

The Interaction of Social and Emotional Processes in the Brain

Catherine J. Norris, E. Elinor Chen, David C. Zhu,
Steven L. Small, and John T. Cacioppo

Abstract

■ Social stimuli function as emotional barometers for the immediate environment and are the catalysts for many emotional reactions, and have inherent value for relationships and survival independent of their current emotional content. We, therefore, propose that the neural mechanisms underlying social and emotional information processing may be interconnected. In the current study, we examined the independent and interactive effects of social and emotional processes on brain activation. Whole-brain images were acquired while participants viewed and categorized affective pictures that varied on two dimensions: emotional content (i.e., neutral, emotional) and social content (i.e., faces/people, objects/scenes). Patterns of activation were consistent with past findings demonstrating that the amygdala and part of the visual cortex were more active to

emotionally evocative pictures than to neutral pictures and that the superior temporal sulcus was more active to social than to nonsocial pictures. Furthermore, activation of the superior temporal sulcus and middle occipito-temporal cortex showed evidence of the interactive processing of emotional and social information, whereas activation of the amygdala showed evidence of additive effects. These results indicate that interactive effects occur early in the stream of processing, suggesting that social and emotional information garner greater attentional resources and that the conjunction of social and emotional cues results in synergistic early processing, whereas the amygdala appears to be primarily implicated in processing biologically or personally relevant stimuli, regardless of the nature of the relevance (i.e., social, emotional, or both). ■

INTRODUCTION

Since Darwin (1872) first proposed that the nervous system mediates the relationship between certain behaviors (e.g., avoidance of rancid food) and states of mind (e.g., disgust), emotion researchers have studied the role of the brain in how we process and react to emotional stimuli. In fact, Cannon (1927), James (1884), and many other researchers have postulated the existence of brain areas specialized for processing emotionally evocative stimuli, such as snakes, spiders, and James' legendary bear. Among the most emotionally evocative stimuli that we encounter, however, are social stimuli. According to multiple sources (Bruskin Associates, 1973; see also <http://tigerx.com/trivia/fears.htm> for recent evidence), speaking in public is the single most prevalent fear of the American people; up to 85% of the general population report experiencing some anxiety about speaking in public (Burnley, Cross, & Spanos, 1993). Social anxiety disorders have received increasing attention by clinical researchers in recent years. Weddings and funerals, both social events involving the gain or loss of a loved one, are two of the most emotionally evoca-

tive events that humans experience. Most of our joys and sorrows, our fears and triumphs, are social in nature.

The primary hypothesis of the current article is that because social stimuli are among the most emotionally evocative stimuli for humans, the neural mechanisms that underlie the processing of social information may be intricately connected with those implicated in emotional networks in the brain. Keltner and Kring (1998) well captured the fundamental connection between emotion and social meaning in their "social-functional" account of emotions. They argue that emotions serve a set of functions that are critical for coordinating social interactions: (a) conspecifics' emotions provide information about the surrounding environment (e.g., fear may indicate the presence of a predator); (b) emotions elicit both complementary and similar emotions in others, depending on the context; and (c) emotions can be incentives that promote social relationships. Keltner and Kring's perspective highlights the highly dependent link between social and emotional processes and suggests that, due to this link, social stimuli may inherently have emotional significance.

Faces, in particular, provide critical information about emotional states, and considerable evidence supports the notion that processing faces is a basic component of social cognition. Infants are predisposed to attend to

facial stimuli (Johnson, Dziurawiec, Ellis, & Morton, 1991) and mimic facial expressions (Field, Woodson, Greenberg, & Cohen, 1982) at a very early age, abilities thought to be central for the development of both emotional and social communication. Kanwisher, McDermott, and Chun (1997) have found that facial stimuli elicit focal activation of a region of the fusiform gyrus (i.e., the fusiform face area [FFA]), suggesting that face processing is such a fundamental component of social cognition that specific neural structures may be specialized for processing faces (but see Gauthier & Tarr, 1997). As faces play an essential role in communicating emotion (Ekman & Oster, 1979; Darwin, 1872), neural regions implicated in face processing may also be sensitive to emotional content. Initial evidence in support of this hypothesis is provided by a recent study using positron emission tomography (PET) that revealed that emotional pictures of faces and social interactions produce greater activation of the posterior fusiform gyrus than do nonemotional pictures with similar content (Geday, Gjedde, Boldsen, & Kupers, 2003).

In addition to face perception and recognition, specific neural regions have been implicated in the perception of biological motion, another fundamentally social function. Both Puce and Perrott (2003) and Grossman and Blake (2002) have provided evidence that the superior temporal sulcus (STS) is selectively active when viewing moving images of bodies. Furthermore, Puce and Perrott provide evidence that the STS is responsive not only to movement of limbs and full bodies, but also to eye gaze direction and mouth movements. They suggest that the STS may decode complex social signals and provide this input to multiple neural regions, including limbic, frontal, and parietal systems. Importantly, perception of biological motion—including eye gaze and mouth movements—is of critical importance for understanding the intentions of a conspecific, including current emotional state and motivation. Thus, the STS may also be sensitive to the emotional content of social stimuli.

Although every social species may possess specialized systems for the perception of social cues including faces and biological motion, humans are unique in their ability to make inferences regarding the intentions of conspecifics, the psychological construct known as “theory of mind” (ToM). Assessing emotional and motivational states is critical for understanding the intentions of others; thus, neural regions implicated in ToM should be sensitive to emotional cues to facilitate rapid and accurate judgments about conspecifics’ intentions. In addition to the STS, the neuroscientific study of ToM has focused on the temporo-parietal junction (Saxe & Kanwisher, 2003), regions of the medial prefrontal cortex (mPFC, a region thought to be involved in representation of states of the self; Gallagher & Frith, 2003; Kelley et al., 2002), and the anterior paracingulate (Gallagher & Frith, 2003). Furthermore, Frith and Frith (1999) have suggested that ToM evolved from a system for repre-

senting actions, similar to current thought regarding the neural mechanisms underlying empathy, a quintessential merging of social and emotional processes. In fact, a recent study provided evidence that empathic responses may be produced via imitation of facial expressions (Carr, Jacoboni, Dubeau, Mazziotta, & Lenzi, 2003), which produces an action representation in premotor areas (including the inferior frontal gyrus [IFG]) that ultimately modulates the activity of emotional networks containing the insula and amygdala.

As we argue that social cues (e.g., faces, movement) often supply emotional information, neural structures implicated in broad emotional networks (e.g., amygdala, insula) may also be sensitive to social information. A great deal of research from the human and animal literature strongly supports the central role of the amygdala in emotional processing. Many neuroimaging studies have demonstrated greater amygdalar activation to negative as compared with neutral or positive stimuli (Lane, Fink, Chau, & Dolan, 1997; Zald & Pardo, 1997; Irwin et al., 1996), and at least one recent study has also reported greater amygdalar activation to positive than to neutral stimuli (Hamann, Ely, Hoffman, & Kilts, 2002). Furthermore, neurobiological research on the role of the amygdala in emotional processes has demonstrated that individuals with bilateral lesions of the amygdala exhibit selective impairment in recognition of emotional facial expressions, especially fear (Adolphs, Tranel, Damasio, & Damasio, 1994). Evidence from both lesion studies (Adolphs, Tranel, & Damasio, 1998) and functional neuroimaging (Winston, Strange, O’Doherty, & Dolan, 2002) suggests that the amygdala plays a critical role in both automatic and conscious evaluations of trustworthiness in faces of unknown people, a task requiring both social and emotional processing. These results suggest that the amygdala is implicated in the extraction of emotional meaning from social stimuli (e.g., faces), in addition to general emotional processing. Nevertheless, the independent and interactive effects of social and emotional information on amygdalar activation have not been addressed.

Finally, many studies investigating the neural mechanisms underlying emotional processing have reported greater activation of extensive regions of the visual cortex (extending from inferior occipital through middle occipital and middle temporal regions) for emotionally arousing than for neutral, unarousing visual stimuli. Using both PET and functional magnetic resonance imaging (fMRI), Lang et al. (1998) and Lane, Reiman, et al. (1997) have demonstrated that emotional pictures produce greater and more distributed activation of the visual cortex than do neutral pictures. Furthermore, these differences in functional activity are not due to differential eye movements (Lang et al., 1998, Study 2), and ERP studies suggest that such findings are not due to systematic variation in picture luminance or color (Junghöfer, Bradley, Elbert, & Lang, 2001) or differences

in complexity (Hamby, Bradley, Junghöfer, & Lang, 2002). As social stimuli may function as an emotional signal regardless of the specific emotions they evoke, we might expect that social stimuli will also elicit greater activation of the visual cortex than nonsocial stimuli. To date, no study has examined this hypothesis.

In sum, researchers have tended to study either social processes or emotional processes, but not both, and have often assumed that the networks that subserve these processes are separate. However, as social stimuli may function as emotional barometers for the immediate environment, are the catalyst for many emotional reactions, and have inherent value for relationships and survival independent of their emotional content, we propose that the neural mechanisms underlying social and emotional information processing may be partly redundant and interactive. In the current article, we first replicate prior findings in the neuroimaging literature concerning the processing of social stimuli (e.g., STS) and emotional stimuli (e.g., middle occipito-temporal cortex, amygdala). More importantly, we predict that regions specialized for processing social information may be especially active when these stimuli also convey emotional information. Although some studies have provided initial evidence for the interactive effects of social and emotional information on neural activity (e.g., Geday et al., 2003), the current study is the first to directly test hypotheses regarding the interaction of these two types of processes.

RESULTS

Whole-brain images were acquired while participants viewed a series of color pictures from the International Affective Picture System (IAPS; Center for the Study of Emotion and Attention [CSEA-NIMH], 1999). Pictures ranged in emotional content from negative to positive; half of the pictures contained human faces or bodies (i.e., had social content) and half did not. Participants were asked to focus on each picture for its entire duration and to categorize each as negative, neutral, or positive using a three-button mouse. For the purposes of the current study, pictures were collapsed into four sets of 50 pictures: neutral pictures of objects and scenes (i.e., neutral nonsocial); neutral pictures containing people (neutral social); emotional pictures of objects and scenes, regardless of valence (emotional nonsocial); and emotional pictures containing people, regardless of valence (emotional social).

Picture Ratings

After the fMRI procedure, participants viewed and rated each picture outside the scanner.¹ Extremity scores, calculated as the absolute value of valence ratings, were analyzed in a 2 (emotional content: neutral, emotional) × 2 (social content: nonsocial, social) analysis of vari-

ance (ANOVA). The main effect for emotional content was significant, $F(1,12) = 207.54$, $p < .001$, and means indicated that emotionally arousing pictures ($M = 2.24$) were rated more extremely than neutral pictures ($M = 0.76$; see Figure 1). These results constitute a manipulation check and indicate that our manipulation of emotional arousal was successful. In addition, the ANOVA also revealed a main effect for social content, $F(1,12) = 7.11$, $p < .05$, such that pictures containing people ($M = 1.60$) were rated more extremely than were pictures that did not depict people ($M = 1.40$; see Figure 1). This result was somewhat surprising, as normative ratings did not differ as a function of social content for either neutral or emotional pictures, $t_s(49) = 1.92$ and 0.23 , respectively, both $p_s > .05$.

Region-of-Interest Analysis

Regions of interest (ROIs) were created using computer-generated images based on the Talairach-defined coordinates for each of the following regions: amygdala, thalamus, insula, mPFC, IFG, anterior cingulate cortex, STS, fusiform gyrus, parahippocampal gyrus, and middle occipito-temporal cortex (see Lancaster et al., 1997, 2000, for an explanation of the application of automated Talairach atlas labels using the Talairach Daemon system). For example, the left amygdala ROI extended from 29 (left) to 15 (right) in the x -plane; from 8 (posterior) to -3 (anterior) in the y -plane; and from -23 (inferior) to -9 (superior) in the z -plane (LPI coordinates). As ROIs were defined following stereotactic normalization, the same ROI template was applied to all participants. For each individual subject, separate impulse response functions (IRFs, i.e., estimates of the hemodynamic response; Glover, 1999) were generated for each condition at each voxel using a deconvolution analysis. IRFs

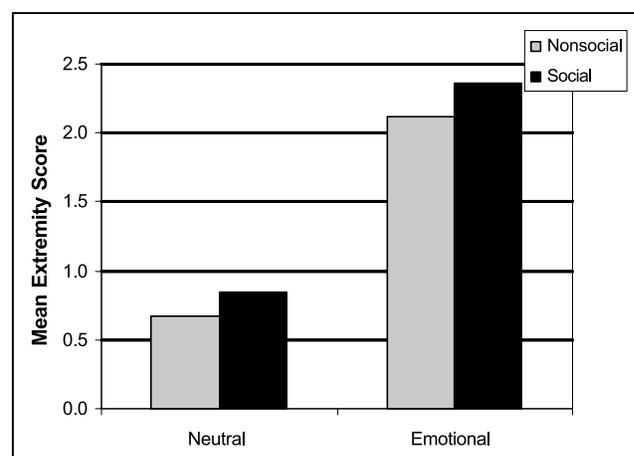


Figure 1. Mean extremity ratings for all four groups of stimuli. As expected, participants rated emotional stimuli as more extreme than neutral stimuli. In addition, social stimuli were rated more extremely than nonsocial stimuli, independent of their emotional content.

(i.e., average percent signal change over time) were averaged across all voxels within each ROI. For purposes of this study, a measure of the peak average signal change was computed from the middle portion of the hemodynamic curve (i.e., from four time points: 6, 8, 10, and 12 sec poststimulus onset).²

We conducted 2 (emotional content: neutral, emotional) × 2 (social content: nonsocial, social) ANOVAs on average percent signal change for each of 10 ROIs. Results are summarized in Table 1.

Both the main effects for emotional and for social content were significant for the amygdala, $F_s(1,13) = 31.19$ and 17.72 , respectively, both $p_s < .01$. Means revealed that percent signal change in the amygdala was larger for emotional ($M = 0.20$) than for neutral pictures ($M = 0.13$) and larger for social ($M = 0.21$) than for nonsocial pictures ($M = 0.12$; see Figure 2). These two main effects were not qualified by any higher order interactions; this pattern of results suggests that the amygdala is responsive to both emotional and social stimuli.

Another subcortical region, the thalamus, was more active to emotional ($M = 0.15$) than to neutral ($M = 0.12$) stimuli, $F(1,13) = 6.76$, $p < .05$. Furthermore, this main effect was qualified by the Emotional × Social Content interaction, $F(1,13) = 4.74$, $p < .05$. Follow-up tests indicated that the emotional content main effect was significant for social stimuli only, $t(13) = 2.67$, $p < .05$. In sum, the thalamus was more active to emotional social stimuli than to any other stimulus set,

consistent with our hypothesis that networks underlying the processing of social and emotional stimuli may interact.

The fusiform and parahippocampal gyri were included as ROIs to both replicate past findings regarding neural activation to faces (FFA; Kanwisher et al., 1997) and places (parahippocampal place area [PPA]; Epstein & Kanwisher, 1998) and to explore an interaction of social and emotional processes that has been reported previously in the FFA (Geday et al., 2003). In this set of analyses, only one effect was significant: The fusiform gyrus was more active to emotional ($M = 0.54$) than to neutral ($M = 0.47$) stimuli, $F(1,13) = 15.34$, $p < .01$. Simple effects analyses on activation of the fusiform gyrus revealed that the main effect for emotional content in the fusiform gyrus was primarily due to responses to social stimuli, as the fusiform gyrus was more active to emotional social stimuli ($M = 0.56$) than to neutral social stimuli ($M = 0.47$), $t(13) = 3.25$, $p < .01$. This finding suggests that the fusiform gyrus, a structure known to be implicated in social processing (i.e., face perception), may also be sensitive to emotional content—at least when the stimulus is social in nature. Importantly, this suggests that even without the main effect for social content, the fusiform gyrus is selectively responding to socially relevant emotional stimuli, replicating findings by Geday et al. (2003). Simple effects analyses conducted on percent signal change in the parahippocampal gyrus indicated greater activation to neutral nonsocial stimuli (i.e., scenes, places; $M = 0.21$)

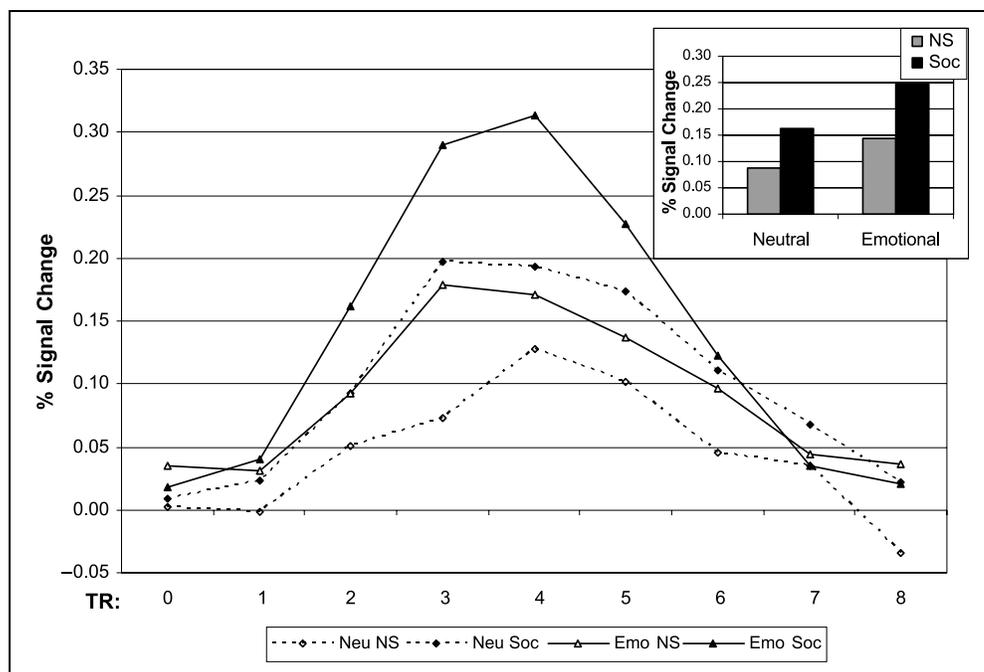
Table 1. Results from 2 (Emotional Content: Neutral, Emotional) × 2 (Social Content: Nonsocial, Social) ANOVAs on Percent Signal Change for Each ROI

ROI	Main Effect		Interaction	Simple Effects <i>t</i> Tests
	Emotional	Social	Emotional × Social	
Amygdala	Emo > Neu	Soc > NS	<i>ns</i>	NeuSoc > NeuNS; EmoSoc > EmoNS EmoNS > NeuNS; EmoSoc > NeuSoc
Thalamus	Emo > Neu	<i>ns</i>	$p < .05$	EmoSoc > NeuSoc
Insula	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>
Medial prefrontal cortex	Emo > Neu	Soc > NS	<i>ns</i>	NeuSoc > NeuNS; EmoSoc > EmoNS EmoSoc > NeuSoc
Inferior frontal gyrus	Emo > Neu	Soc > NS	<i>ns</i>	EmoSoc > EmoNS EmoNS > NeuNS; EmoSoc > NeuSoc
Anterior cingulate cortex	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>
Superior temporal sulcus	Emo > Neu	Soc > NS	$p < .05$	NeuSoc > NeuNS; EmoSoc > EmoNS EmoNS > NeuNS; EmoSoc > NeuSoc
Fusiform gyrus	Emo > Neu	<i>ns</i>	<i>ns</i>	EmoSoc > NeuSoc
Parahippocampal gyrus	<i>ns</i>	<i>ns</i>	<i>ns</i>	NeuSoc < NeuNS
Middle Occipito-temporal cortex	Emo > Neu	Soc > NS	$p < .05$	EmoSoc > EmoNS EmoNS > NeuNS; EmoSoc > NeuSoc

All effects listed are significant at $p < .05$, two-tailed.

Emo = emotional; Neu = neutral; Soc = social; NS = nonsocial; *ns* = nonsignificant.

Figure 2. IRFs depicting activation in the amygdala for each condition. Inset: Percent signal change averaged across the middle of the hemodynamic response (TRs 2, 3, 4, and 5; 4–10 sec poststimulus onset).



than to neutral social stimuli ($M = 0.18$), $t(13) = 2.57$, $p < .05$, replicating previous research (e.g., Epstein & Kanwisher, 1998).

The STS is another neural region often implicated in social cognition, especially in studies of the perception of biological motion and ToM. A 2 (neutral, emotional) \times 2 (nonsocial, social) ANOVA on activation of the STS revealed two significant main effects: one for social content, such that social stimuli elicited greater activation than did nonsocial stimuli, $F(1,13) = 36.11$, $p < .001$, and a second for emotional content, such that emotional pictures elicited greater activation than did neutral pictures, $F(1,13) = 39.32$, $p < .001$ (see Figure 3). Importantly, the interaction between social and emotional content was also significant, $F(1,13) = 5.05$, $p < .05$. Simple effects analyses indicated that activation of the STS was larger for social than for nonsocial stimuli whether they contained emotional or neutral content, $ts(13) = 4.66$ and 2.53 , respectively, both $ps < .05$. These results are a direct replication of past studies indicating greater activation of the STS to social than to nonsocial stimuli. In addition, the STS was more active to emotional than to neutral stimuli whether pictures contained social or nonsocial content, $ts(13) = 4.16$ and 2.49 , respectively, both $ps < .05$. These findings suggest that the STS is also sensitive to emotional content, regardless of the social nature of the stimulus. The interaction is due to a stronger effect of emotional content on social stimuli (see Figure 3).

Results from another neural region associated with social processing and specifically with ToM tasks and empathy, the IFG, showed two significant main effects for emotional and social content, $Fs(1,13) = 7.51$ and

4.95, respectively, both $ps < .05$. Means indicated that the IFG was more active to emotional ($M = 0.14$) than to neutral ($M = 0.10$) stimuli and more active to social ($M = 0.13$) than to nonsocial stimuli ($M = 0.11$). Simple effects tests revealed that the emotional content main effect held for both social and nonsocial stimuli, $ts(13) = 2.42$ and 2.36 , respectively, both $ps < .05$, whereas the social content main effect was driven by activation to emotional stimuli, $t(13) = 2.60$, $p < .05$. Although the interaction between social and emotional content was not significant, results from the simple effects tests suggest that the IFG may also be a region implicated in interactions between social and emotional processing.

Activation of the mPFC, a third region implicated in ToM (Frith & Frith, 1999), showed a similar pattern to that of the IFG; both the main effects for social and emotional content were significant, $Fs(1,13) = 11.06$ and 5.82 , respectively, both $ps < .05$. Again, these effects were due to greater activation for emotional ($M = 0.01$) than for neutral ($M = -0.01$) stimuli and greater activation to social ($M = 0.03$) than to nonsocial ($M = -0.02$) stimuli. Although the interaction was not significant, simple effects analyses hinted at the possibility of an interaction. The main effect for social content held for both social and nonsocial stimuli in the mPFC, $ts(13) = 2.89$ and 2.30 , respectively, both $ps < .05$; but the main effect for emotional content was significant only for social stimuli, $t(13) = 2.31$, $p < .05$.

Finally, the middle occipito-temporal cortex was chosen as an ROI due to the robust effect of emotional arousal on activation of this area (e.g., Lang et al., 1998). As expected, we replicated the finding that emotional stimuli ($M = 0.77$) activated the middle occipito-temporal

cortex to a greater degree than did neutral stimuli ($M = 0.66$), $F(1,13) = 41.83$, $p < .001$. In addition, the middle occipito-temporal cortex was more active to social ($M = 0.75$) than to nonsocial ($M = 0.69$) stimuli, $F(1,13) = 15.63$, $p < .01$. The main effects were qualified by the emotional \times social content interaction, $F(1,13) = 7.29$, $p < .05$ (see Figure 4). Simple effects tests indicated that the middle occipito-temporal cortex was more active to emotional than to neutral stimuli when stimuli were social or nonsocial, $t_s(13) = 5.39$ and 3.62 , respectively, both $p_s < .01$, and that the middle occipito-temporal cortex was more active for emotional social than for emotional nonsocial stimuli, $t(13) = 3.92$, $p < .01$. Thus, the middle occipito-temporal cortex was most active when participants viewed stimuli that were both social and emotional in nature.

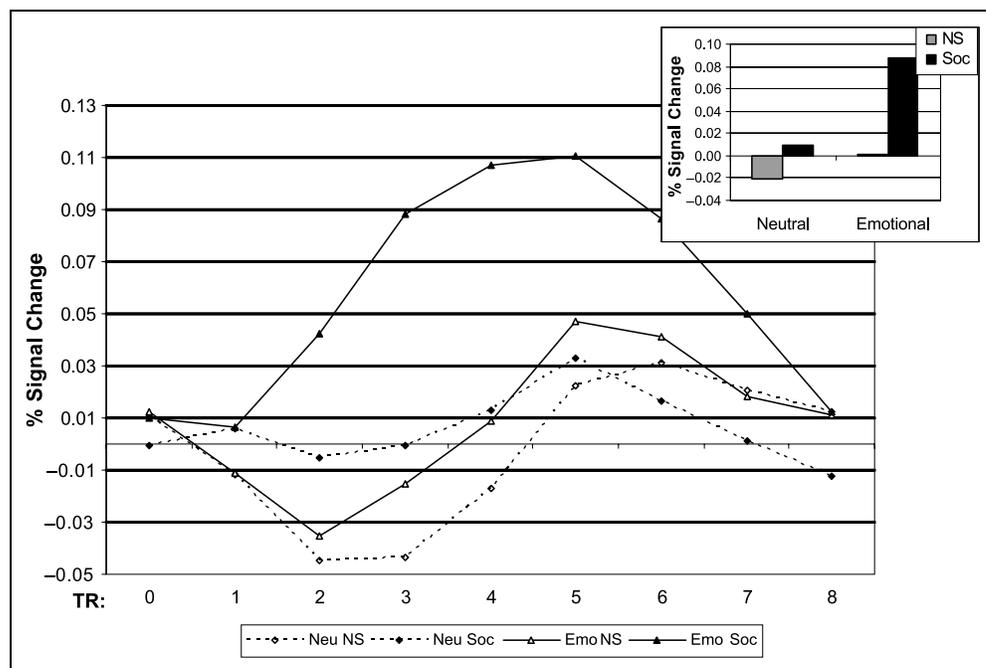
Are Social Stimuli Just More Emotional?

One possible explanation for the apparent interaction of emotional and social processes is that social stimuli are just more emotional. In fact, participants rated social stimuli more extremely than they did nonsocial stimuli.³ If this is true, then every interaction between the processing of emotional and social stimuli (e.g., interaction of emotional and social content in the middle occipito-temporal gyrus) is open to the criticism that it may be driven by the greater emotionality of social stimuli. To test this hypothesis, we calculated the mean difference between extremity scores of social and nonsocial stimuli for each participant. Using this variable as a covariate, we conducted a second set of 2 (emotional content: neutral, emotional) \times 2 (social content: non-

social, social) analyses of covariance (ANCOVAs) on percent signal change in each ROI.⁴ If effects involving social content in the primary analyses were due to the greater emotionality of social stimuli, we would expect them to be nonsignificant when controlling for the difference in ratings between social and nonsocial stimuli.

Results from the set of ANCOVAs controlling for differences in participants' ratings of social and nonsocial stimuli were largely consistent with results from the primary analyses (i.e., not controlling for these differences) in all regions, with the following exceptions. First, the main effect for emotional content on activation of the thalamus was nonsignificant in the ANCOVA analysis, $F(1,12) = 2.58$, $p = .14$, although the means were in the same direction, with activation to emotional stimuli ($M = 0.15$) slightly greater than that to neutral stimuli ($M = 0.12$). However, two simple effects tests were marginally significant for the thalamus: First, activation to emotional social pictures ($M = 0.17$) was marginally greater than activation to neutral social pictures ($M = 0.12$), $F(1,12) = 4.13$, $p = .07$, consistent with results from the original ANOVA; second, activation to emotional social pictures ($M = 0.17$) was marginally greater than activation to emotional nonsocial pictures ($M = 0.13$), $F(1,12) = 4.18$, $p = .06$. For the IFG, activation to emotional stimuli ($M = 0.14$) was no longer significantly greater than that to neutral stimuli ($M = 0.10$), $F(1,12) = 2.54$, $p = .14$. Finally, the interaction between emotional and social processing in the STS was no longer significant in the ANCOVA analysis, $F(1,12) = 2.48$, $p = .14$. However, simple effects analyses continued to suggest that the STS might be implicated in the interactive processing of emotional and social stimuli, as the STS

Figure 3. IRFs for activation of the STS in each condition. Inset: Activation of the STS depicted as percent signal change averaged across the middle of the hemodynamic response.



was more active to social than to nonsocial stimuli regardless of whether they contained emotional or neutral content, $F_s(1,12) = 12.69$ and 5.03 , respectively, both $p_s < .05$; but the STS was only more active to emotional than to neutral stimuli when they were also social in content, $F(1,12) = 7.54$, $p < .05$.⁵

In sum, the striking finding from this set of analyses controlling for differences in participants' ratings of social and nonsocial stimuli was that overall the results were consistent with the primary set of analyses, suggesting that effects due to the social content of stimuli are not attributable to the greater emotionality of social stimuli.

DISCUSSION

Human beings are fundamentally social creatures. Social information is highly valued and critical for survival throughout the life span as it contributes to successful attachment, reproduction, vigilance toward threatening encounters, and protection of territory and significant others. Thus, conspecifics are the primary elicitors of emotions designed to promote both affiliative and protective behaviors. We argue in the current study that the neural mechanisms that underlie social and emotional processes may be partly redundant and interactive; specifically, regions of the brain previously implicated in social and/or emotional processes may exhibit evidence of an interaction in processing.

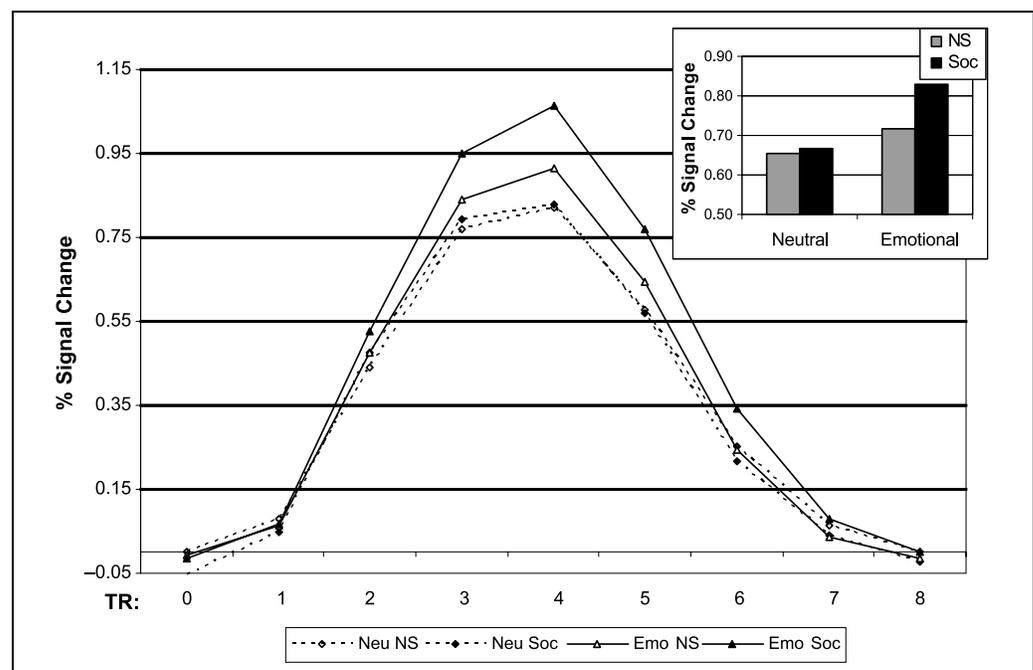
Evidence for such an interaction in social and emotional processing was provided by patterns of brain activation in the STS, the middle occipito-temporal cortex, and the thalamus. The form of the interaction

for all three sites clearly demonstrated that activation was significantly greater for emotional stimuli depicting conspecifics than for all other groups of pictures (see Figures 3 and 4). Importantly, these regions have all been implicated in relatively early stages of processing; the STS in perception of biological motion, the middle occipito-temporal cortex in processing emotionally arousing visual stimuli, and the thalamus (especially the pulvinar nucleus) in visual attention.

One possible explanation for the interaction between social and emotional processes observed in the STS, however, is that, as the STS has been shown to be active during the perception of biological motion, it is possible that emotional social stimuli simply involve more biological motion than do all other groups of stimuli. This is an unlikely explanation for our findings for two reasons: First, the emotional and neutral groups of stimuli both included pictures with active (e.g., involving movement) and passive (e.g., portraits, facial expressions) content; second, if the interaction was due only to excessive depiction of biological motion in the emotional social stimuli, additional simple effects tests would not have been significant (e.g., neutral social vs. neutral nonsocial).

It is also important to note that the main effect for emotional content was significant for the middle occipito-temporal cortex, replicating a robust finding in the neuroimaging literature. Greater activation of this region of visual association cortex to emotional than to neutral stimuli is consistent with results from ERP studies suggesting that emotional stimuli (especially negative) may receive greater attentional resources at early stages of processing (e.g., Smith, Cacioppo, Larsen, & Chartrand,

Figure 4. Activation of the middle occipito-temporal cortex for each condition, presented as IRFs and (inset) average percent signal change for TRs 2–5.



2003). Furthermore, many researchers have suggested that this effect is a manifestation of “natural selective attention,” or the tendency for individuals to attend to stimuli with inherent significance for survival. Thus, our results suggest that emotional stimuli that have social significance may be selectively attended to and receive even greater attentional resources at early stages of processing.

In contrast to these results indicating an interaction between social and emotional processing, three neural regions demonstrated overlap (but no interaction) between social and emotional processes. Results for the amygdala, the mPFC, and the IFG all indicated main effects for social and for emotional content, but no significant interaction between the two. However, simple effects tests for the mPFC and IFG did hint at a potential interaction, such that the mPFC was sensitive to social content regardless of emotional content, but was only sensitive to emotional content when the stimulus was social, whereas the IFG was sensitive to emotional content regardless of social content, but was only sensitive to social content when the stimulus was also emotional. Thus, the amygdala is the only region that appears to be activated additively, not interactively, by social and emotional information (see Figure 2).

Why might social and emotional information be processed interactively in some regions of the brain (e.g., STS, middle occipito-temporal cortex, thalamus) and additively in others (e.g., amygdala)? Observed interactions between social and emotional information processing were all located in regions implicated in relatively early stages of processing, potentially indicating greater attentional allocation to conspecifics in emotional contexts. The thalamus, middle occipito-temporal cortex, and STS all project to regions involved in assessing relevance and, ultimately, regulating behavior; for example, the STS has connections with the amygdala, which is reciprocally connected with the orbito-frontal cortex, two regions implicated in social perception, cognition, and representation of reward and punishment (Allison, Puce, Spencer, & McCarthy, 1999). Thus, the conjunction of social and emotional cues results in synergistic early processing (which may or may not be maintained through the processing stream; e.g., producing an interaction in the mPFC). The amygdala, however, may be involved in processing any stimulus that has potential personal significance. If conspecifics and emotionally provocative stimuli have potential personal significance, both sets of stimuli may produce comparable activation of the amygdala. Existing literature on appetitive behaviors and threat responses and activation of the amygdala are consistent with this hypothesis.

It is important to note that our results did not show greater activation of the fusiform gyrus to social stimuli (i.e., faces, people) than to nonsocial stimuli (i.e., objects, scenes) or greater activation of the parahippocampal gyrus to nonsocial than to social stimuli, both of

which are robust findings in the neuroimaging literature. One potential explanation is that most studies of the FFA and the PPA define the ROI functionally rather than anatomically. For example, participants are shown a series of faces and a series of objects, and the region of the fusiform gyrus that is selectively more active to faces than to objects is chosen as the FFA (the same procedure is undertaken for defining the PPA). In the current study, we chose both ROIs based on anatomy, not function. This methodological difference could contribute to a less powerful test of the replication. In addition, our stimulus selection was not ideal to replicate either of these results. Activation of the FFA has been shown to depend on the orientation (Tong, Nakayama, Moscovitch, Weinrib, & Kanwisher, 2000) and coverage (e.g., eyes; Bentin, Allison, Puce, Perez, & McCarthy, 1996) of the facial stimuli. Thus, our categorization of any picture containing a person (whether a full face, torso, profile, or multiples bodies) as “social,” as well as the inclusion of objects as well as places/scenes in the “non-social” category, may have weakened our ability to observe the FFA and PPA effects.

However, simple effects tests for both the fusiform gyrus and parahippocampal gyrus provide some evidence for a replication of previous results. First, the fusiform gyrus was more active for emotional than for neutral stimuli—but only for those that were social, suggesting that the fusiform was sensitive to the social content of the pictures. Similarly, the parahippocampal gyrus was more active for nonsocial than for social stimuli—but only for those that had neutral content, suggesting that the parahippocampal gyrus was sensitive to social content. Although these findings do not constitute a robust replication, tempered with the methodological differences discussed previously, they provide evidence for the consistency of our results with previous studies.

As previous research has demonstrated sex differences in neural activation to emotional stimuli and in consideration of a vast literature on sex differences in emotion more generally, a brief discussion of the generalizability of our results to men is warranted. A recent fMRI study indicated that men showed greater activation of the inferior temporal visual cortex when viewing erotic pictures than did women (Sabatinelli, Flaitsh, Bradley, Fitzsimmons, & Lang, 2004). Results from a second study demonstrated greater activation of the right extrastriate visual cortex when women viewed unpleasant as compared with pleasant pictures, whereas men showed the opposite trend (Lang et al., 1998). However, it is important to note that male and female participants provide very different ratings for these categories of pictures, with men responding more positively to erotica than do women and women responding more negatively to unpleasant pictures than do men (CSEA, 1999). These observed sex differences, therefore, are likely a function of differences in the motivational significance of these stimuli for men and women rather

than sex differences in the neural substrates underlying emotional processing. In sum, to the extent that stimuli differ for men and women along specific dimensions, such as motivational significance, we might predict differences in neural activation between the two sexes. However, social and emotional stimuli retain much of their significance for both men and women; therefore, we suggest that our results should generalize in large part to men.

In conclusion, social stimuli have inherent emotional value for members of a social species, as they provide information about both the shared environment and mutual relationships. We have provided initial evidence that neural regions implicated in social networks may also be sensitive to emotional information, and that regions activated by stimuli with emotional significance may also be sensitive to the social content of those stimuli. Further studies are needed to investigate the relative contributions of negative and positive stimuli to social information processing, as well as to explore interactions between emotional and social processes under more specific conditions.

METHODS

Participants

Seventeen right-handed, healthy female⁶ University of Chicago students (ages 18–25) participated in the current study; however, fMRI data from two subjects were lost or incomplete due to equipment problems and fMRI data from one subject were discarded due to excessive head movement (>5 mm). Participants were recruited through the use of a study pool maintained by the Department of Psychology at the University of Chicago and were paid approximately \$12/hr for their participation.

Stimuli

Sixty negative, 120 neutral, and 60 positive pictures were chosen from the IAPS (CSEA-NIMH, 1999) according to female-only normative ratings (Lang, Bradley, & Cuthbert, 1999); however, for the purposes of the current study, only 50 negative ($M_{\text{valence}} = 2.54$, $SD = 0.52$; $M_{\text{arousal}} = 5.59$, $SD = 0.77$), 100 neutral ($M_{\text{valence}} = 5.08$, $SD = 0.53$; $M_{\text{arousal}} = 3.40$, $SD = 0.71$), and 50 positive ($M_{\text{valence}} = 7.31$, $SD = 0.43$; $M_{\text{arousal}} = 5.65$, $SD = 0.76$) pictures were included in the analysis.⁷ Negative, neutral, and positive pictures were matched in dominant colors, complexity, and content (i.e., half of the pictures in each valence category contained some form of a person, the other half was composed of pictures of objects and scenes). In addition, negative and positive pictures were chosen to be equally extreme from the midpoint of the normative scale and to be matched in terms of normative arousal ratings.⁸ Neutral pictures were divided into two sets of 50 pictures each; one

set was always shown in the same blocks as negative stimuli, the other was always shown in the same blocks as positive stimuli.

Equipment

All instructions and images were backward projected onto a screen inside the scanner room and reflected on a mirror mounted on the top of the head coil approximately 6 in. above the participant's eyes. Participants made responses using a three-button mouse held in their right hand, with their index finger on the left button, middle finger on the middle button, and ring finger on the right button. Responses and response times were recorded on a Dell Pentium III 800-MHz processor with 512 MB of RAM using E-Prime 1.1 (<http://www.pstnet.com>).

Procedure

Participants were told that they would view a series of emotional pictures and their task was to focus on their emotional reactions to the content of each picture. During the viewing period, participants categorized each picture as negative, neutral, or positive using the three-button mouse. Each picture was presented for 6 sec and followed by a variable intertrial interval, consisting of white crosshairs on a black background, ranging from 0 to 24 sec in duration. Following a set of 30 practice trials and before entering the scanner, participants were given an opportunity to ask questions and were reminded that it was very important that they not move at any time while in the scanner. Participants completed four blocks of trials in the scanner, each consisting of half neutral pictures and half negative or positive pictures (i.e., participants did not view negative and positive pictures in the same block). The same set of neutral pictures was always shown with the same set of negative or positive pictures; participants were randomly assigned to one of two block orders, each block contained one predetermined quasi-random stimulus order. After scanning, participants rated each picture using the affect matrix, a 5×5 grid with positive affect represented on the horizontal axis and negative affect on the vertical axis (Larsen, Norris, & Cacioppo, 2004). A traditional bipolar valence measure was calculated as the difference between the positive affect rating and the negative affect rating, resulting in a possible valence range of -4 (*very negative*) to 4 (*very positive*). In addition, an extremity measure was calculated as the distance of each valence score from the midpoint (0).

Image Acquisition

Imaging was performed on a 3-T GE Signa scanner (GE Medical Systems, Milwaukee, WI) with a standard quadrature GE head coil. High-resolution volumetric T1-

weighted spoiled gradient-recalled images were obtained for each subject in one hundred twenty-four 1.5-mm sagittal slices with 10° flip angle and 24 cm field of view (FOV) for use as anatomical images. Functional images were acquired using a gradient-echo spiral-in/out pulse sequence (Glover & Law, 2001) with 27 contiguous 5-mm sagittal slices in an interleaved order spanning the whole brain (TR = 2000 msec, TE = 26 msec, flip angle = 77°, FOV = 22 cm, 64 × 64 matrix size, fat suppressed). Each set of slices was acquired 270 times during each of four blocks while participants viewed the pictures, resulting in a total of 1080 sets of images collected over the course of the entire experiment.

Image Processing

Image and data processing were done off-line. The spiral-in and spiral-out images were reconstructed first separately and then combined using a weighted-average algorithm that maximizes signal-to-noise ratio while reducing signal loss in the orbito-frontal cortex (Preston, Thomason, Ochsner, Cooper, & Glover, 2004; Glover & Law, 2001). Further image processing was performed using AFNI software (Cox, 1996). For each subject, motion detection and correction was undertaken using a six-parameter, rigid-body transformation. For group analysis, images were interpolated to volumes with 3-mm³ voxels, coregistered, and converted to Talairach stereotaxic coordinate space (Talairach & Tournoux, 1988).

Functional Magnetic Resonance Imaging Data Analyses

Preliminary analyses were performed for each participant using a “deconvolution” analysis to generate IRFs of the fMRI signal on a voxel-wise basis (Ward, 2001; Glover, 1999). This analysis produces an estimate of the hemodynamic response for each condition relative to a baseline state without a priori assumptions about the IRF. The deconvolution analysis uses a separate regressor for each time point of each condition and fits these regressors using a linear least squares model to each time point of the hemodynamic response. Each of the four conditions in the current study (i.e., neutral/nonsocial, neutral/social, emotional/nonsocial, and emotional/social) had nine regressors, one for each TR between 0 and 18 sec. In addition, we included a regressor for the constant, linear, and quadratic trends for each of the four blocks. Output from the deconvolution analyses was submitted to an ROI analysis.

ROIs were chosen based on existing literature and were drawn using stored representations included in AFNI. The following ROIs were drawn separately in each hemisphere: amygdala, insula, mPFC (middle frontal gyrus, modified by hand to include only the mPFC), IFG, anterior cingulate cortex, STS (defined as the region encompassing both the STG and MTG), fusiform gyrus,

parahippocampal gyrus, and middle occipito-temporal cortex (defined as posterior portions of MTG and anterior portions of middle occipital cortex). IRFs were averaged across all voxels within each ROI. To better compare peaks of the hemodynamic responses to each of the four conditions, data were averaged across the four TRs under the peak. These data were submitted to a 2 (emotional content: neutral, emotional) × 2 (social content: nonsocial, social) ANOVA separately for each ROI.

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Reprint requests should be sent to Catherine J. Norris, Institute for Mind and Biology, The University of Chicago, 940 East 57th Street, Chicago, IL, 60637, or via e-mail: cjnorris@uchicago.edu.

The data reported in this experiment have been deposited in the fMRI Data Center (<http://www.fmridc.org>). The accession number is 2-2004-1172A.

Notes

1. Postscan ratings for one participant were lost due to experimenter error. Therefore, analyses on participants' ratings of the stimuli are based on data from 13 participants.
2. Note that the method used to create the ROIs in the current article has been used in previous published research (cf. Mather et al., 2004). Due to space constraints, coordinates for all ROIs are not included in the article, but are available as supplementary material on the journal website. Two ROIs required modification from the TD system. First, the mPFC was chosen to be the anterior, inferior portion of the medial frontal gyrus. Second, data from the superior temporal gyrus (STG) and middle temporal gyrus (MTG) and their mean (a broad approximation of the STS, which separates the two gyri) were analyzed separately. Analyses produced very similar results for the STG, MTG, and their mean; therefore, we present data here for the mean (e.g., the STS). Finally, we conducted preliminary analyses including hemisphere (left and right) as a factor. However, as none of our predictions involve questions of lateralization and none of the effects listed here were qualified by an interaction with hemisphere, we collapsed across this factor to simplify presentation of results.
3. This difference in ratings may be due to faster habituation to nonsocial than to social stimuli, as participants made ratings of the pictures outside the scanner following a second observation. However, we do not have data to directly address this hypothesis.
4. Recall that self-report data were lost for one participant. To maintain the same statistical power for this set of ANCOVAs, we replaced the missing data with the mean from all other participants' scores, a standard practice in statistical analyses for dealing with missing data points. Importantly, results from the ANCOVAs were generally consistent whether this participant's data were missing or replaced with the mean.
5. Some effects were weakened when controlling for the difference in ratings of social and nonsocial stimuli, but all showed the same pattern. For example, the main effect of emotional

content on activation of the mPFC was still marginally significant, $F(1,12) = 4.47, p = .06$, and the interaction between social and emotional content in the thalamus was marginally significant, $F(1,12) = 4.48, p = .06$. The effects discussed in text were those that were weakened a great deal ($p > .10$). Importantly, all means showed the same pattern as the original ANOVAs.

6. Only women were recruited to participate in the current study for two reasons. First, men and women express divergent reactions to the color photographs included in the IAPS (e.g., women rate mutilations as much more negative; men rate erotica as much more positive). This problem has been addressed previously by either selecting different sets of pictures for male and female participants or only including participants of one gender. Second, women often exhibit stronger emotional responses than men (Kring & Gordon, 1998), and prior research has suggested that women respond more strongly and more reliably to the IAPS (Ito, Cacioppo, & Lang, 1998).

7. Five pictures were excluded from both the negative and positive sets and 10 from the neutral set because they depicted animals, which are nonsocial stimuli that have faces and are thus problematic for the current analysis. An additional five pictures were excluded from both the negative and positive sets and 10 from the neutral set to match the number of stimuli that centrally depicted people and the number that did not (i.e., objects, scenes), resulting in 25 pictures depicting people and 25 nonpeople pictures within both the negative and positive sets and 50 pictures depicting people and 50 nonpeople pictures in the neutral set. In addition, the IAPS did not contain sufficient neutral pictures to allow a match with the negative and positive sets on all dimensions. Thus, 65 of the final neutral pictures were selected from the IAPS and 35 additional neutral pictures were chosen from the PC Paintbrush PhotoLibrary CD (1994) to bring the total in the neutral set to 100.

8. A 4 (valence category: negative, neutral (in a negative block), neutral (in a positive block), positive) \times 2 (content: objects and scenes, pictures with people) ANOVA on normative extremity scores (i.e., distance from the midpoint of the normative scale) revealed only a main effect for valence category, $F(3,192) = 301.53, p < .001$. Pairwise comparisons confirmed that negative ($M = 2.46$) and positive ($M = 2.31$) pictures were equally extreme, $p > .05$, and that ratings of both of these categories of pictures were significantly more extreme than ratings of the neutral categories of pictures ($M_s = 0.47$ and 0.52), $p_s < .001$. Importantly, extremity ratings did not differ as a function of the social content of the pictures. The same pattern of results emerged for normative arousal ratings: negative ($M = 5.62$) and positive ($M = 5.66$) pictures were equally arousing and both categories were more arousing than the neutral pictures ($M_s = 3.47$ and 3.20). Again, the main effect for social content was not significant.

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