Adolphs et al., 2002; Davis and Whalen, 2001). In addition, it is not surprising that social negative conditions activated more significantly, given the amygdala's preferential involvement in processing negative emotions. Given the findings, the amygdala/sublenticular extended amygdala may preferentially respond to salient emotional properties that are specifically social.

Social emotions of joy and sadness also activated the superior temporal gyrus. This region has been associated with processing facial features and with paying attention to facial expressions (Narumoto et al., 2001); thus, its preferential involvement in processing of social emotions in our study is not surprising. The activation in the superior temporal gyrus reflects the emotional processing demands beyond those required to process facial features, which were isolated by using a nonemotional neutral comparison controlling for human figures. In concert with our findings, this region is also associated with social cognition—social schema, perceptions of social signs, and the mental states of others (Adolphs, 1999; Haxby et al., 2000).

The activations in hippocampus and posterior cingulate may reflect memory processing. The hippocampus is involved in memory retrieval (Stark and Squire, 2001), and the posterior cingulate responds to the interaction between emotion and episodic memory (Maddock, 1999). One participant reported recognizing the social negative video, *Steel Magnolias*, and another reported personal memories associated with the social neutral video, deck-making. Thus, the social stimuli presented in our study may have triggered individual's memories and personal reflection (i.e., remembering personal accounts associated the comedy routine and/or remembering personal accounts associated with death), which may account for the hippocampus and poster cingulate activation (Addis et al., 2004; Gilboa et al., 2004).

To mediate some social interactions, self-referential processing may be engaged. For instance, social emotional processing may require relating/distinguishing the “self” and the “other”. The interplay of these constructs is difficult, if not impossible, to disentangle; however, it is an important feature of sociality. Studies have suggested that the amygdala plays a role in stimulus salience, assessing the meaningfulness of stimuli (Liberzon et al., 2003). In addition, the amygdala has also been shown to detect racial outgroup status, suggesting that the amygdala detects a social “other” (Hart et al., 2000). Several studies have investigated “self” processing through autobiographical memory (Cabeza et al., 2004; Levine et al., 2004), self-association tasks (Phan et al., 2004), and self-related judgments (Johnson et al., 2002; Kelley et al., 2002). Those studies of self-referential processing have implicated the posterior cingulate and medial prefrontal cortex. The posterior cingulate activates with self-generated emotions (Damasio et al., 2000), listening to autobiographical scripts (Fink et al., 1996) and viewing personally familiar faces (Gobbini et al., 2004). Interestingly, dorsomedial prefrontal cortex activation was not detected in social or nonsocial conditions. The mPFC has been shown to be activated during explicit self-association task and modulated in part by self-relevance. On the other hand, mPFC deactivates when making judgments pertaining to “other”, showing less deactivation with self-related processing (Johnson et al., 2002; Kelley et al., 2002). In our study, participants were not directly asked to make personal judgments or personal associations during the emotional task; thus, the failure to find dmPFC may not be surprising as dmPFC is activated with cognitive task (Taylor et al., 2003). According to meta-analysis, dorsomedial prefrontal cortex is

thought to be involved in general emotional processing (e.g., emotional evaluation/appraisal and emotion regulation); thus, it is assumed that these general emotional processes were present in all conditions. In fact at a lower threshold (FDR of 0.05), dmPFC was detected in all conditions. Thus, these regions that process social emotions may be processing the dynamic process of assessing self-relevance in the social interactions presented.

### *Specific emotions*

Anterior cingulate was activated by nonsocial appetite and social sadness but not by the other two emotions. In the case of appetite, anterior cingulate activation may aid in the generation of visceral responses, evidenced by correlations with cardiovascular and skin conductance responses (Critchley et al., 2000, 2001, 2005). In addition, the anterior cingulate activation could reflect attentional control, inhibition of a prepotent response, or conflict monitoring (Devinsky et al., 1995). Attention tasks such as the modified Stroop or dot-probe tasks have shown increased attention to food words in healthy and eating disorder participants (Channon et al., 1988; Mogg et al., 1998), suggesting a heightened salience or increased conflict, internal or otherwise, to the food cues. Anterior cingulate activation was also observed in induction of social sadness. Other studies have reported that sadness activates the anterior cingulate (Prohovnik et al., 2004). However, in this case, a lack of rostral anterior cingulate (BA25) activation is somewhat surprising since sadness induction studies typically activate this region (Mayberg et al., 1999; Phan et al., 2002). In the current study, dorsal anterior cingulate, typically activated in cognitive tasks, was activated rather than a more rostral region of the anterior cingulate, typically activated in emotional tasks (Bush et al., 2000). Conceivably sadness could have had less self-relevance and more cognitive processing (Reiman et al., 1997), though this interpretation is clearly speculative. For example, anterior cingulate activation may reflect participants distancing themselves from the bereavement scenes to avoid becoming overly sad.

Regions involved in reward processing have been reported to respond to positive valence, and we observed activation of these regions with social positive emotion. Specifically, orbitofrontal cortex and nucleus accumbens are associated with positive motivational significance (Berridge, 1996; Kelley, 2004; O'Doherty et al., 2000; Rolls, 2000; Rolls and Baylis, 1994). Orbitofrontal cortical activation has also been associated with appraising social-emotional stimuli and guiding goal-directed behavior (Bechara et al., 2000; Damasio et al., 2000) and with response to the valence of odors (Anderson et al., 2003). Basal ganglia activation including the ventral striatum has been reported in 70% of happiness induction studies (Phan et al., 2002), including pleasant pictures (Lane et al., 1997a,b), happy faces (Morris et al., 1996; Whalen et al., 1998), and happiness recall (George et al., 1996; Phan et al., 2002). In previous studies, orbitofrontal cortex activation has been detected when viewing food stimuli (Rolls and Baylis, 1994) and correlated with hunger ratings (Morris and Dolan, 2001). In our study, it is not entirely clear why appetizing pizza failed to activate nucleus accumbens or orbitofrontal cortex. This difference in response to social and visceral rewards might reflect a difference between obtained reward and anticipated reward. (Knutson et al., 2001). In this case, the comedy routine seems to be an immediate rewarding experience for participants; whereas the pizza scenes

may not be directly rewarding since food was not tasted (Arana et al., 2003). Alternatively, it might reflect an intensity difference, if the pizza image was not sufficiently potent to activate reward circuitry. Our participants were not required to fast prior to this study, which may have diminished the motivational salience of the pizza scenes (Critchley and Rolls, 1996; Wang et al., 2004), and no odor or sight of real pizza was presented here. Future studies could explore the role of these factors in determining activation of orbitofrontal cortex and nucleus accumbens.

### *General findings*

All the stimuli used in this study activated the thalamus, a central sensory gateway. Prior work from other groups using positive and negative IAPS pictures to elicit emotional responses also reported activation of the thalamus (Lane et al., 1997b). Similarly, other emotion activation paradigms that used film and script-driven recall to induce happy, sad, and disgust also elicited thalamic activation (Lane et al., 1997a).

Several limitations of this study should be noted. In trying to underscore the importance of characterizing emotions based on a social dimension, this design contrasted two important factors, a social dimension (social, nonsocial) and a valence dimension (positive, negative); therefore, this design did not fully account for all potential differences (e.g., physiological, cognitive mechanisms, cognitive effort) among the conditions; however, we have attempted to match the stimuli on multiple dimensions within social and nonsocial conditions. Our previous study indicated that differences in physiological arousal (skin conductance response) cannot account for the differences in emotional responses to social and nonsocial stimuli that were used (Britton et al., *in press*). Reaction time differences between social and nonsocial emotions were detected, suggesting that the social emotional conditions may involve additional cognitive demands (e.g., cognitive effort, heightened salience/attention, personal recollection). These differences, however, are unlikely to stem from simple stimuli processing differences since we matched stimuli and used a “subtraction” technique, and actually might be an integral component of “sociality” processing. Processing and understanding the films may require different cognitive mechanisms (e.g., inferential reasoning) and associated regions; therefore, the still frames were introduced to provide a more controlled period as the stimuli are only visual reminders of an emotionally laden event. All conditions required cognitive recall during the still frame period, and the fMRI acquisition that took place at that time captured episodic memory retrieval and associated emotional state. Like the reaction time differences, episodic memory retrieval component is essentially “subtracted out” when emotional and neutral conditions are compared. To minimize the effort required for maintaining the emotions, the still frames immediately followed the eliciting films. Of note, no participants reported any difficulty in maintaining the emotions during the still frame period. The emotions that represented each cell were chosen to maximize the social/nonsocial and positive/negative distinction and only two social emotions (joy and sadness) and two nonsocial emotions (appetite/food desire and bodily disgust) were studied. According to Adolphs, the selected social emotions would be classified as “basic” social emotions; however, future investigations could explore “other” social emotions, such as embarrassment, guilt, and shame, and additional nonsocial emotions, such as thirst, pain, and object fear. In

addition, emotions may occupy both ends of the social dimension. For example, disgust can be evoked by body mutilation or by moral differences. Future investigation is needed to determine if these types of disgust can be dissociated based on this social dimension. Although our conservative random effects analysis and SVC protects against Type I errors, other sources of error (i.e., Type II error due to reduced power) may explain the data; thus, conclusive evidence for absence of activation awaits replication. Finally, this analysis assumed a canonical hemodynamic response function; however, emotions along the sociality dimension may have different temporal dynamics (Siegle et al., 2002), and this deserves further exploration.

Despite these limitations, future directions should also investigate the effect of sociality as a defining feature of emotion in patient populations. Many disorders have both social and emotional components to the symptomatology. Patients with autism and Asperger's syndrome, a high functioning form of autism, have difficulties in face processing (Hobson, 1986; Hobson et al., 1988a,b; Pierce et al., 2001), show reduced eye contact with others (Hobson and Lee, 1998), and have an impaired ability to attribute emotions to others (Adolphs et al., 2002). Diminished eye gaze may explain diminished amygdala and fusiform activation when viewing faces (Dalton et al., 2005). Schizophrenia is composed of both affective and social deficits (Dworkin, 1992). Elevated tonic amygdala activity, inversely correlated with overall schizophrenic symptoms (Taylor et al., 2005), and exaggerated amygdala activation to emotional faces has been detected in schizophrenic patients (Bediou et al., 2005; Kosaka et al., 2002), suggesting abnormal processing of social emotions may play a role in schizophrenia. Patients with social phobia have an intense fear of social situations resulting in inhibited social behavior (DSM-IV). Social phobics have shown increased amygdala activation in an aversive conditioning task with neutral faces (Veit et al., 2002). In addition, patients with specific phobia (e.g., spider, snakes) have shown increased insula but similar amygdala responses to facial expressions as healthy controls (Wright et al., 2003). These disorders highlight a key intersection between social and emotional processes; however, few neuroimaging studies have attempted to examine these factors, sociality and emotion, simultaneously.

Using a combination of film induction and picture recall, we demonstrated that a social dimension of emotion may be as neurobiologically distinct and meaningful as the valence dimension for brain activation. Nonsocial (appetite/food desire and disgust) and social emotions (joy and sadness) activate partially overlapping but somewhat separate neural patterns. All conditions (nonsocial positive, nonsocial negative, social positive, social negative) activated the thalamus. Nonsocial conditions activated insula and visual cortex, whereas social conditions activated amygdala/sublenticular extended amygdala, superior temporal gyrus, hippocampus, and posterior cingulate. Activations within the amygdala, anterior cingulate, nucleus accumbens, and orbitofrontal cortex depended complexly on both social context and valence. Overall, these findings highlight the key role of sociality in eliciting emotion and may have implications for patient populations.

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#### References

- Addis, D.R., Moscovitch, M., Crawley, A.P., McAndrews, M.P., 2004. Recollective qualities modulate hippocampal activation during autobiographical memory retrieval. *Hippocampus* 14 (6), 752–762.
- Adolphs, R., 1999. Social cognition and the human brain. *Trends Cogn. Sci.* 3 (12), 469–479.
- Adolphs, R., Tranel, D., Damasio, A.R., 1998. The human amygdala in social judgment. *Nature* 393 (6684), 470–474.
- Adolphs, R., Baron-Cohen, S., Tranel, D., 2002. Impaired recognition of social emotions following amygdala damage. *J. Cogn. Neurosci.* 14 (8), 1264–1274.
- Anderson, A.K., Phelps, E.A., 2001. Lesions of the human amygdala impair enhanced perception of emotionally salient events. *Nature* 411 (6835), 305–309.
- Anderson, A.K., Christoff, K., Stappen, I., Panitz, D., Ghahremani, D.G., Glover, G., et al., 2003. Dissociated neural representations of intensity and valence in human olfaction. *Nat. Neurosci.* 6 (2), 196–202.
- Arana, F.S., Parkinson, J.A., Hinton, E., Holland, A.J., Owen, A.M., Roberts, A.C., 2003. Dissociable contributions of the human amygdala and orbitofrontal cortex to incentive motivation and goal selection. *J. Neurosci.* 23 (29), 9632–9638.
- Ashburner, J., Neelin, P., Collins, D.L., Evans, A., Friston, K., 1997. Incorporating prior knowledge into image registration. *NeuroImage* 6 (4), 344–352.
- Augustine, J.R., 1996. Circuitry and functional aspects of the insular lobe in primates including humans. *Brain Res. Brain Res. Rev.* 22 (3), 229–244.
- Bechara, A., Damasio, H., Damasio, A.R., 2000. Emotion, decision making and the orbitofrontal cortex. *Cereb. Cortex* 10 (3), 295–307.
- Bediou, B., Franck, N., Saoud, M., Baudouin, J.Y., Tiberghien, G., Dalery, J., et al., 2005. Effects of emotion and identity on facial affect processing in schizophrenia. *Psychiatry Res.* 133 (2–3), 149–157.
- Berridge, K.C., 1996. Food reward: brain substrates of wanting and liking. *Neurosci. Biobehav. Rev.* 20 (1), 1–25.
- Bradley, M.M., Sabatinelli, D., Lang, P.J., Fitzsimmons, J.R., King, W., Desai, P., 2003. Activation of the visual cortex in motivated attention. *Behav. Neurosci.* 117 (2), 369–380.
- 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 (5), 875–887.
- Britton, J.C., Taylor, S.F., Berridge, K.C., Mikels, J.A., Liberzon, I., in press. Differential subjective and psychophysiological responses to socially and nonsocially generated emotional stimuli. *Emotion*.
- Bush, G., Luu, P., Posner, M.I., 2000. Cognitive and emotional influences in anterior cingulate cortex. *Trends Cogn. Sci.* 4 (6), 215–222.
- Calder, A.J., Keane, J., Manes, F., Antoun, N., Young, A.W., 2000. Impaired recognition and experience of disgust following brain injury. *Nat. Neurosci.* 3 (11), 1077–1078.
- Cabeza, R., Prince, S.E., Daselaar, S.M., Greenberg, D.L., Budde, M., Dolcos, F., et al., 2004. Brain activity during episodic retrieval of autobiographical and laboratory events: an fMRI study using a novel photo paradigm. *J. Cogn. Neurosci.* 16 (9), 1583–1594.
- Channon, S., Hemsley, D., de Silva, P., 1988. Selective processing of food words in anorexia nervosa. *Br. J. Clin. Psychol.* 27 (Pt. 3), 259–260.
- Craig, A.D., 2003. Interoception: the sense of the physiological condition of the body. *Curr. Opin. Neurobiol.* 13 (4), 500–505.
- Critchley, H.D., Rolls, E.T., 1996. Hunger and satiety modify the responses of olfactory and visual neurons in the primate orbitofrontal cortex. *J. Neurophysiol.* 75 (4), 1673–1686.
- Critchley, H.D., Elliott, R., Mathias, C.J., Dolan, R.J., 2000. Neural activity relating to generation and representation of galvanic skin conductance responses: a functional magnetic resonance imaging study. *J. Neurosci.* 20 (8), 3033–3040.
- Critchley, H.D., Melmed, R.N., Featherstone, E., Mathias, C.J., Dolan, R.J.,

2001. Brain activity during biofeedback relaxation: a functional neuroimaging investigation. *Brain* 124 (Pt. 5), 1003–1012.
- Critchley, H.D., Wiens, S., Rotshtein, P., Ohman, A., Dolan, R.J., 2004. Neural systems supporting interoceptive awareness. *Nat. Neurosci.* 7 (2), 189–195.
- Critchley, H.D., Tang, J., Glaser, D., Butterworth, B., Dolan, R.J., 2005. Anterior cingulate activity during error and autonomic response. *NeuroImage* 27 (4), 885–895.
- Dalton, K.M., Nacewicz, B.M., Johnstone, T., Schaefer, H.S., Gernsbacher, M.A., Goldsmith, H.H., et al., 2005. Gaze fixation and the neural circuitry of face processing in autism. *Nat. Neurosci.* 8 (4), 519–526.
- Damasio, A.R., Grabowski, T.J., Bechara, A., Damasio, H., Ponto, L.L., Parvizi, J., et al., 2000. Subcortical and cortical brain activity during the feeling of self-generated emotions. *Nat. Neurosci.* 3 (10), 1049–1056.
- Darwin, C., 1998. *The Expressions of Emotions in Man and Animals*, 3rd edition. Oxford University Press, New York.
- Davis, M., Whalen, P.J., 2001. The amygdala: vigilance and emotion. *Mol. Psychiatry* 6 (1), 13–34.
- Devinsky, O., Morrell, M.J., Vogt, B.A., 1995. Contributions of anterior cingulate cortex to behaviour. *Brain* 118 (Pt. 1), 279–306.
- Do-It-Yourself (Writer), 1985. Vinyl floors. In D.V. Corp (Producer), *Home Improvement videos; Hands-on series*. Charlotte, NC.
- Drevets, W.C., Price, J.L., Simpson Jr., J.R., Todd, R.D., Reich, T., Vannier, M., et al., 1997. Subgenual prefrontal cortex abnormalities in mood disorders. *Nature* 386 (6627), 824–827.
- Dworkin, R.H., 1992. Affective deficits and social deficits in schizophrenia: what's what? *Schizophr. Bull.* 18 (1), 59–64.
- Fink, G.R., Markowitsch, H.J., Reinkemeier, M., Bruckbauer, T., Kessler, J., Heiss, W.D., 1996. Cerebral representation of one's own past: neural networks involved in autobiographical memory. *J. Neurosci.* 16 (13), 4275–4282.
- Fitzgerald, D.A., Posse, S., Moore, G.J., Tancer, M.E., Nathan, P.J., Phan, K.L., 2004. Neural correlates of internally-generated disgust via autobiographical recall: a functional magnetic resonance imaging investigation. *Neurosci. Lett.* 370 (2–3), 91–96.
- Frijda, N.H., 1988. The laws of emotion. *Am. Psychol.* 43 (5), 349–358.
- Friston, K.J., 1998. Generalisability, random effects and population inference. *NeuroImage* 7, S754.
- Friston, K., Holmes, A.P., K.J., W., Poline, J.B., Frith, C.D., Frackowiak, R.S. (1995). Statistical parametric maps in functional imaging: a general linear approach. 1995, 2, 189–210.
- Frith, U., Frith, C.D., 2003. Development and neurophysiology of mentalizing. *Philos. Trans. R. Soc. London, Ser. B Biol. Sci.* 358 (1431), 459–473.
- Geday, J., Gjedde, A., Boldsen, A.S., Kupers, R., 2003. Emotional valence modulates activity in the posterior fusiform gyrus and inferior medial prefrontal cortex in social perception. *NeuroImage* 18 (3), 675–684.
- Genovese, C.R., Lazar, N.A., Nichols, T., 2002. Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *NeuroImage* 15 (4), 870–878.
- George, M.S., Ketter, T.A., Parekh, P.I., Herscovitch, P., Post, R.M., 1996. Gender differences in regional cerebral blood flow during transient self-induced sadness or happiness. *Biol. Psychiatry* 40 (9), 859–871.
- Gilboa, A., Winocur, G., Grady, C.L., Hevenor, S.J., Moscovitch, M., 2004. Remembering our past: functional neuroanatomy of recollection of recent and very remote personal events. *Cereb. Cortex* 14 (11), 1214–1225.
- Gobbini, M.I., Liebenluft, E., Santiago, N., Haxby, J.V., 2004. Social and emotional attachment in the neural representation of faces. *NeuroImage* 22, 1628–1635.
- Gross, J.J., Levenson, R.W., 1995. Emotion elicitation using films. *Cogn. Emot.* 9 (1), 87–108.
- Grossman, E.D., Blake, R., 2002. Brain areas active during visual perception of biological motion. *Neuron* 35 (6), 1167–1175.
- Hart, A.J., Whalen, P.J., Shin, L.M., McInerney, S.C., Fischer, H., Rauch, S.L., 2000. Differential response in the human amygdala to racial outgroup vs ingroup face stimuli. *NeuroReport* 11 (11), 2351–2355.
- Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2000. The distributed human neural system for face perception. *Trends Cogn. Sci.* 4 (6), 223–233.
- Hinton, E.C., Parkinson, J.A., Holland, A.J., Arana, F.S., Roberts, A.C., Owen, A.M., 2004. Neural contributions to the motivational control of appetite in humans. *Eur. J. Neurosci.* 20 (5), 1411–1418.
- Hobson, R.P., 1986. The autistic child's appraisal of expressions of emotion: a further study. *J. Child. Psychol. Psychiatry* 27 (5), 671–680.
- Hobson, R.P., Lee, A., 1998. Hello and goodbye: a study of social engagement in autism. *J. Autism Dev. Disord.* 28 (2), 117–127.
- Hobson, R.P., Ouston, J., Lee, A., 1988a. Emotion recognition in autism: coordinating faces and voices. *Psychol. Med.* 18 (4), 911–923.
- Hobson, R.P., Ouston, J., Lee, A., 1988b. What's in a face? The case of autism. *Br. J. Psychol.* 79 (Pt. 4), 441–453.
- IBEX (Writer), 1990. Cast jewelry. In G.P.N.I.T. Library (Producer), *Artsmart*. Lincoln, NE.
- Johnson, S.C., Baxter, L.C., Wilder, L.S., Pipe, J.G., Heiserman, J.E., Prigatano, G.P., 2002. Neural correlates of self-reflection. *Brain* 125 (Pt. 8), 1808–1814.
- Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* 17 (11), 4302–4311.
- Kelley, A.E., 2004. Ventral striatal control of appetitive motivation: role in ingestive behavior and reward-related learning. *Neurosci. Biobehav. Rev.* 27 (8), 765–776.
- Kelley, W.M., Macrae, C.N., Wyland, C.L., Caglar, S., Inati, S., Heatherton, T.F., 2002. Finding the self? An event-related fMRI study. *J. Cogn. Neurosci.* 14 (5), 785–794.
- Knutson, B., Fong, G.W., Adams, C.M., Varner, J.L., Hommer, D., 2001. Dissociation of reward anticipation and outcome with event-related fMRI. *NeuroReport* 12 (17), 3683–3687.
- Kosaka, H., Omori, M., Murata, T., Iidaka, T., Yamada, H., Okada, T., et al., 2002. Differential amygdala response during facial recognition in patients with schizophrenia: an fMRI study. *Schizophr. Res.* 57 (1), 87–95.
- 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. *Behav. Neurosci.* 115 (2), 493–500.
- Lane, R.D., Reiman, E.M., Ahern, G.L., Schwartz, G.E., Davidson, R.J., 1997a. Neuroanatomical correlates of happiness, sadness, and disgust. *Am. J. Psychiatry* 154 (7), 926–933.
- Lane, R.D., Reiman, E.M., Bradley, M.M., Lang, P.J., Ahern, G.L., Davidson, R.J., et al., 1997b. Neuroanatomical correlates of pleasant and unpleasant emotion. *Neuropsychologia* 35 (11), 1437–1444.
- Lane, R.D., Chua, P.M., Dolan, R.J., 1999. Common effects of emotional valence, arousal and attention on neural activation during visual processing of pictures. *Neuropsychologia* 37 (9), 989–997.
- LeDoux, J., 1998. Fear and the brain: where have we been, and where are we going? *Biol. Psychiatry* 44 (12), 1229–1238.
- Levine, B., Turner, G.R., Tisserand, D., Hevenor, S.J., Graham, S.J., McIntosh, A.R., 2004. The functional neuroanatomy of episodic and semantic autobiographical remembering: a prospective functional MRI study. *J. Cogn. Neurosci.* 16 (9), 1633–1646.
- Liberzon, I., Phan, K.L., Decker, L.R., Taylor, S.F., 2003. Extended amygdala and emotional salience: a PET activation study of positive and negative affect. *Neuropsychopharmacology* 28 (4), 726–733.
- Maddock, R.J., 1999. The retrosplenial cortex and emotion: new insights from functional neuroimaging of the human brain. *Trends Neurosci.* 22 (7), 310–316.
- Mayberg, H.S., Liotti, M., Brannan, S.K., McGinnis, S., Mahurin, R.K., Jerabek, P.A., et al., 1999. Reciprocal limbic–cortical function and negative mood: converging PET findings in depression and normal sadness. *Am. J. Psychiatry* 156 (5), 675–682.
- Mayberg, H.S., Brannan, S.K., Tekell, J.L., Silva, J.A., Mahurin, R.K., McGinnis, S., et al., 2000. Regional metabolic effects of fluoxetine in major depression: serial changes and relationship to clinical response. *Biol. Psychiatry* 48 (8), 830–843.

- Mobbs, D., Greicius, M.D., Abdel-Azim, E., Menon, V., Reiss, A.L., 2003. Humor modulates the mesolimbic reward centers. *Neuron* 40 (5), 1041–1048.
- Mogg, K., Bradley, B.P., Hyare, H., Lee, S., 1998. Selective attention to food-related stimuli in hunger: are attentional biases specific to emotional and psychopathological states, or are they also found in normal drive states? *Behav. Res. Ther.* 36 (2), 227–237.
- Moll, J., de Oliveira-Souza, R., Eslinger, P.J., Bramati, I.E., Mourao-Miranda, J., Andreiuolo, P.A., et al., 2002. The neural correlates of moral sensitivity: a functional magnetic resonance imaging investigation of basic and moral emotions. *J. Neurosci.* 22 (7), 2730–2736.
- Moran, J.M., Wig, G.S., Adams Jr., R.B., Janata, P., Kelley, W.M., 2004. Neural correlates of humor detection and appreciation. *NeuroImage* 21 (3), 1055–1060.
- Morris, J.S., Dolan, R.J., 2001. Involvement of human amygdala and orbitofrontal cortex in hunger-enhanced memory for food stimuli. *J. Neurosci.* 21 (14), 5304–5310.
- Morris, J.S., Frith, C.D., Perrett, D.I., Rowland, D., Young, A.W., Calder, A.J., et al., 1996. A differential neural response in the human amygdala to fearful and happy facial expressions. *Nature* 383 (6603), 812–815.
- Narumoto, J., Okada, T., Sadato, N., Fukui, K., Yonekura, Y., 2001. Attention to emotion modulates fMRI activation in human right superior temporal sulcus. *Brain Res. Cogn. Brain Res.* 12 (2), 225–231.
- Nelson, J., Nelson, R., Hungate, T. (Writer), 1991. The Nelson video on chair caning with Jane. In N. Videos (Producer). Cashmere, WA.
- O'Doherty, J., Rolls, E.T., Francis, S., Bowtell, R., McGlone, F., Kobal, G., et al., 2000. Sensory-specific satiety-related olfactory activation of the human orbitofrontal cortex. *NeuroReport* 11 (2), 399–403.
- Ochsner, K.N., Knierim, K., Ludlow, D.H., Hanelin, J., Ramachandran, T., Glover, G., et al., 2004. Reflecting upon feelings: an fMRI study of neural systems supporting the attribution of emotion to self and other. *J. Cogn. Neurosci.* 16 (10), 1746–1772.
- Oppenheim, A., Schafer, R., 1989. *Discrete-Time Signal Processing*. Prentice Hall, Englewood Cliffs, NJ.
- Pelchat, M.L., Johnson, A., Chan, R., Valdez, J., Ragland, J.D., 2004. Images of desire: food-craving activation during fMRI. *NeuroImage* 23 (4), 1486–1493.
- Pelphrey, K.A., Morris, J.P., Michelich, C.R., Allison, T., McCarthy, G., 2005. Functional anatomy of biological motion perception in posterior temporal cortex: an fMRI study of eye, mouth and hand movements. *Cereb. Cortex* 15 (12), 1866–1876.
- Pessoa, L., Kastner, S., Ungerleider, L.G., 2002. Attentional control of the processing of neural and emotional stimuli. *Brain Res. Cogn. Brain Res.* 15 (1), 31–45.
- Phan, K.L., Wager, T., Taylor, S.F., Liberzon, I., 2002. Functional neuroanatomy of emotion: a meta-analysis of emotion activation studies in PET and fMRI. *NeuroImage* 16 (2), 331–348.
- Phan, K.L., Taylor, S.F., Welsh, R.C., Ho, S.H., Britton, J.C., Liberzon, I., 2004. Neural correlates of individual ratings of emotional salience: a trial-related fMRI study. *NeuroImage* 21 (2), 768–780.
- Phillips, M.L., Young, A.W., Senior, C., Brammer, M., Andrew, C., Calder, A.J., et al., 1997. A specific neural substrate for perceiving facial expressions of disgust. *Nature* 389 (6650), 495–498.
- Pierce, K., Muller, R.A., Ambrose, J., Allen, G., Courchesne, E., 2001. Face processing occurs outside the fusiform 'face area' in autism: evidence from functional MRI. *Brain* 124 (Pt. 10), 2059–2073.
- Prohovnik, I., Skudlarski, P., Fulbright, R.K., Gore, J.C., Wexler, B.E., 2004. Functional MRI changes before and after onset of reported emotions. *Psychiatry Res.* 132 (3), 239–250.
- Puce, A., Syngneniotis, A., Thompson, J.C., Abbott, D.F., Wheaton, K.J., Castiello, U., 2003. The human temporal lobe integrates facial form and motion: evidence from fMRI and ERP studies. *NeuroImage* 19 (3), 861–869.
- Reiman, E.M., Lane, R.D., Ahern, G.L., Schwartz, G.E., Davidson, R.J., Friston, K.J., et al., 1997. Neuroanatomical correlates of externally and internally generated human emotion. *Am. J. Psychiatry* 154 (7), 918–925.
- Rolls, E.T., 2000. The orbitofrontal cortex and reward. *Cereb. Cortex* 10 (3), 284–294.
- Rolls, E.T., Baylis, L.L., 1994. Gustatory, olfactory, and visual convergence within the primate orbitofrontal cortex. *J. Neurosci.* 14 (9), 5437–5452.
- Schneider, W., Eschman, A., Zuccolotto, A., 2002a. *E-Prime Reference Guide*. Psychology Software Tools, Inc, Pittsburgh.
- Schneider, W., Eschman, A., Zuccolotto, A., 2002b. *E-Prime User's Guide*. Psychology Software Tools, Inc, Pittsburgh.
- Shamay-Tsoory, S.G., Tomer, R., Goldsher, D., Berger, B.D., Aharon-Peretz, J., 2004. Impairment in cognitive and affective empathy in patients with brain lesions: anatomical and cognitive correlates. *J. Clin. Exp. Neuropsychol.* 26 (8), 1113–1127.
- Sheehan, D., Janavs, J., Baker, R., Harnett-Sheehan, K., Knapp, E., Sheehan, M., et al., 1998. *Mini International Neuropsychiatric Interview, English Version 5.0.0, DSM-IV*.
- Siegle, G.J., Steinhauer, S.R., Thase, M.E., Stenger, V.A., Carter, C.S., 2002. Can't shake that feeling: event-related fMRI assessment of sustained amygdala activity in response to emotional information in depressed individuals. *Biol. Psychiatry* 51 (9), 693–707.
- Simmons, W.K., Martin, A., Barsalou, L.W., 2005. Pictures of appetizing foods activate gustatory cortices for taste and reward. *Cereb. Cortex* 15 (10), 1602–1608.
- Somerville, L.H., Kim, H., Johnstone, T., Alexander, A.L., Whalen, P.J., 2004. Human amygdala responses during presentation of happy and neutral faces: correlations with state anxiety. *Biol. Psychiatry* 55 (9), 897–903.
- Sprengelmeyer, R., Rausch, M., Eysel, U.T., Przuntek, H., 1998. Neural structures associated with recognition of facial expressions of basic emotions. *Proc. R. Soc. London, Ser. B Biol. Sci. Biol. Sci.* 265 (1409), 1927–1931.
- Stark, C.E., Squire, L.R., 2001. Simple and associative recognition memory in the hippocampal region. *Learn. Mem.* 8 (4), 190–197.
- Stark, R., Schienle, A., Walter, B., Kirsch, P., Sammer, G., Ott, U., et al., 2003. Hemodynamic responses to fear and disgust-inducing pictures: an fMRI study. *Int. J. Psychophysiol.* 50 (3), 225–234.
- TauntonPress (Writer), 1993. *Building decks with Scott Schuttner*. In T. Press (Producer), *A Fine Homebuilding Video Workshop*. Newton, CT.
- Taylor, S.F., Phan, K.L., Decker, L.R., Liberzon, I., 2003. Subjective rating of emotionally salient stimuli modulates neural activity. *NeuroImage* 18 (3), 650–659.
- Taylor, S.F., Phan, K.L., Britton, J.C., Liberzon, I., 2005. Neural response to emotional salience in schizophrenia. *Neuropsychopharmacology* 30 (5), 984–995.
- Veit, R., Flor, H., Erb, M., Hermann, C., Lotze, M., Grodd, W., et al., 2002. Brain circuits involved in emotional learning in antisocial behavior and social phobia in humans. *Neurosci. Lett.* 328 (3), 233–236.
- Wang, G.J., Volkow, N.D., Telang, F., Jayne, M., Ma, J., Rao, M., et al., 2004. Exposure to appetitive food stimuli markedly activates the human brain. *NeuroImage* 21 (4), 1790–1797.
- 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. *J. Neurosci.* 18 (1), 411–418.
- Woods, R.P., Grafton, S.T., Watson, J.D., Sicotte, N.L., Mazziotta, J.C., 1998. Automated image registration: II. Intersubject validation of linear and nonlinear models. *J. Comput. Assist. Tomogr.* 22 (1), 153–165.
- Wright, C.I., Martis, B., McMullin, K., Shin, L.M., Rauch, S.L., 2003. Amygdala and insular responses to emotionally valenced human faces in small animal specific phobia. *Biol. Psychiatry* 54 (10), 1067–1076.
- Wright, P., He, G., Shapira, N.A., Goodman, W.K., Liu, Y., 2004. Disgust and the insula: fMRI responses to pictures of mutilation and contamination. *NeuroReport* 15 (15), 2347–2351.
- Yang, Y., Gu, H., Zhan, W., Xu, S., Silbersweig, D.A., Stern, E., 2002. Simultaneous perfusion and BOLD imaging using reverse spiral scanning at 3T: characterization of functional contrast and susceptibility artifacts. *Magn. Reson. Med.* 48 (2), 278–289.